

Adaptive maternal effects and rapid population differentiation

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How rapidly can two populations diverge when exposed to different selection pressures? And what mechanisms contribute to rapid population divergence? A remarkable new study by Badyaev *et al.* of house finches *Carpodacus mexicanus* suggests that simultaneous maternal adjustment of offspring sex ratio and growth rates has played an important role in rapid population differentiation associated with an explosive range expansion.

Introductions of alien species can have disastrous consequences for native fauna, but might also provide important evidence relating to pattern and process in evolution [1–3]. House finches *Carpodacus mexicanus* (Fig. 1a) are small granivorous passerine birds, formerly confined to western North America. In 1939, between 40 and 100 house finches, originally from California, were released near New York and, in a rapid range expansion, colonized much of the eastern USA and south-eastern Canada within the next 50 years (Fig. 1b).

Simultaneously, house finches in the original range expanded to the north and east, colonizing formerly unoccupied areas (Fig. 1b). A new paper by Badyaev *et al.* [4] shows that adaptive maternal effects might have played a crucial role in enabling populations to adapt to new environments, in spite of this very rapid colonization.

In previous work, Badyaev and colleagues [5–10] compared sexual size dimorphism in house finches comprising recently established populations. Most of the population comparisons have been between a population in Alabama (representing the New York introduction) and a population in Montana (representing one of the range extensions of the original population; Fig. 1b). These comparisons, between populations inhabiting very different environments (hot and humid versus cold and dry, respectively) have shown that the two populations have evolved different patterns of sexual size dimorphism (males are larger than females), the dimorphism being more

marked in Alabama than in Montana [7]. In addition, the relative difference between the sexes also varied for different traits in different populations [7]. In both populations, the pattern of sexual size dimorphism for individual traits matched empirically derived differences in selection on the two sexes [5,7].

This latter observation suggests that the differences in sexual size dimorphism represent adaptive responses to sex differences in selection, but there is a problem. Genetic correlations in morphology between the sexes in this species are high [6], as in many other organisms, and this should constrain the response to selection [11]. Badyaev and colleagues suggest that one way to overcome these constraints is if sexual size dimorphism is affected by sex differences in growth, and demonstrate that these two populations differ in the ontogeny of sexual size dimorphism [9,10]. In addition, the patterns of differences in growth rates of different morphological traits between

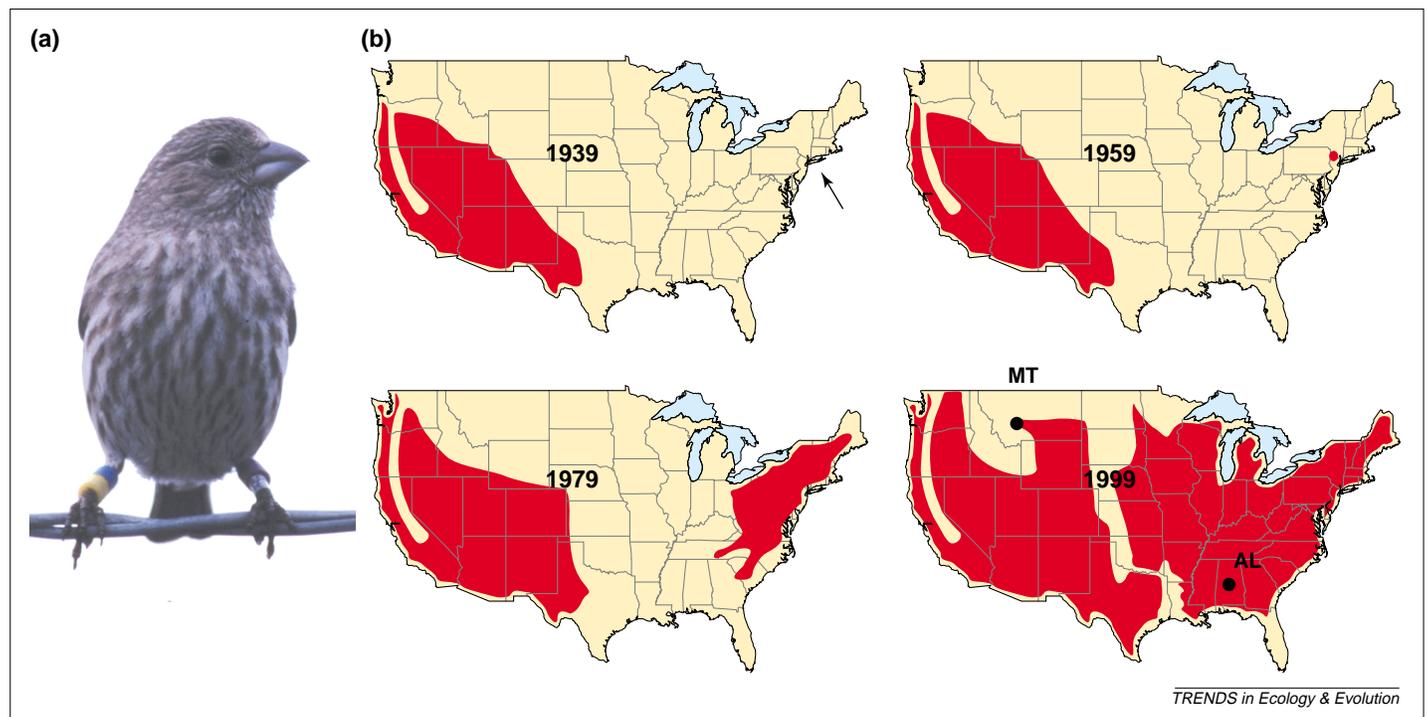


Fig. 1. The house finch *Carpodacus mexicanus* and its spread through North America. (a) Female house finch. (b) Change in distribution of the house finch in North America from 1939 (introduction in New York arrowed) to 1999. Photograph in (a) reproduced with permission from A.V. Badyaev.

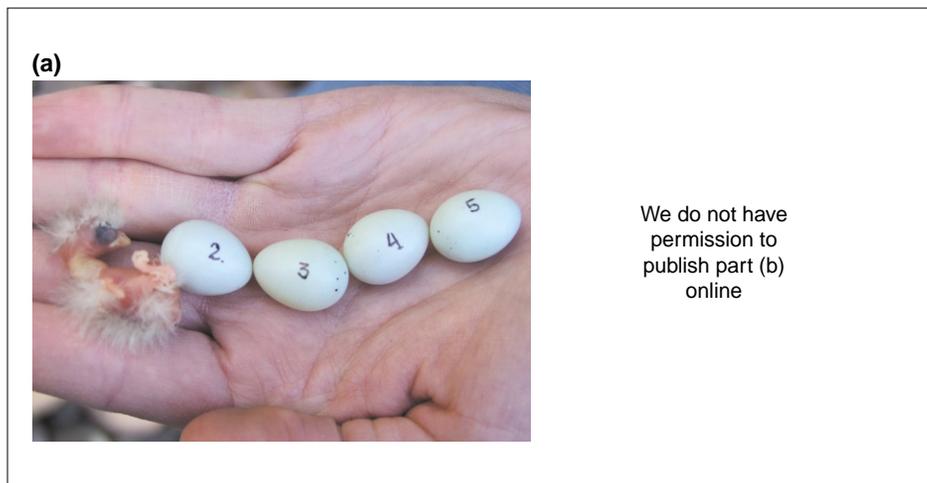


Fig. 2. Maternal adjustment of sex ratio within families. (a) By careful monitoring around hatching, individual house finch *Carpodacus mexicanus* nestlings can be matched to eggs laid in a known sequence. (b) The sex of a nestling house finch varies with respect to position in the laying sequence, such that the sex with the highest survival probability for that position, in each population, is overproduced. Numbers indicate the position within the hatching order, and asterisks indicate individual positions that showed a significant deviation from an equal sex ratio; triangles, Montana data; squares, Alabama data. Photograph in (a) reproduced with permission from A.V. Badyaev. (b) reproduced, with permission, from [4].

populations match the sexual size dimorphism found among the adults in the two populations [10].

However, although these studies have been invaluable in demonstrating differences between populations, the important question of what has caused the differences between the populations remains. This is answered by the new study [4]. By careful monitoring of nests close to hatching (Fig. 2a), Badyaev and colleagues were able to match the laying order of individual eggs to the hatching order of individual nestlings (they were identical), and then by marking those nestlings, follow their fate through to independence from their parents. Within unmanipulated nests, the order of hatching had a strong, sex-specific effect on the survival probability of the nestling, and this effect differed between the populations, so that, generally speaking, early hatching favoured females in Montana and males in Alabama (Fig. 2b). Remarkably, within each population, the sex ratio of eggs laid at different positions within the clutch was such that it favoured the sex that was more likely to survive if laid at that position (Fig. 2b). Females tended to be laid first in clutches from Montana, whereas they tended to be laid last in clutches from Alabama. These patterns were found consistently in data from several years (up to six) from the same populations. Thus, within these two different populations of the same species, the association between laying order and

sex ratio was of different direction, and, in both cases, it matched that favoured by natural selection in that population.

However, the associations between laying sequence and sex ratio of the eggs were only part of the story. In both populations, the growth rate and final size of nestlings differed with respect to the position that they were in in the laying sequence, and between sexes. For example, in Montana, males grew fastest, and reached their largest size when hatching from first-laid eggs, whereas females grew fastest and reached their largest size when hatching from last-laid eggs. Because body size predicted survival probability in both sexes, it seems that growth rate was adjusted to favour rapid growth in the sex that was at a disadvantage because of its laying and hatching position. In the Alabama population, differences between the sexes were less marked, but females grew faster relative to the males when they were hatched late in the clutch.

Such hatching-order sex-specific growth effects could be a result of either an effect of hatching order itself (e.g. if hatching order determined a competitive hierarchy within the nest that differentially affected the sexes), or could be caused by differences among the eggs associated with their laying order. A simple experiment distinguished between these two [4]. By cross-fostering nestlings into broods where their relative hatching order was changed, and then measuring

final body size, Badyaev *et al.* showed that the original hatching order of a nestling affected its growth much more than its experimentally assigned hatching order did. Hence, because the original hatching order corresponded exactly to laying order, the differential growth was due to differences among eggs that were already present when they were laid.

In combination, Badyaev *et al.* demonstrate two adaptive maternal effects, but were able to go further and ask the question: how much greater would mortality of juveniles have been if females had not adjusted sex ratio or growth rate in the two populations? Calculations based on observed selection intensities suggest that the reduction in mortality of both male and female offspring was 10–20% in both populations. This substantial reduction might be one of the key factors behind the extraordinarily rapid spread of this species (Fig. 1b).

Several aspects of these results are novel. First, the demonstration of repeatable patterns of sex-ratio bias within clutches, differing in direction between two presumably recently diverged populations. In birds, associations between laying order and sex ratio are reported quite frequently [12–14], but it is rare that evidence showing that selection favours the association is available simultaneously, as was provided in this study (Fig. 2b). That the laying order–sex ratio correlation was in different directions in different populations suggests a surprising degree of plasticity in this trait. Either different sex allocation rules have evolved in the two populations, or (perhaps less likely) this trait is phenotypically plastic and females are able to assess jointly the relative fitness prospects of sons and daughters, and adjust their sex ratio accordingly. Second, the results demonstrate, as have other recent studies [15], that females can adjust the phenotype of individual offspring by changing characteristics of the eggs, but, again, the demonstration that these effects can evolve rapidly is novel. In combination, the two maternal effects might also have played an important role in the adaptation of these colonizing populations to their new environments [4].

Like all the best studies, this one raises several intriguing questions. First, although the divergence between the two populations with respect to the

two maternal effects might well have been extremely rapid, that the source of the introduction to eastern North America was different from that from which the Montana population arose means that the time in which the divergence occurred is not known exactly. Studies of finches in other parts of the range that inhabit different environments would be invaluable. Second, although there are strong differential effects of hatching position on the size and hence survival of male and female offspring, why is survival strongly dependent on size? Third, how much of the difference between the populations can be attributed to adaptive evolution, and how much to phenotypic plasticity of individuals? Transplant experiments between populations might yield valuable insights here. Finally, by what mechanism do females adjust simultaneously growth rates and the sex of eggs within the clutch? Might there be some connection in birds between hormonal favouritism [15] and associations among steroid hormones and sex ratio [4,16]? Because house finches are common and, as this study demonstrates, extremely amenable to field observation

and experimentation, we can expect that these and other questions will soon be under concerted empirical attack.

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