Evolution, 57(2), 2003, pp. 384–396

THE EVOLUTION OF SEXUAL SIZE DIMORPHISM IN THE HOUSE FINCH.
V. MATERNAL EFFECTS

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Abstract.—The phenotype of a mother and the environment that she provides might differentially affect the phenotypes of her sons and daughters, leading to change in sexual size dimorphism. Whereas these maternal effects should evolve to accommodate the adaptations of both the maternal and offspring generations, the mechanisms by which this is accomplished are rarely known. In birds, females adjust the onset of incubation (coincident with the first egg or after all eggs are laid) in response to the environment during breeding, and thus, indirectly, determine the duration of offspring growth. In the two house finch (*Carpodacus mexicanus*) populations that breed at the extremes of the species' distribution (Montana and Alabama), females experience highly distinct climatic conditions during nesting. We show that in close association with these conditions, females adjusted jointly the onset of incubation and the sequence in which they produced male and female eggs and consequently modified the growth of sons and daughters. The onset of incubation in newly breeding females closely tracked ambient temperature in a pattern consistent with the maintenance of egg viability. Because of the very different climates in Montana and Alabama, females in these populations showed the opposite patterns of seasonal change in incubation onset and the opposite sex bias in egg-laying order. In females with breeding experience, incubation onset and sex bias in laying order were closely linked regardless of the climatic variation. In nests in which incubation began with the onset of egg laying, the first-laid eggs were mostly females in Montana, but mostly males in Alabama. Because in both populations, male, but not female, embryos grew faster when exposed to longer incubation, the sex-bias produced highly divergent sizes of male and female juveniles between the populations. Overall, the compensatory interaction between the onset of incubation and the sex-biased laying order achieved a compromise between maternal and offspring adaptations and contributed to rapid morphological divergence in sexual dimorphism between populations of the house finch breeding at the climatic extremes of the species range.

Key words.—*Carpodacus mexicanus*, egg-laying order, growth, incubation, maternal effects, sex ratio.

Received June 24, 2002. Accepted September 19, 2002.

Parental effects are components of offspring phenotype that are the result of the parental phenotype and the parental environment (Rutledge et al. 1972; Kirkpatrick and Lande 1989; Rossiter 1996). Such effects may be due to allocation of parental products (e.g., parental hormones or enzymes); effects of social, physiological, and ecological environment provided by parents (e.g., nest or mate choice, body condition); and the interactions of these factors (Cheverud and Moore 1994; Bernardo 1996; Rossiter 1996; Fig. 1). When parental effects are sex biased, they can be a powerful force in shaping change in the growth of male and female progeny and degree of sexual size dimorphism (SSD; Fig. 1).

Sex-biased parental effects may evolve to optimize parental investment in sons and daughters by either capitalizing on the different environmental sensitivity of the sexes during growth or by direct modifications of male and female size and growth (Stamps 1990; Badyaev 2002; Lessells 2002). Thus, depending on the ecological and social contexts of breeding and on the patterns of selection experienced by parental and offspring generations, parental (maternal hereafter) effects can either constrain or enhance the growth and size potential of male and female offspring (Proudfoot and Hulan 1981; Bandyopadhyay and Ahuja 1990; Clark and Galef 1995; Sasvári et al. 1999). For example, prenatal exposure to steroids of maternal origin can permanently affect the sensitivity of growth hormone receptors in male and female embryos to subsequent exposure to steroids and in this way influence growth (Gatford et al. 1998; Brandstetter et al. 2000). In many animals, the limitation imposed by maternal size on SSD at birth (Mascie-Taylor and Boldsen 1988; Smith and Leigh 1998; Guégan et al. 2000) and the bias (or the lack thereof) in provisioning of sons and daughters (Teather and Weatherhead 1988; Holden and Mace 1999; Wilkinson and van Aarde 2001) is a powerful selection pressure on the ontogeny of the larger sex, leading to the evolution of an increased rate and duration of growth as well as adaptations that allow greater sensitivity to (and capitalization on) environmental variation during growth (Ono and Boness 1996; Guinet et al. 1999). More generally, maternal effects on growth of sexes are maternal adaptations that represent the outcome of the interaction between maternal modifications of offspring growth potential and offspring counter-adaptations to influence these modifications. Thus, to understand the importance of maternal effects on SSD evolution, we need to address causes and consequences of maternal effects in both maternal and offspring generations.

The onset of incubation in birds is uniquely suited to affect both maternal and offspring generations (Fig. 2; Stoleson and Beissinger 1995; Hébert 2002). Birds are unusual among animals in that they have direct control over developmental time of their offspring because embryos cannot develop before eggs are incubated (Fig. 3). Females lay at most one egg per day, but then modify the onset of incubation (coincident with the first egg or after all eggs are laid) in response to *their* environment at the time of breeding (e.g., food availability, predation risk, mate provisioning, temperature;

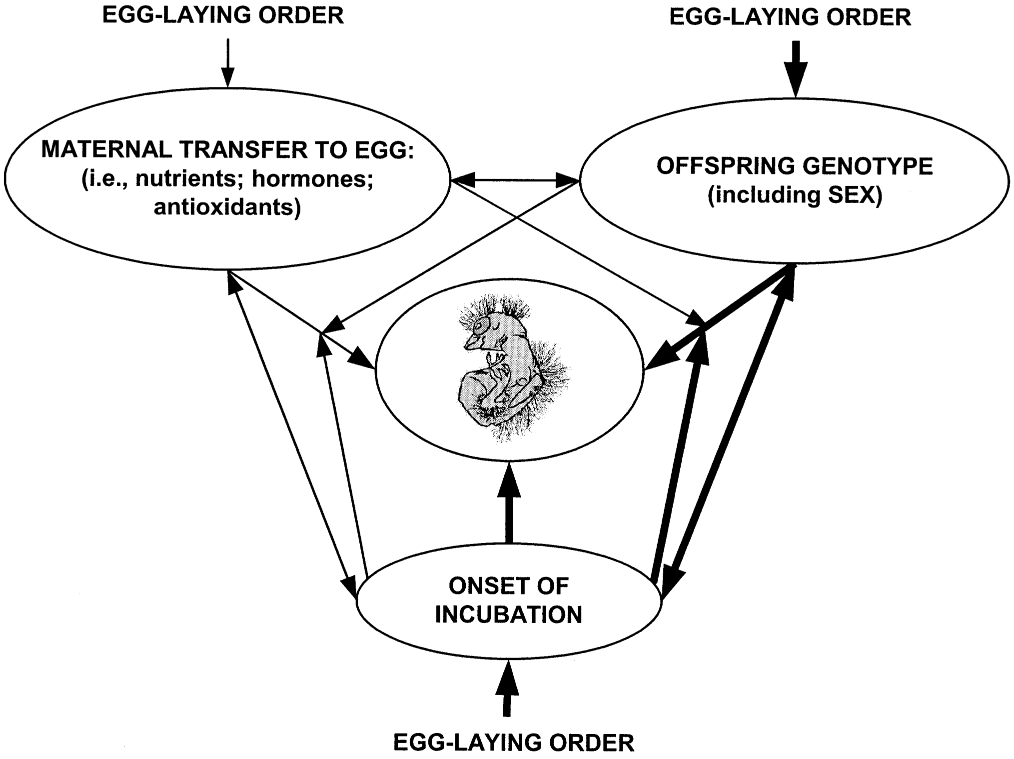

FIG. 1. Outline of direct and indirect maternal influences on offspring during egg laying and incubation in birds. The growth and morphology of the offspring are influenced by its own genotype, maternal transfer of growth and immune factors into eggs, and the duration of growth, which is determined by the onset of incubation. Egg-laying order influences offspring growth by modifying each of these effects. Differences between males and females in growth and morphology can arise when either of these factors or their interactions are different between the sexes. Thick lines indicate the effects examined in this study; thin lines show the effects proposed in other studies (see introduction). Sexual size dimorphism can be due to direct and sex-biased maternal effects, sex-biased interactions between multiple maternal effects, or differential sensitivity of male and female offspring to maternal effects.

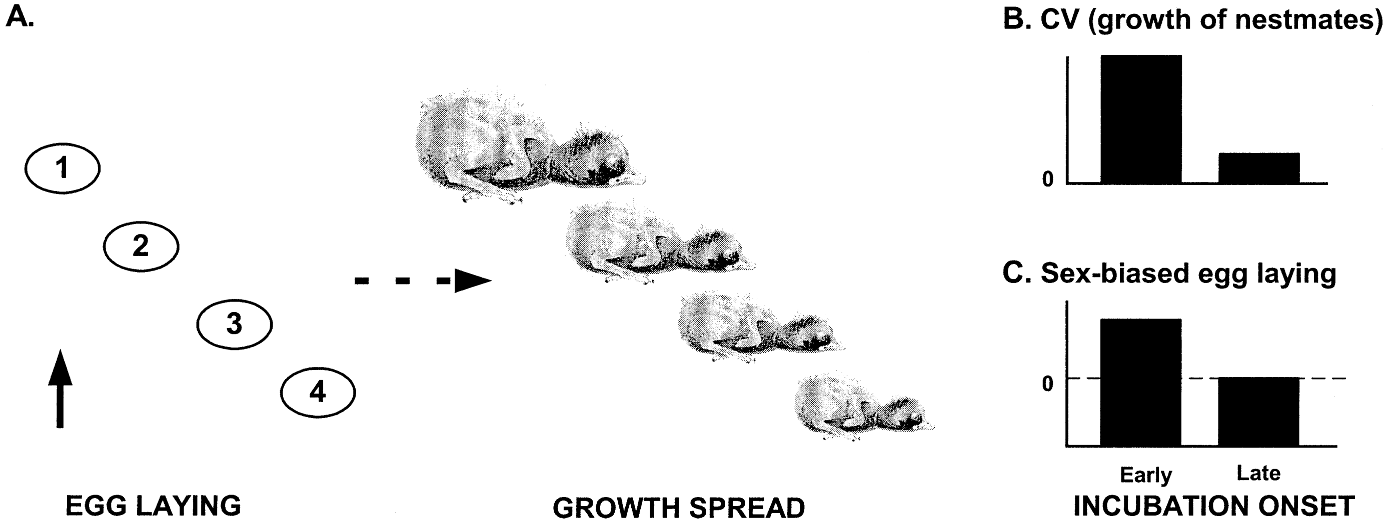

FIG. 2. (A) Onset of incubation from the first egg (solid arrow) leads to different growth patterns among nest mates. (B) In the absence of compensatory maternal effects, the variable developmental time among nestmates will lead to greater variation in the rates of growth (CV) among nest mates in nests with early onset of incubation versus nests with late onset of incubation. (C) If mothers compensate for the effects of variable incubation onset by modifying laying order of male and female eggs, then sex-bias in egg-laying order is expected to be greater in nests with early onset of incubation versus nests with late onset of incubation.

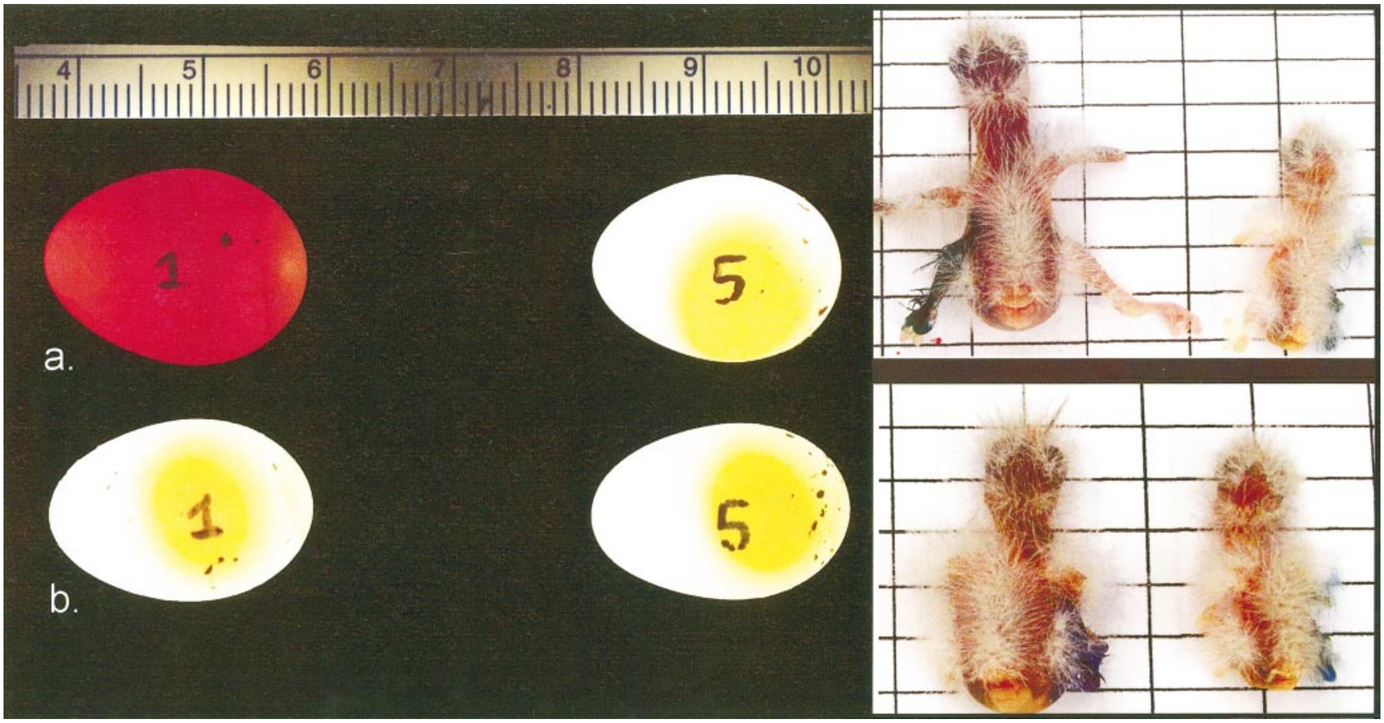

FIG. 3. Differences in embryo development and nestling growth resulting from differences in the extent of overlap between incubation and egg laying in the house finch. Shown are the first- and the last-laid egg photographed on the last (fifth) day of egg-laying period and the nestlings hatched from these eggs (photographed 48 h after the hatch). In nest A full incubation started with the first egg. On the last day of egg laying, the embryo in the first-laid egg has clearly visible blood circulation system, whereas the last-laid egg shows no development as indicated by clearly delineated yolk. In nest B full incubation started with the last egg and both first-laid and the last-laid eggs are at the same developmental stages at the end of egg-laying period.

Amundsen 1999; Stoleson 1999; Conway and Martin 2000; Vinuela 2000; Martin 2002). The variable developmental times of offspring from different egg-laying orders have strong effects on offspring growth and fitness (Griffiths 1992; Bradbury and Griffiths 1999; Fig. 3). Mothers can either enhance or mitigate these effects by modifying the sequences in which they lay male and female eggs (in sexually dimorphic species; Weatherhead 1985; Bortolotti 1986; Bednarz and Hayden 1991; Nager et al. 1999; Blanco et al. 2002; Krebs et al. 2002) or by differentially allocating nutrients or growth enhancers or suppressors to eggs in relation to laying order (Schwabl 1993; Hillström 1999; Sockman and Schwabl 2000; Cordero et al. 2001; Eising et al. 2001; Fig. 2). Whereas compensatory maternal effects on offspring phenotype, especially in relation to flexible onset of incubation, may be common (Howe 1979; Slagsvold et al. 1984; Slagsvold and Amundsen 1992; Schwabl 1996a; Schwabl et al. 1997; Lipar et al. 1999; Royle et al. 2001; Blanco et al. 2002), the causes of such compensation and its variation among females are rarely known in natural populations.

We studied the interaction between ambient temperature, the onset of incubation, sex-biased laying order, and offspring growth in populations of the house finch (*Carpodacus mexicanus*) that recently colonized two climatic extremes of the species range (northwestern Montana and eastern Alabama; Badyaev and Hill 2000). Ambient temperatures below and above the range of physiological tolerance of unincubated house finch eggs (~2°C and 27°C, respectively; Webb 1987) are routinely observed early in the season in the Montana population and late in the season in the Alabama population, leading to corresponding changes in onset of incubation. In the absence of compensatory maternal effects, variable incubation times should lead to an increase in hatching asynchrony and to variation in growth among nestmates (Fig. 2). However, in both populations the onset of incubation and the sequence in which females lay male and female eggs are closely linked (Badyaev et al. 2003). Here we examine the joint effects of sex bias in the egg-laying order and flexible incubation onset on male and female growth and on SSD at fledgling. We show that joint modification of incubation and egg-laying patterns produces widely divergent patterns of SSD between the populations and may represent a compromise between maternal and offspring adaptations in the two highly distinct breeding environments.

MATERIALS AND METHODS

Study Populations and General Protocols

We studied house finches in two recently established resident populations: Missoula, in northwestern Montana, and Auburn, in east-central Alabama. The study site in Montana has been maintained since 1995, when the local population was 25–30 years old, and the study site in Alabama has been maintained since 1993, when the local population was 10–15 years old (detailed description of the study sites are in Hill et al. 1999; Badyaev and Martin 2000). All resident

TABLE 1. Effects of incubation onset (onset), sex laying order (sex order), female breeding age (age), and their interactions on tarsus growth during pre-hatching (i.e., size at hatching) and post-hatching (from hatching to growth completion) growth periods in the Montana and Alabama populations of the house finch. The analyses are at the nest level.

Population	Effects									
	Onset		Sex order		Age (mother)		Age × onset		Age × sex order	
Sex	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Montana					Pre-hatch growth (n = 33 nests)					
Males	6.13	**0.02**	2.97	0.07	5.45	**0.03**	7.19	<**0.01**	3.95	**0.05**
Females	5.34	**0.02**	8.64	<**0.01**	20.6	<**0.01**	0.10	0.76	5.41	**0.02**
					Post-hatch growth (n = 52 nests)					
Males	8.62	<**0.01**	4.16	**0.04**	2.46	0.12	19.06	<**0.01**	9.04	<**0.01**
Females	4.62	**0.02**	1.93	0.10	0.01	0.97	9.90	<**0.01**	0.59	0.45
Alabama					Pre-hatch growth (n = 31 nests)					
Males	3.86	**0.05**	15.71	<**0.01**	22.5	<**0.01**	8.41	<**0.01**	7.26	<**0.01**
Females	1.71	0.19	4.73	**0.03**	0.10	0.75	4.34	**0.04**	0.22	0.64
					Post-hatch growth (n = 44 nests)					
Males	8.20	<**0.01**	14.21	<**0.01**	0.01	0.92	3.70	0.06	7.33	<**0.01**
Females	2.35	0.12	3.79	0.06	1.68	0.20	0.10	0.75	5.12	**0.03**

adults were trapped 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, at both sites, all nests included in this study were found during building. Based on the records of previous captures as juveniles and breeding history at the study site, females were classified into two categories: females that bred for the first time (''young'' females hereafter) and females that bred at the site more than once (''older'' females). Daily ambient temperature (24-h average) for all years of the study was recorded by permanent weather stations at the Missoula Airport, located 1 km from the Montana study site, and on the campus of Auburn University. Data on the onset of incubation and ambient temperature were collected in 1995–2001 in Montana and in 2000–2001 in Alabama. Complete data on the onset of incubation, nestling growth, and offspring sex in relation to egg-laying order were available for 1997 and 1999–2001 in Montana and for 2000–2001 in Alabama.

Egg Laying, Incubation, and Nestling Growth

All females laid one egg per day until the clutch was complete. We did not observe any female skipping a day during the egg-laying period. Egg-laying and hatching were monitored closely and eggs were numbered sequentially on the day of laying. Nestlings were marked within a few hours of hatching. In some nests in 2000 and 2001 in both populations, eggs were not numbered during egg laying and the laying order was inferred from the hatching order, which has been shown to be identical in these populations (Badyaev et al. 2002). Individual marking was renewed every second day until nestlings could be banded with an aluminum ring at 7–8 days of age (protocols in Badyaev et al. 2001). Onset of full incubation was determined by daily monitoring of female presence on the nest during egg laying and by inferring incubation patterns from thermocouples (iButton-TMEX, Dallas Semiconductor, Sunnyvale, CA; and HOBO ProSeries, Onset Computer Corporation, Pocasset, MA) which were installed in each nest at the time of nest building (Montana) or at the onset of egg laying (Alabama). The devices were set to record egg temperature every 5 min. Trials in 2002 showed that the observational and thermocouple data were identical, which together with the observations of egg development (e.g., Fig. 3) and hatching asynchrony (unpubl. ms.) shows that the continuous presence of the female on the nest during egg laying is indicative of full incubation.

We separated the entire growth period of a nestling into pre-hatching (growth within an egg until hatching) and post-hatching (growth from hatching to fledging). We used a combined pre-hatching and post-hatching growth—measured as the final tarsus size (achieved by days 11–13 post-hatch; Badyaev et al. 2001)—as an estimate of overall nestling growth. There were several reasons to use final size as a proxy for overall growth. First, duration of egg laying (4–5 days) was always longer than the duration of hatching (typically $<$ 24 h); thus, in nests where incubation started during egg laying, nestlings hatched at different developmental stages and different sizes (Table 1). Second, more than 20% of tarsus growth takes place before hatching and, most importantly, the growth rate of tarsus differs between pre- and post-hatching periods (Badyaev et al. 2001). Thus, an estimation of daily gains in growth may be confounded by differences in timing of nestling development in relation to a nestling's position in a clutch. We measured left and right tarsus of nestlings twice (using Mitutoyo calipers, to an accuracy of 0.02 mm), and the average of repeated measures was used for the analyses. A. V. Badyaev measured all nestlings used in this study in Montana in 1997, 1999, and part of 2000, as well as in Alabama in 2000 and early 2001, M. L. Beck measured all nestlings in Alabama in late 2001, and a technician measured nestlings in Montana in a part of 2000. Repeatabilities for all traits were high (Badyaev and Martin 2000), and interobserver bias in measurements were negligible for the purposes of this study (Badyaev et al. 2001). Nestlings were measured every second day starting within a few hours of hatching and continuing until they left the nest (days 16–18 post hatch; see Badyaev et al. 2001 for details of nestling handling and prevention of premature fledgling).

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). We collected a 5- to 10-μl blood sample when each nestling was 8 days old. Details of molecular work and tests of verification of the molecular sexing methods are in Badyaev et al. (2001).

Statistical Analysis

House finches typically lay clutches of either four or five eggs. To include both of these clutch sizes, we recorded egg-laying sequence as the first, second, third, and the last (the fourth or fifth) egg. Clutches with less than four or more than five eggs ($n = 12$) were excluded from this study. We recorded the onset of incubation as the proportion of the total number of eggs that had been laid when incubation started (i.e., small values indicate early onset of incubation; see Fig. 4). Sex-ratio bias was tested with the binomial test (see Fig. 5). We used the generalized linear mixed models (SAS 8.12 macro GLIMIX modified from www.sas.com/service/techsup/faq/stat_macro/glimacr.html and PROC NLMIXED) with nest identity as a random effect to analyze the among-clutch trends in the egg-laying order, while accounting for interdependency of egg-laying positions within each clutch and for the binomial error variance of the sex data (after Krackow and Tkadlec 2001).

We analyzed the factors contributing to male and female growth at the brood (nest) level (see Fig. 6). Sex-laying order was recorded as a dummy variable representing the first two eggs (e.g., FM when female egg was laid first and male egg was laid the second; four combinations, df = 3) for each nest. The sex of the third and last eggs was always strongly biased in both populations (Badyaev et al. 2002), thus it was not used in the analyses. The sexes of some adjacent egg positions were not independent statistically and the sex ratio of the first egg was highly biased (Badyaev et al. 2003), thus reducing the number of observed values of the dummy variable. Variance of all effects was standardized before the analyses. For each nest, we included the nest-initiation date (breeding date), incubation onset, sex-laying order (first two eggs), growth of males (i.e., the mean size of all fully grown brothers), growth of females (the mean size of all fully grown sisters), and the SSD at fledgling (difference between mean male size and mean female size). Only paths drawn in Figure 6 were tested because of the limitations of the sample sizes. The path coefficient were estimated in two ways: by fitting reduced path diagram (see Fig. 6) in PROC CALIS of SAS 8.12 and by multiple regression analysis. Both procedures produced similar results, so only the path analysis output is shown in Figure 6. For ease of interpretation, only absolute values of the paths are shown (except for the paths from male and female growth to SSD). The total effects on SSD (see Fig. 7) were calculated from the path diagram by combining the direct and indirect effects and excluding the effects of unmeasured variables (unknown variance).

To analyze the effect of onset of incubation on growth of males and females, we compared growth of the preferred sex (i.e., sex biased for) with the growth of the avoided sex (i.e., sex biased against) in nests with early and late incubation initiations (see Fig. 9). The difference in growth gains was compared with two-tailed *t*-tests.

RESULTS

Ambient Temperature, Onset of Incubation, and Sex Ratio

In young females, the onset of incubation closely corresponded with ambient temperature; as a result, the seasonal pattern was opposite between Montana and Alabama (Fig. 4A,B). In Montana, young females started incubation from the first-laid eggs early in the season, and then as the season progressed and the ambient temperature increased, delayed the onset of incubation until the laying of the last egg. In Alabama, young females showed the opposite seasonal pattern (test of differences between populations: $F_{\text{population}} = 116.8$, $P < 0.001$; $F_{\text{population} \times \text{initiation date}} = 169.4$, $P < 0.001$). Older females in both populations varied extensively in the onset of incubation and were different between the populations, but within each population did not show pronounced patterns related to season or ambient temperature (Fig. 4C,D; test of differences between populations: $F_{\text{population}} = 2.75$, $P = 0.10$, $F_{\text{population} \times \text{initiation date}} = 5.24$, $P = 0.03$; test of differences between young and older females in Montana: $F_{\text{age}} = 21.08$, $P = 0.002$; $F_{\text{initiation date}} = 49.65$, $P < 0.001$; $F_{\text{initiation date} \times \text{age}} = 10.95$, $P = 0.003$; in Alabama: $F_{\text{age}} = 1.29$, $P = 0.27$; $F_{\text{initiation date}} = 24.82$, $P < 0.001$; $F_{\text{initiation date} \times \text{age}} = 7.87$, $P = 0.01$).

The sex of eggs in the laying sequence was closely related to the onset of incubation. In both young and older females and in both populations, clutches that were incubated from the first-laid eggs had highly sex-biased laying order (Fig. 5A,C). The bias was due mostly to sex of the first and the second eggs in Montana and the first egg in Alabama. In nests where incubation coincided with the onset of egg laying, the first egg produced mostly females in Montana (young females: 80%, older females: 83%; binomial test, both *P*-values < 0.02; Fig. 5A) and males in Alabama (young females: 82%, $P = 0.014$, and older females: 60%, $P = 0.09$, Fig. 5C). In nests where incubation started with the last egg, the sex of the first and second eggs was not biased in either population (Fig. 5B,D). The only exceptions were older females in Montana that produced mostly males (80%, $P = 0.016$) in first-laid eggs in nests with late onset of incubation (Fig. 5B). The sex of the last-laid egg did not vary with the onset of incubation and was strongly biased in both populations: these eggs produced mostly males in Montana (young: 70%; older: 100%; both *P*-values < 0.03; Fig. 5A,B) and mostly females in Alabama (young: 67%; older: 100%, both *P*-values < 0.03; Fig. 5C,D). Older females had greater sex bias in the egg-laying order, especially in the last-laid egg in both populations (above; both *Z*-values < -2.4; $P < 0.01$) and in the third-laid position in Alabama (early onset, young: 43% males, binomial $P = 0.13$; older: 100% males, $P < 0.01$; test for difference: $Z = -4.42$, $P < 0.01$; late onset, young: 62% males; older: 30% males; both *P*-values < 0.02; test for difference: $Z = 2.48$, $P < 0.01$).

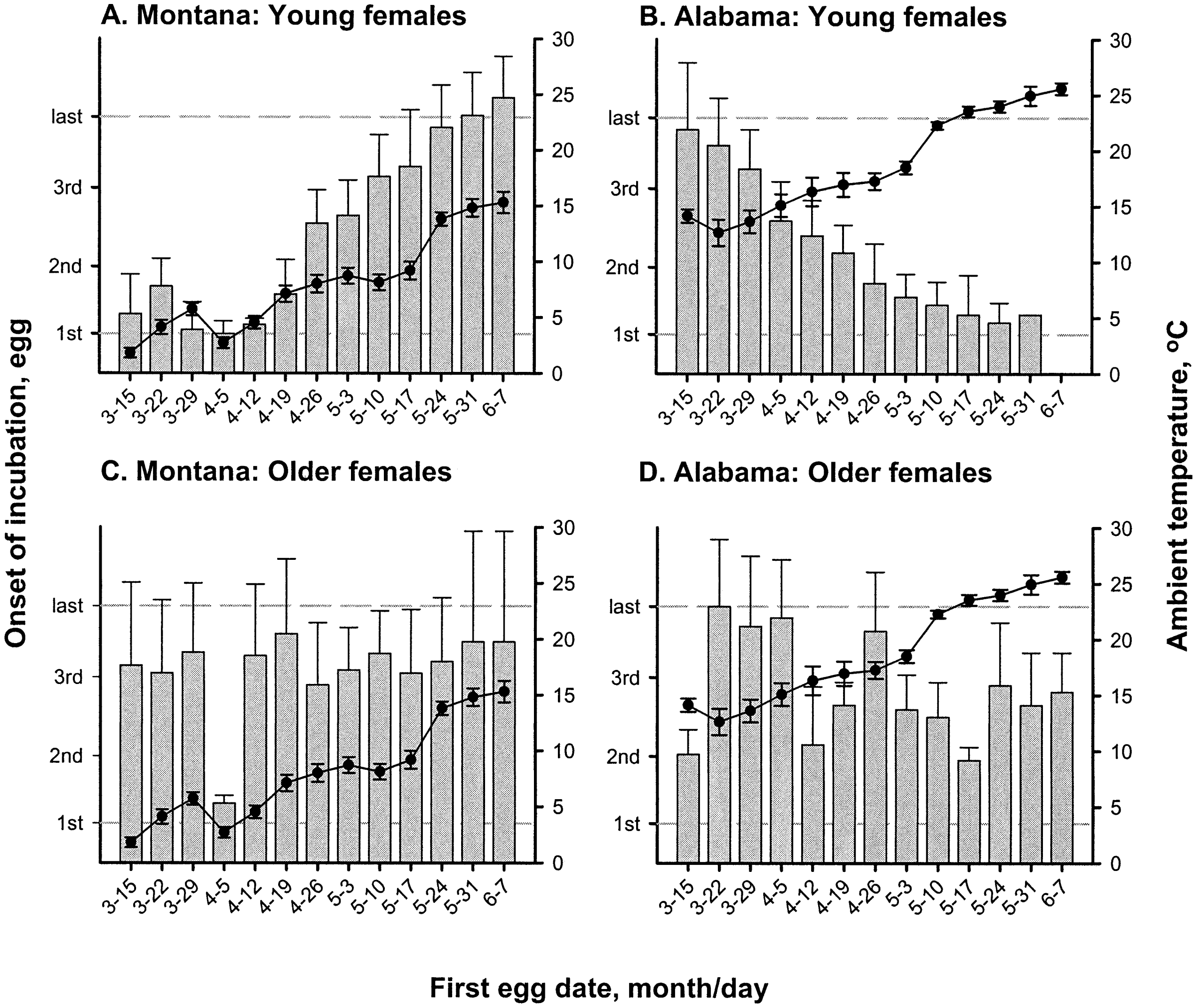

FIG. 4. The onset of incubation in house finch nests (gray bars, proportion of the egg number on which incubation started to the total number of eggs in a clutch, mean ± 1 SE) in relation to the first-egg date (one-week intervals) and the ambient temperature (black line, 24 h average, mean ± 1 SE) in (A) young females in Montana; (B) young females in Alabama; (C) older females in Montana; and (D) older females in Alabama. Dashed lines indicate the onset of incubation coincident with the first egg (lower) and with the last egg (upper).

Male and Female Growth and Sexual Size Dimorphism at Fledgling

Total growth

The effects of the onset of incubation and the position of the sexes in the laying order on growth of males and females were remarkably similar between the populations (Figs. 6, 7; Table 1). In both populations, the effects of incubation onset on offspring growth were stronger in the nests of young females compared to older females (Figs. 7, 8). In contrast, the effects of sex-biased egg-laying order were more pronounced in older females compared to young females (Figs. 6, 7). In both populations and age classes, the growth of males was affected by incubation onset more than the growth of females (Fig. 6; Table 1). In Montana, the growth of both sexes was equally affected by sex-biased egg-laying order, whereas in Alabama, growth of males was more affected (Fig. 6; Table 1). SSD at fledging was female biased in Montana and male biased in Alabama (Badyaev et al. 2002), and growth of male and female offspring contributed differently to SSD at fledging. In nests of young females in both populations, growth of females contributed more to SSD than did growth of males; in Montana, SSD was greater in nests with faster female growth, whereas in Alabama, SSD was greater in nests with slower female growth (Fig. 6). In nests of older females, male growth contributed more to SSD in both populations than did female growth. In both populations, faster male growth produced greater SSD (Fig. 6).

Pre-hatch growth

In both populations, the effects of incubation onset and sex-biased egg-laying order on pre-hatching growth (size at hatching) of males were strongly dependent on the breeding age of the female (Table 1). In Montana, nests of young and older females differed in the effects of the position of the sexes in the laying order on female pre-hatching growth. In Alabama, nests of young and older females differed in the

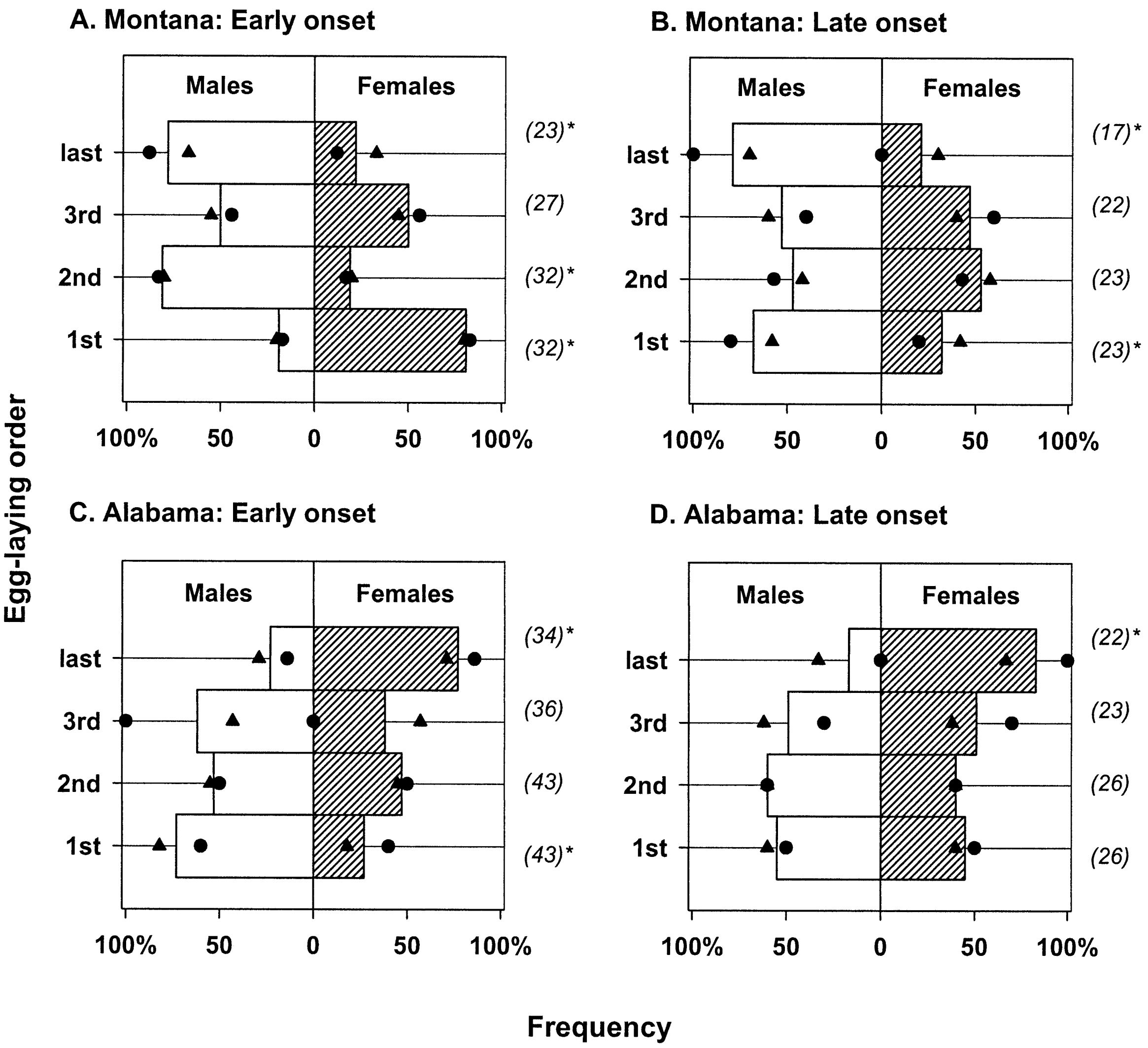

FIG. 5. The ratio of sons and daughters in relation to the egg-laying sequence in house finch nests in (A) Montana with early onset of incubation (from first-laid egg); (B) Montana with late onset of incubation (from the last-laid egg); (C) Alabama with early onset of incubation; and (D) Alabama with late onset of incubation. Numbers in parentheses show the number of nests. Asterisks indicate significantly biased sex ratio. Triangles indicate young females, circles indicate older females.

effects of incubation onset on female pre-hatching growth (Table 1). In both populations, pre-hatching growth of males was most affected by the onset of incubation, whereas pre-hatching growth of females was most affected by sex-biased egg laying in Alabama and was equally strongly affected by incubation onset and sex-biased egg laying in Montana (Table 1).

Post-hatching growth

In both populations, post-hatching growth of males was strongly affected by both sex-biased egg-laying order and, especially, the onset of incubation (Fig. 6, Table 1). In both populations, these effects were distinct between young and older mothers (Figs. 7, 8; Table 1). In Montana, the post-hatching growth of females was affected mostly by the onset of incubation and this effect differed between young and older mothers. In Alabama, the post-hatching growth of females was only weakly affected by sex-biased egg-laying order, and this effect differed between young and older mothers (Table 1).

In nests with early onset of incubation, variation among nestmates in post-hatching growth was more pronounced in young females compared to older females (Fig. 8). In nests of young females in both populations, variation in post-hatching growth was greater for nestling of the sex preferred in the first-laid position within a clutch (females in Montana and males in Alabama; Figs. 5, 8). Older females that incubated from the first egg did not show the predicted increase in variance in post-hatching growth of nest-mates (cf. Figs. 2 and 8).

The effects of sex-bias in egg-laying order and the modification of incubation onset were complementary in both populations (Fig. 9). In both populations, when male offspring were produced in the first egg in nests with early incubation onset, they grew faster and to a larger size (Fig. 9). In Montana, female offspring were preferred and male

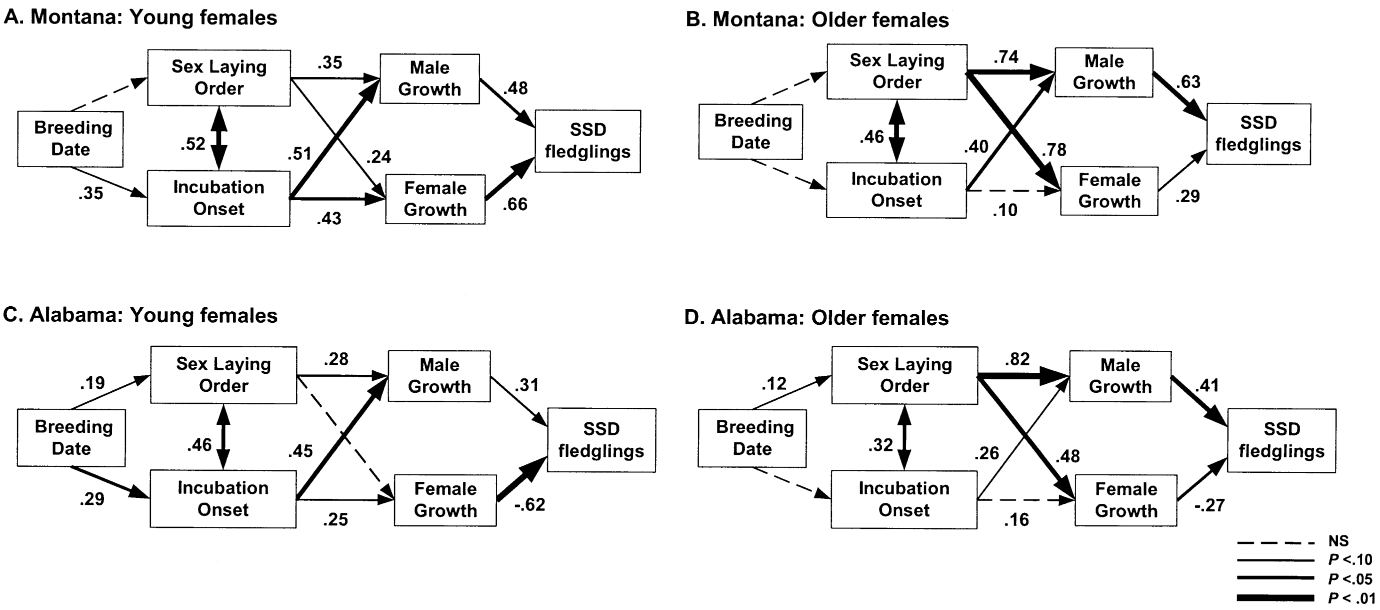

FIG. 6. Effects of breeding date, incubation onset, and the position of males and females in the laying order (sex-laying order) on male and female tarsus growth (pre- and post-hatching combined) and on sexual size dimorphism (SSD) in the nests of (A) young females in Montana; (B) older females in Montana; (C) young females in Alabama; and (D) older females in Alabama. The single-headed arrows indicate causal effect (in standard deviations). The effect of onset of incubation on sex-laying order is shown as bidirectional, but estimated as the effect of incubation onset influencing sex-laying order. Dashed lines indicate nonsignificant effects.

offspring were avoided in the first egg in nests with early onset of incubation, whereas the pattern was opposite in Alabama. Thus, in Montana mothers produced the sex that was less sensitive to the duration of incubation in the first egg, whereas in Alabama, mothers produced in the first egg the sex that grew faster and to a larger size when incubated for longer (Fig. 9). Hence the sex-bias in the first-laid eggs was concordant with the divergence in SSD between the two populations.

DISCUSSION

We found that by simultaneously adjusting both incubation onset (which determines developmental time) and the sequence in which male and female eggs were laid within a clutch, female house finches were able to strongly modify the growth of their sons and daughters at two climatic extremes of the species' geographical range. In both populations, differential environmental sensitivities of male and female growth enabled breeding females either to compensate for the effects of flexible incubation onset (Montana) or to enhance them (Alabama). Interestingly, in each population, maternal modifications of male and female growth produced patterns of SSD that were qualitatively concordant with those favored by survival selection on the offspring generation (i.e., larger females in Montana and larger males in Alabama; Badyaev et al. 2002). Such precision in maternal effects may be expected if the environmental conditions are shared between maternal and offspring generations (Rossiter 1996; Mousseau and Fox 1998; Wolf and Wade 2001; Komdeur and Pen 2002). More generally, the complementary interactions between the two maternal effects on offspring phenotype can produce a compromise between maternal and offspring adaptations under a wide range of breeding environments.

The relative strength and pathways by which mothers modified SSD of their offspring differed between young (first-time breeders) and older (experienced breeders) females (Figs. 6–8). In young females, environmentally induced onset of incubation was the most important factor contributing to male and female growth, with sex-ratio adjustment playing mostly a compensatory role. In contrast, in older females, strong modification of the sequence in which male and female offspring were produced played the most important role in their growth (Figs. 7, 8). These differences may be attributed to two factors. The effects of climate on females' decisions regarding when to begin incubation were distinct between young and older females (Fig. 4). Only in young females did the onset of incubation closely track seasonal changes in ambient temperature. Nevertheless, the onset of incubation was closely linked with the position of males and females in the laying order in both young and older females and in both populations (Fig. 5). Because the effect of climate on the onset of incubation was significantly weaker in older females, the onset of incubation in these females may represent a secondary, complimentary effect to the primary manipulation of the sex-ratio (Fig. 6; see also Blank and Nolan 1983; Sheldon et al. 1999). In contrast, in young females, the environmentally induced onset of incubation strongly affected growth of both sexes and was only weakly compensated for by the sex bias in egg-laying sequence (Figs. 7, 8).

The strong effects of sex bias in egg-laying order on growth of nestlings is expected if it is accompanied (or caused, see below) by the sex-biased allocation of growth factors into the eggs (Cordero et al. 2001; Petrie et al. 2001). Interestingly, in both populations, pre-hatch growth, but not post-hatch growth, was strongly affected by breeding age of the mother (Table 1), suggesting that the effects of sex-ratio ad-

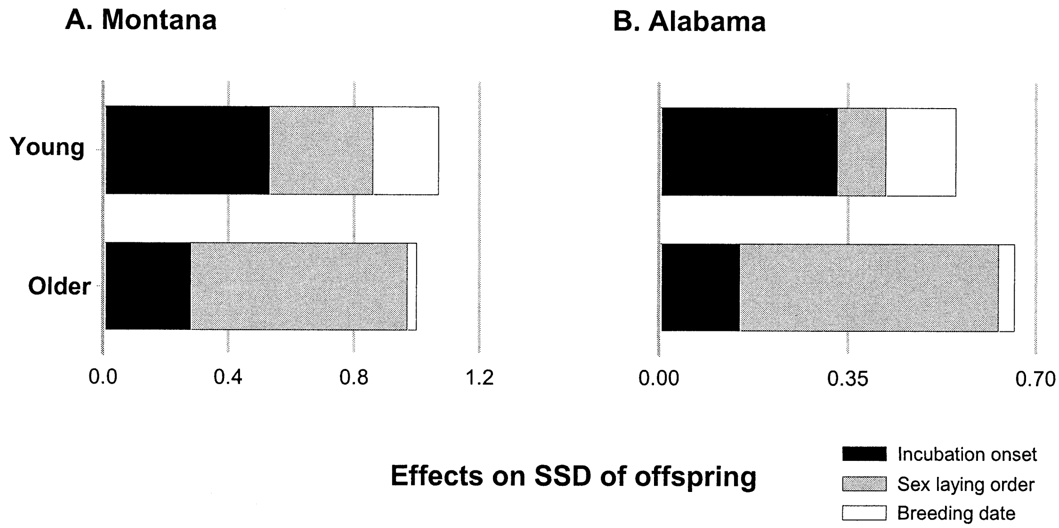

FIG. 7. Total (direct and indirect) effects (in standard deviations) of incubation onset, sex-laying order, and breeding date on sexual size dimorphism in tarsus at the end of growth in (A) Montana; (B) Alabama population of the house finch. Calculated from Figure 6.

justment were accompanied by different growth factors in females of different ages (Fig. 8). More generally, because all nestlings were provisioned with food equally (Stoehr et al. 2001), it is unclear how sex-biased egg-laying order per se can influence the dynamics of nestling growth other than by coinciding with the allocation of sex-specific growth factors (such as growth-inducing hormones). The results presented here suggest that the maternal transfer of growth factors should be more prevalent in older versus younger females (Table 1) and should be especially strong in nests of older females that undertake early onset of incubation (Fig. 8). Consistent with this prediction, allocation of maternal steroids into eggs (K. Navara, unpubl. data) was highest in the nests with early onset of incubation. In many species the magnitude and patterns of maternal effects on offspring growth change with a female's age, social rank, or condition, and these age-related changes can have unequal effects on male and female offspring (Bradbury and Blakey 1998; Nager et al. 1999; reviewed in Badyaev 2002; Lessells 2002). These findings and the results presented here suggest that the demographic composition of a population can play an important role in SSD divergence and should be investigated further.

Our results raise three questions: (1) Why do young and older females differ in their incubation strategies in relation to the ambient temperature at the time of egg-laying? (2) Why is the sex-bias associated with the early onset of incubation the opposite between the populations? (3) What is the contribution of the maternal effects described here to the adaptive population divergence in SSD that accompanied recent colonization of ecologically distinct areas of North America by the house finch (Badyaev and Hill 2000)?

In most passerine birds, unincubated eggs can remain viable for several days, during which they can tolerate a wide range of temperatures (~2–27°C; Webb 1987; Hébert 2002). The temperatures below the physiological tolerance of unincubated eggs were frequently recorded early in the season in Montana, whereas temperatures above the physiological tolerance were common late in the season in Alabama. Repeated exposure to these temperatures is expected to cause high mortality and aberrations in development of an embryo (Stoleson 1999). Correspondingly, the seasonal change in incubation onset in young females is most easily explained by the need to maintain egg viability in relation to ambient temperature (Veiga 1992; Vinuela 2000). In older females, lack of close association between incubation onset and ambient temperature (Fig. 4) have several potential explanations. First, the onset of incubation depends on female familiarity with breeding environment (reviewed in Hébert 2002) and older females in our populations may be responding only to extreme temperature fluctuations. Indeed in older females in Montana, more individuals incubated from the first egg early in the season compared to later in the season, but the pattern was the opposite in Alabama (Fig. 4). Second, in the house finch, full incubation is enabled by obligatory provisioning of the incubating female by her mate (Hill 1993; Badyaev and Hill 2002). Females with no prior breeding experience with their partners may induce greater paternal investment into the current reproductive attempt by initiating incubation early and thus extending the period of parental investment by a male (Slagsvold and Lifjeld 1989). Because of strong pair fidelity, older females may have previous familiarity with their breeding partners (Badyaev and Hill 2002) and may have more flexible incubation strategies (Amundsen 1999). Interestingly, older females vary extensively in the onset of incubation throughout the season (note the large standard errors for older females in Fig. 4). Thus, a substantial part of the variation in onset of incubation in older females is due to variation in individual strategies and not to seasonal temperature trends.

In both populations, the growth of males was influenced more by the flexible incubation periods than was the growth of females (Figs. 6, 9; Table 1), which corroborates the results of other studies (Bortolotti 1986; Anderson et al. 1997; Albrecht 2000; Blanco et al. 2002). In both populations, males in the first-laid eggs within a clutch grew faster and to a larger size compared to female offspring in the first-laid eggs

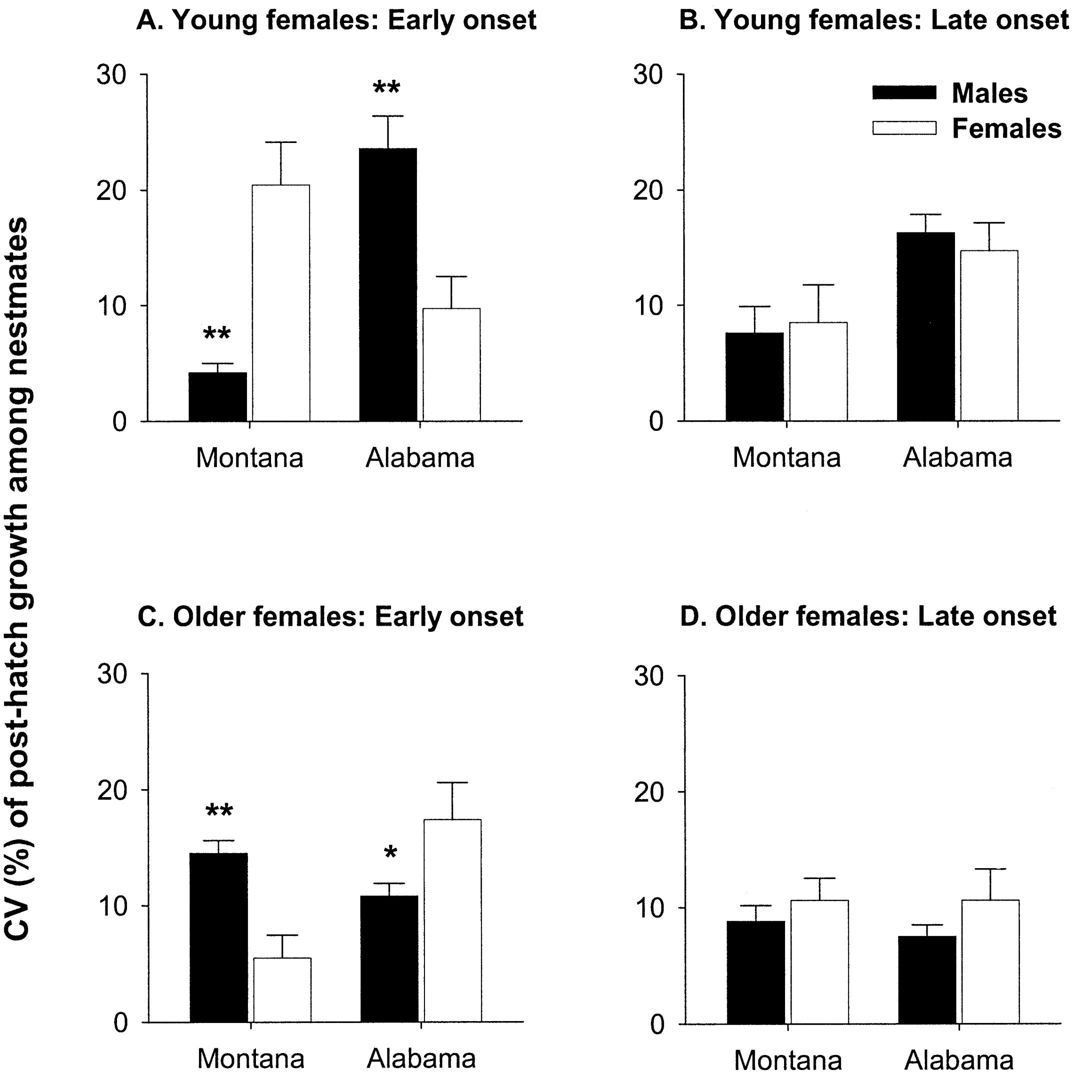

FIG. 8. Variability in growth among male and female offspring in nests of (A) young females with early onset of incubation; (B) young females with late onset of incubation; (C) older females with early onset of incubation; and (D) older females with late onset of incubation. Asterisks indicate significant difference by two-tailed *t*-test: $^*P < 0.05$; $^{**}\ P < 0.01$.

(Fig. 9). Thus, biasing the sex of the first offspring in relation to the onset of incubation provides the female with an opportunity to manipulate growth of males and females and hence to change the SSD of progeny (Legge et al. 2001; Blanco et al. 2002; Krebs et al. 2002). Indeed, the joint manipulation of onset of incubation and the position of males and females in the egg-laying sequence produced highly distinct SSD in Montana and Alabama juveniles. In Montana, where larger juvenile females have higher survival, the first-laid egg was strongly female biased in the nests with early onset of incubation. In Alabama, where larger juvenile males have higher survival, the first-laid egg was male biased (Badyaev et al. 2002).

The close link between onset of incubation and bias in the position of males and females in the egg-laying sequence may be due to changes in the hormonal profile of breeding females. The onset of incubation is associated with a sharp increase in circulating prolactin and with a decrease in testosterone in female's plasma (Schwabl 1996a; Crisostomo et al. 1998; Vleck 2002). Indeed, we found that in the Montana population prolactin profiles differed between females that incubated from the first versus last egg. Moreover, the mother's prolactin profile at the time of ovulation of male follicles was lower than the prolactin profile during ovulation of female follicles (A. Badyaev, R. Duckworth, and H. Schwabl, unpubl. ms.). Mothers commonly transfer hormones that influence growth into eggs, and several studies have documented differential maternal allocation in relation to egg-laying order (Schwabl 1996b; Eising et al. 2001; Reed and Vleck 2001; Royle et al. 2001) and offspring sex (Schwabl et al. 1997; Petrie et al. 2001). Moreover, maternal hormones, such as steroids, may differentially affect prenatal and postnatal growth of males and females (Gatford et al. 1998; Henry and Burke 1999) and fluctuations in maternal hormones during egg laying (e.g., due to social interactions; Whittingham and Schwabl 2002), correlates with maternal transfer of hormones into eggs (Zadworny et al. 1986; Schwabl 1996a; Sockman et al. 2001). Thus, the link between the sex-biased

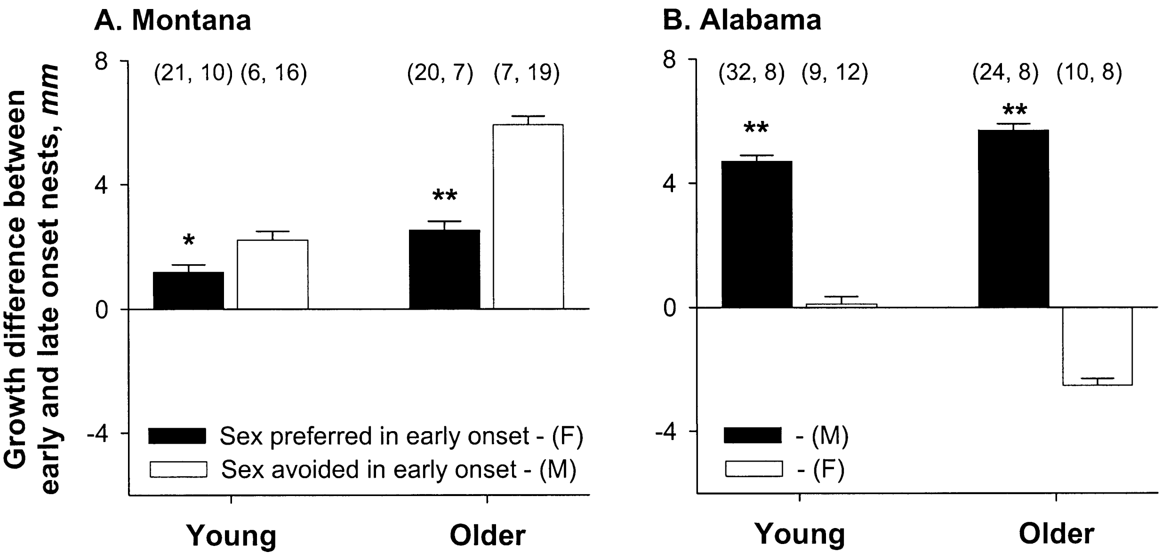

FIG. 9. Effect of onset of incubation on post-hatching tarsus growth of the offspring in the first-laid position within a clutch in (A) Montana; (B) Alabama population. Preferred (i.e., biased for) sex for the first-laid egg in nests with early onset of incubation is females in Montana and males in Alabama (Fig. 5). Bars show the difference in growth gains (mm per 48 h) in offspring raised in the nests with the early versus late onset of incubation. Black bars above the zero line indicate that the sex preferred in the first position in nests with early onset grows faster that it does in nests with late incubation onset. White bars above the zero line show that sex that is avoided in the first position in nests with early incubation onset grows faster in these nests than in the nests with late onset of incubation. Asterisks indicate significant difference by two-tailed *t*-test: $*P < 0.05$; $**P < 0.01$. Numbers in parentheses are sample sizes (early onset, late onset).

laying order and the onset of incubation might be due to temporal variation in the ability of breeding females to transfer particular hormones into eggs (Schwabl 1999; Komdeur and Pen 2002).

Whereas the patters of SSD produced by the maternal effects were clearly adaptive for offspring (Badyaev et al. 2002), it is unclear how the maternal ability to achieve such precision can evolve (Komdeur and Pen 2002). Biasing sex ratio in relation to the onset of incubation may enable females to produce more synchronous growth and fledging despite flexible incubation periods among nestmates (cf. Figs. 2 and 8). Indeed, the precise adjustment of offspring sex to modify the effects of variable developmental periods of nestmates (due to either pronounced sexual dimorphism or early incubation onset) is frequently found in birds (Bortolotti 1986; Slagsvold 1990; Lessells et al. 1996; Bradbury and Griffiths 1999; Legge et al. 2001; Blanco et al. 2002). Mothers can modify the sex of their offspring seasonally in the close concordance with the seasonal changes in fitness of male and female progeny (Dijkstra et al. 1990; Daan et al. 1996; Cordero et al. 2001; Velando et al. 2002) and depending on changes in breeding habitat and social status, mate choice, or environmental conditions (reviewed in Hasselquist and Kempenaers 2002; Komdeur and Pen 2002). Recent meta-analysis showed that when the offspring environment is predictable for mothers (e.g., when maternal and offspring environments are correlated) and when the costs of sex-ratio adjustment is low (e.g., limited SSD in offspring) birds can manipulate the sex of their progeny strongly and precisely (West and Sheldon 2002; see also Komdeur and Pen 2002). The results presented here show that selection acting on females during egg laying, in combination with active maternal effects, affects the morphology of male and female offspring and thus facilitates evolution of maternal effects that may be adaptive for both generations.

ACKNOWLEDGMENTS

We are grateful to R. Duckworth, F. James, J. Merilä, L. Oring, and anonymous reviewers for many helpful suggestions. We thank J. Ariail, L. Cole, W. Deschamps, A. Dervan, P. Hendricks, C. Glen, H. Mays, K. Navara, and A. Rapone for help with the field and laboratory work. The personnel of the Vigilante MiniStorage in Missoula, Montana, kindly allowed us to work on their property and helped with the logistics. We thank Beth Archie for preparing drawings for the cover. This research was supported by the National Science Foundation (NSF) (DEB-0075388, IBN-9722171, and IBN-0218313). High school and undergraduate interns K. Anderson, H. Williams, J. Dacy, and S. Terry, who assisted with this study, were supported by the NSF Research Experiences for Undergraduates program (DEB-0077804).

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Corresponding Editor: J. Merilä