# Population consequences of maternal effects: sex-bias in egg-laying order facilitates divergence in sexual dimorphism between bird populations

A. V. BADYAEV,*† G. E. HILL† & L. A. WHITTINGHAM‡

*Division of Biological Sciences, The University of Montana, Missoula, MT, USA
†Department of Biological Sciences, Auburn University, Auburn, AL, USA
‡ Department of Biological Sciences, University of Wisconsin, Milwaukee, WI, USA

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## Abstract

When costs and benefits of raising sons and daughters differ between environments, parents may be selected to modify their investment into male and female offspring. In two recently colonized environments, breeding female house finches (*Carpodacus mexicanus*) modified the sex and growth of their offspring in relation to the order in which eggs were laid in a clutch. Here we show that, in both populations, these maternal effects strongly biased frequency distribution of tarsus size of fully grown males and females and ultimately produced population divergence in this trait. Although in each population, male and female offspring show a wide range of growth patterns, maternal modifications of sex-ratio in relation to egg-laying order resulted in under-representation of the morphologies that were selected against and over-representation of morphologies that were favoured by the local selection on juveniles. The result of these maternal adjustments was fast phenotypic change in sexual size dimorphism within and between populations. Maternal manipulations of offspring morphologies may be especially important at the initial stages of population establishment in the novel environments and may have facilitated recent colonization of much of North America by the house finch.

## Introduction

When costs and benefits of raising male and female offspring differ between environments, parents are expected to adjust their investment to sons and daughters (Williams, 1979; West & Sheldon, 2002). In birds, sex-biased parental effects include modification of primary sex ratio of offspring (Komdeur *et al.*, 1997, 2002; Sheldon *et al.*, 1999), differential allocation of nutrients, hormones and antibodies into male and female eggs (Cordero *et al.*, 2000; Petrie *et al.*, 2001), sex-biased egg laying and hatching order (Bortolotti, 1986; Bednarz & Hayden, 1991; Legge *et al.*, 2001; Krebs *et al.*, 2002), as well as sex-biased provisioning of nestlings (reviewed in Lessells, 2002).

Egg-laying sequence may represent a particularly predictable gradient of environmental condition for offspring growth because birds lay just one egg a day until the clutch is completed, and females are in control of initiation of incubation. Indeed, egg-laying order has a profound effect on growth and fitness of offspring (Griffiths, 1992; Bradbury *et al.*, 1997; Torres & Drummond, 1999; Blanco *et al.*, 2002). Consequently, differential parental allocation in offspring in relation to egg-laying order is often documented (Schwabl, 1996a; Lipar *et al.*, 1999; Royle *et al.*, 2001) and, depending on environmental conditions, could either mitigate or exaggerate the effects of hatching asynchrony (Bortolotti, 1986; Anderson *et al.*, 1997; Hillström, 1999; Cordero *et al.*, 2001). Thus, when costs of raising sons and

*Correspondence and present address:* A. V. Badyaev, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721 USA.
e-mail: abadyaev@selway.umt.edu

daughters differ, parents may be selected to adjust the sex of offspring relative to their position in the laying order (Slagsvold *et al.*, 1986; Slagsvold, 1990).

However, sex-biased parental allocation is a parental adaptation, and to fully understand its evolution it is necessary to take into account costs and benefits of sex-allocation strategies for both parental and offspring generations (Wolf & Wade, 2001; Hasselquist & Kempenaers, 2002; West & Sheldon, 2002). Yet, most studies had focused only on parental generation, partly because it is easier to identify the factors that should favour changes in sex-allocation and to predict its outcome for parental fitness. For example, females of many avian species were shown to predictably modify their allocation to sons and daughters in relation to changes in social environment (e.g. mate quality) (Svensson & Nilsson, 1996; Sheldon *et al.*, 1999; Westerdahl *et al.*, 2000), variation in individual health and condition (Nager *et al.*, 1999; Whittingham & Dunn, 2000), environmental variation (Komdeur *et al.*, 1997), or interaction between these factors. A particularly good illustration are the studies that documented close correspondence between predictable changes in ecological and social environments during breeding and changes in parental sex-allocation in successive breeding attempts (Dijkstra *et al.*, 1990; Dzus *et al.*, 1996; Bensch *et al.*, 1999; Bradbury & Griffiths, 1999; Torres & Drummond, 1999; Questiau *et al.*, 2000; Westerdahl *et al.*, 2000; Cordero *et al.*, 2001).

Less attention has been paid to the effects of parental sex-allocation on offspring fitness, and especially to the population consequences of these parental strategies (but see Daan *et al.*, 1996; Appleby *et al.*, 1997; Cordero *et al.*, 2001). The challenge for empirical studies has been the identification of selection pressures on offspring generation that may favour biases in parental sex allocation. Such parental effects may be especially pronounced during initial stages of population establishment in novel environments when the contrast between selection pressures on parental and offspring generations is especially pronounced and predictable, and when selection pressures on offspring morphologies are strong (Miao *et al.*, 1991). Parental modifications of offspring morphology may facilitate adaptation to novel environment by reducing mortality of offspring and thus allowing population to persist during initial colonization stages (Fear & Price, 1998; Mousseau & Fox, 1998).

In the house finch (*Carpodacus mexicanus*), extensive colonization of new areas in North America over the last 60 years was accompanied by population divergence in sexual size dimorphism that was the result of adaptive and rapid changes in morphology of both males and females (Badyaev & Hill, 2000). For example, establishment of house finch populations in highly distinct environments of Montana (north-west US) and Alabama (south-east US) 20–30 years ago was accompanied by wide divergence of morphological appearances of both sexes (i.e. in Montana, female tarsus at the end of growth is 2.5% longer than male tarsus, whereas in Alabama, female tarsus is 3.2% shorter than male tarsus), apparently because of rapid population divergence in the ontogeny of sexual size dimorphism (Badyaev *et al.*, 2001a).

This divergence in growth was facilitated by population differences in maternal allocation into eggs in relation to egg-laying order (Badyaev *et al.*, 2002). Here we evaluate the contribution of these maternal effects to population divergence in sexual dimorphism in tarsus length. We first show that nestlings in both populations show a wide range of growth patterns that can produce a wide range of adult sizes. We then show that, in the absence of maternal modification of sex-ratio in relation to egg-laying order, population divergence in nestling growth rates cannot account for population divergence in adult morphologies. We discuss implications of sex-biased parental investment for rapid range expansion of the house finch.

## Materials and methods

### Study populations and field methods

We studied the house finches in two recently established resident populations – in Missoula, north-western Montana and in Auburn, east-central Alabama. The study site in Montana was maintained since 1995 when the local population was 25–30 years old, the study site in Alabama was maintained since 1993 when the local population was 10–15 years old (Badyaev & Hill, 2000). For detailed description of the study sites see Hill *et al.* (1999) and Badyaev & Martin (2000). Here we summarize the most relevant details of data collection.

All pairing and nesting affiliations of breeding adults were determined reliably and all nests were found during nest building. Hatching was monitored continuously and nestlings were individually marked within few hours of hatching (for details see Badyaev *et al.*, 2001b). Individual markings of nestlings were renewed every second day until nestlings could be banded with a permanent ring. House finches lay one egg a day which results in distinct hatching sequence of nestlings. In 2 years, in both populations, we examined concordance between egg-laying and egg-hatching sequence, by numbering each newly laid egg with permanent nontoxic marker and recording its hatching sequence. In all years, egg-laying sequence corresponded with egg-hatching sequence (e.g. Clotfelter *et al.*, 2000). By cross-fostering eggs between nests where their laying order was different and recording the growth and final size of nestlings we established that maternal effects were the result of differential allocation into eggs in relation to egg-laying sequence and not due to hatching hierarchy or within-nest competition (Badyaev *et al.*, 2002; see also below). Thus, only egg-laying order is used in this study.

**Table 1** Tarsus length (mean ± SE, mm) in relation to the egg-laying order in male and female house finches in Montana and Alabama.

| | Egg-laying order | | | | |
|---|---|---|---|---|---|
| Sex | 1st | 2nd | 3rd | 4th | 5th |
| Montana | | | | | |
| Males | 20.00 (0.20)$^{*}$ | 19.46 (0.17)$^{*}$ | 19.10 (0.18)$^{\dagger}$ | 18.50 (0.27)$^{\dagger}$ | 17.49 (0.25)$^{\ddagger}$ |
| Females | 18.54 (0.39)$^{*}$ | 19.12 (0.27)$^{*}$ | 19.25 (0.13)$^{*\dagger}$ | 19.58 (0.30)$^{\dagger}$ | 19.89 (0.34)$^{\dagger}$ |
| Alabama | | | | | |
| Males | 20.21 (0.12)$^{*}$ | 20.35 (0.50)$^{*}$ | 20.72 (0.13)$^{*}$ | 19.80 (0.20)$^{\dagger}$ | 18.90 (0.21)$^{\dagger}$ |
| Females | 20.60 (0.15)$^{*}$ | 20.38 (0.16)$^{*}$ | 19.73 (0.15)$^{\dagger}$ | 19.55 (0.17)$^{\dagger\ddagger}$ | 19.40 (0.35)$^{\ddagger}$ |

Values with the same superscript symbols are not significantly different within sex and population after sequential Bonferonni adjustment ($n = 5$ egg-laying positions).

The sex-ratio data used in this study was collected in 1998–2001 in Montana and 2000–2001 in Alabama populations. Data on sexual dimorphism in tarsus of fully grown juveniles (18–30 days of age) were collected in 1995–2000 in Montana (Badyaev *et al.*, 2001b) and in 1997–2000 in Alabama (G. E. Hill, unpubl. data). We measured (with Mitutoyo calipers with accuracy of 0.02 mm) left and right tarsus of nestlings at the time they left the nest (*c.* 16 days). The tarsus attains its full size in the house finches by the 12–13 days post-hatching (Badyaev *et al.*, 2001b) and thus well suited for the purpose of our study. The measures were repeated twice for left and right tarsus and the average of repeated measures was used for further analyses. To exclude any interobserver bias in measurements, AVB and a technician measured all nestlings used in this study. Hatch date and mite infestation have a strong influence on sex-specific growth in birds (e.g. Cooch *et al.*, 1996; Potti, 1999). Mite infestation is not recorded in the Montana population, although it is a common cause of nestling mortality during late spring and summer in Alabama (Stoehr *et al.*, 2000). Thus, to control for effects of hatch date and mite infestation we only used the subset of nestlings (Montana: $n = 26$ nests, 119 nestlings; Alabama: 40 nests, 153 nestlings) from the first breeding attempt (late February–late April) where the entire brood survived till the end of the nestling period.

### Statistical analysis

To examine the effects of sex and egg-laying order on the tarsus size at the end of growth, we performed mixed-model analyses of variance on the data. The random effects were sex and egg-laying order. The tarsus length data were natural log-transformed and standardized to a mean zero and unit variance.

### Molecular sexing

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 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 blood sample when each nestling was 8 days old. For details of DNA extraction, PCR, and electrophoresis see Badyaev *et al.* (2001a).

## Results

### Tarsus size in relation to sex and egg-laying order

Tarsus size at the end of growth strongly depended on egg-laying order, but these effects were opposite between the sexes and populations. In Montana, males hatched from the first and second eggs grew to be larger than males hatched from the third, fourth and fifth eggs, and males that hatched from the third egg were larger than males hatched from the fifth egg (Table 1; ANOVA $F$-values >8.0, $P < 0.001$). Females hatched from eggs laid later in the sequence grew to be the largest – females from the last egg were larger than females hatched from the first and second eggs (Table 1, $F$-values >6.7, $P < 0.001$). In Montana juveniles, tarsus size depended on interaction of laying order and sex ($F_{4,119} = 6.50$, $P < 0.001$) and the laying order ($F_{4,119} = 2.88$, $P = 0.04$), but not the sex itself ($F_{1,119} = 1.02$, $P = 0.36$).

In Alabama, males hatched in the middle of the egg-laying sequence grew to be the largest, whereas males hatched from the fourth and fifth eggs were the smallest (Table 1, $F$-values >5.3, $P < 0.01$). Females hatched from eggs laid in the beginning of laying sequence were larger than females that hatched from the third and fourth eggs (Table 1, $F$-values >8.00, $P < 0.001$). In Alabama juveniles, tarsus size depended on interaction of laying order and sex ($F_{4,\ 153} = 4.44$, $P = 0.006$) and the laying order ($F_{4,\ 153} = 3.65$, $P = 0.01$), but not the sex ($F_{1,153} = 0.63$, $P = 0.56$).

In Montana, sexual dimorphism (male minus female) in tarsus size at the end of growth depended mostly on male position in egg-laying sequence (Fig. 1a). Sexual dimorphism was male-biased in cohorts where males hatched from eggs laid early in the sequence (#1–3), and female-biased in cohorts where males hatched from eggs laid later in the sequence (#4–5). In Alabama, sexual dimorphism at the end of growth depended mostly on female position in egg-laying sequence (Fig. 1b). Sexual dimorphism was female-biased in cohorts where females hatched from eggs laid early in the sequence (#1–2), and male-biased in cohorts where females hatched from eggs laid in the middle or the end of sequence (#3–5).

### Sex-biased egg-laying order and population divergence

In both populations egg-laying order was strongly sex-biased (tests in Badyaev *et al.*, 2002), resulting in biased representation of different cohorts of males and females among fully grown juveniles (Fig. 2). In the absence of sex-bias in egg-laying order, sexual dimorphism in tarsus length at the end of growth (calculated as the mean of values of all cohorts from Fig. 1a for Montana and Fig. 1b for Alabama), was not significantly different from zero in either populations [Montana: 0.09 ± 0.12 (SE), $t = 0.13$, $P = 0.89$; Alabama: 0.12 ± 0.14, $t = 1.58$, $P = 0.14$; Fig. 3] and was highly dissimilar to the observed level of sexual dimorphism of juveniles in both populations (both $t$-values >16.0, $P < 0.001$; Fig. 3). Weighting the means of sexual size dimorphism of different male–female cohorts (Montana: Fig. 1a; Alabama: Fig. 1b) by the frequency of their occurrence (Montana: Fig. 2a; Alabama: Fig. 2b) produced significant and highly distinct levels of sexual size dimorphism in both populations (Montana: −0.20 ± 0.11; Alabama: 0.55 ± 0.12; Fig. 3), that were qualitatively similar to the levels of sexual dimorphism observed in both populations over all years of study (Fig. 3; Montana: −0.47 ± 0.07 mm; Alabama: 0.65 ± 0.07 mm).

## Discussion

We found that pronounced population difference in both sex-ratio in relation to egg-laying order and in the effect of egg-laying order on offspring growth resulted in significant population divergence in morphology of juvenile males and females. Moreover, in the absence of biases in sex-ratio and growth in relation to egg-laying sequence, growth divergence between the populations could not account for the observed population divergence in the tarsus size. Thus, by simultaneously adjusting sex and growth of offspring in relation to egg-laying order, breeding females biased frequency distribution of fully grown males and females. These results raise several questions. First, why do populations differ in growth patterns and sex-ratio in relation to egg-laying order? More specifically, because differential maternal allocation into eggs produces these patterns, why are different maternal strategies favoured in different populations? Secondly, what are the population-level consequences of these effects? Could these effects facilitate rapid

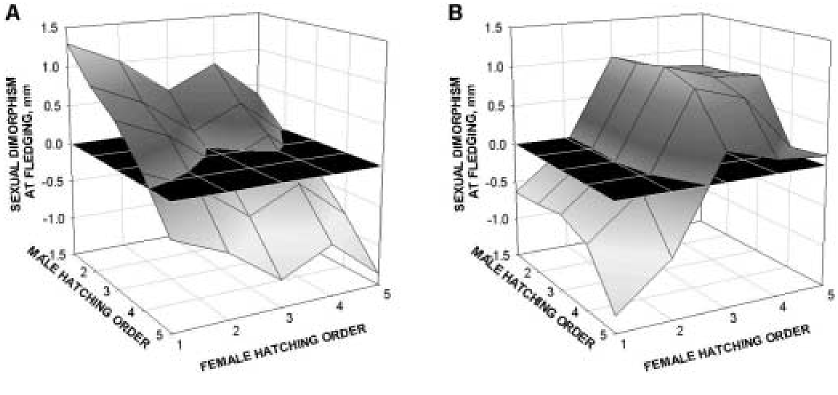

**Fig. 1** Sexual dimorphism in tarsus length (male minus female) at the end of growth in different cohorts of sexes in relation to hatching order ( = egg-laying order) in (a) Montana and (b) Alabama populations. Black plane indicates no sexual dimorphism. Values above the plane represent male-biased dimorphism, values below the plane represent female-biased dimorphism. In Montana, sexual dimorphism at the end of growth is mostly affected by male position in egg-laying sequence, whereas in Alabama it is mostly affected by female position in egg-laying sequence.

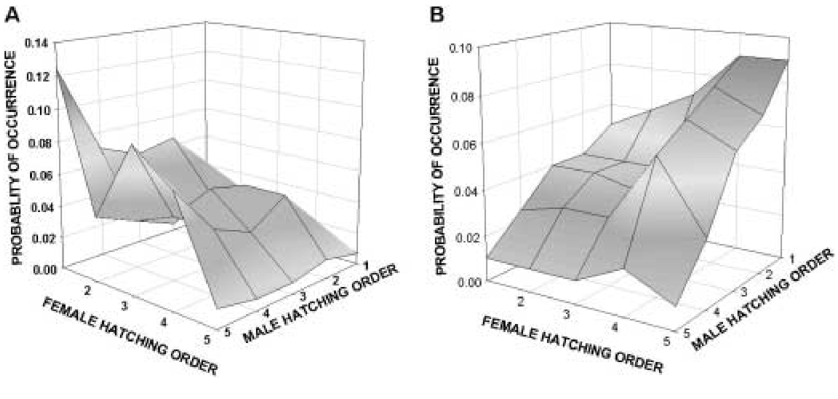

**Fig. 2** Probability of occurrence of a particular combination of sex and hatching order ( = egg-laying order) in (a) Montana and (b) Alabama. Nestlings hatched from the first-laid eggs are most often females in Montana and males in Alabama.

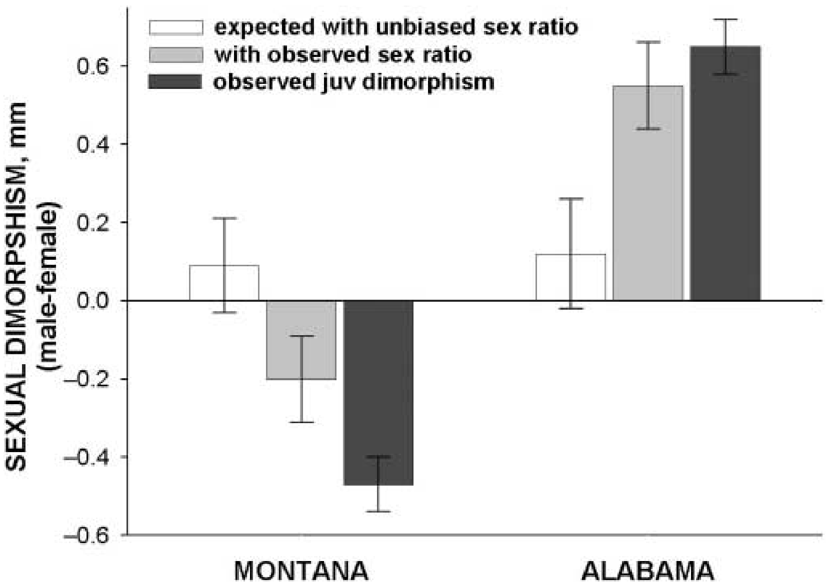

**Fig. 3** Sexual dimorphism in tarsus size at the end of growth in Montana and Alabama. White bars show mean level of sexual dimorphism in the absence of sex-bias in egg-laying order. Calculated from Fig. 1a and b. Standard errors are from bootstrapping of the mean. Grey bars show mean levels of sexual dimorphism adjusted by the probability of occurrence of a particular sex and laying order combination. Calculated by weighting means shown in Fig. 1a and b by the probabilities shown in Fig. 2a and b for Montana and Alabama correspondingly. Dark bars show observed level of sexual dimorphism in tarsus in Montana and Alabama. In the absence of sex-biased egg-laying order, divergence in growth cannot account for observed divergence in sexual size dimorphism of juvenile house finches between Montana and Alabama populations.

establishment of the house finches across much of North America in the last 60 years? Finally, by what mechanisms females adjust sex and growth of nestlings in relation to egg-laying order and why do females vary in this ability?

Consistent population differences in patterns of maternal sex-allocation in relation to egg-laying order (Fig. 2) suggest that populations differ in either costs and benefits of producing sons and daughters of a particular morphology or in sex-specific costs of offspring growth *per se*. Precision and consistency of sex-ratio manipulation may be facilitated by strong and predictable ecological differences between the populations. Correspondingly, adult and juvenile finches of both sexes experience strongly distinct selection on survival between the populations. Indeed, maternal adjustment of sex-ratio in relation to egg-laying order was closely concordant with the patterns of juvenile survival in both populations: maternal modifications of sex and growth enabled an estimated 10–20% reduction in juvenile mortality compared with that expected if sex and growth were random in relation to egg-laying order (Badyaev *et al*., 2002). Alternatively, population differences in sex-ratio in relation to egg-laying order may represent an adaptation to population differences in costs of male and female growth *per se* – such as different sensitivity of males and females to environmental condition during growth, e.g. to the presence of nest mites or to variable onset of incubation (unpubl. manuscript; Potti & Merino, 1996). Interestingly, differential parental allocation in relation to egg-laying order appears to be more widespread in birds than the modification of the primary sex ratio of entire broods, as it may allow parents a more flexible way to maximize parental investment in relation to their own condition and to environmental variation (Hasselquist & Kempenaers, 2002; Komdeur & Pen, 2002).

By adjustment of sex and growth of offspring in relation to egg-laying order, breeding females biased the morphology of offspring so that the morphologies that were locally selected against were under-produced (and thus excess mortality avoided), whereas locally favoured morphologies were overproduced (and thus increased fitness consequences of parental effort) (selection measures in Badyaev *et al*., 2002). On a population level, these maternal effects can enable population persistence under novel selection pressures, which is likely to be important for colonizing abilities of the house finch. More generally, maternal effects on morphology of offspring can, by virtue of trans-generational transmission or plasticity (Rossiter, 1996), modify the selection pressures on offspring genotype and thus influence character evolution (Larsson & Forslund, 1992; Watson & Hoffmann, 1996), population dynamics (Ginzburg, 1998), population differentiation and establishment in novel environments (Miao *et al*., 1991; Fear & Price, 1998).

Despite the ubiquity of maternal effects in birds (Price, 1998), our progress in understanding their contribution to fitness and the mechanisms behind their evolution is limited by the lack of clear understanding of both adaptive value of such effects and variation in maternal effects in natural populations. For example, although it is frequently documented that maternal transfer of steroids modifies growth of embryos and nestlings (Schwabl, 1996b, 1999; Eising *et al*., 2001), we do not yet know why mothers vary in these effects or how these effects can evolve. Does the often-documented within-clutch variation in steroid transfer represent a passive consequence of endocrinological changes in the female during egg-laying (Sockman *et al*., 2000; Vleck, 2002), differential allocation to embryos of different sex (Petrie *et al*., 2001), or active differential allocation in relation to egg-laying order (Cunningham & Russell, 2001)? Moreover, females may differ in steroid allocation to eggs depending on ecological and social environment during breeding, as well as age and physiological condition (Gil *et al*., 1999; Reed & Vleck, 2001; Whittingham & Schwabl, 2002). Consistent population differences in either of these parameters could produce divergence in maternal effects on growth and sex of offspring documented in this study. Our findings of adaptive and opposite patterns of maternal sex allocation in different environments may provide a framework in which to test proximate mechanisms behind variation in maternal effects.

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