

# Forum

## Genetic correlation complicates the interpretation of phylogenetic transitions in sexually selected traits

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Hill (1994) proposed that under special circumstances the models of nonadaptive (arbitrary) mate choice can be rejected on phylogenetic grounds. Specifically, in the absence of changes in female preferences or viability costs, Hill argued, the sensory exploitation (Basolo, 1990; Ryan et al., 1990) and runaway (Fisher, 1958; Lande, 1981) models provide no mechanism for reduction of a sexually selected trait. Although the sensory exploitation model clearly generates unique historical predictions (Basolo, 1990; Meyer et al., 1994; Ryan et al., 1990), the runaway model was previously thought phylogenetically indistinguishable from models of adaptive mate choice (Kirkpatrick and Ryan, 1991). Hill's method, if valid, would be a major breakthrough in the study of sexual selection. Unfortunately, I think Hill overlooked a factor that invalidates his method for the example he provided and in general. To illustrate my argument with a concrete example, I first summarize key results from Hill's exemplary study of house finches (*Carpodacus mexicanus*).

Hill (1990, 1994) demonstrated that female house finches from several populations prefer males with brighter and larger red patches, and given a choice between males with large drab or small bright patches, females choose the latter. Several indirect lines of evidence suggest that larger patches are not more costly to survival (Hill, 1991, 1994). Nevertheless, patch size and brightness vary geographically (Hill, 1993). A phylogenetic analysis indicates that the small patched subspecies *C. m. griseus* probably descended from an ancestor with medium sized patches (Hill, 1994). Thus, the *griseus* lineage appears to meet all of the conditions Hill claimed are necessary for rejecting the nonadaptive models of mate choice. Based on aviary diet experiments, Hill (1993, 1994) inferred that carotenoid availability places an upper limit on the size of patch that a male house finch can pigment to maximum brightness. Since females value patch brightness over size, he proposed that a low carotenoid availability in the ancestral *griseus* population favored males with smaller, hence brighter, patches.

The problem with Hill's argument is that it relies on a physiological trade-off between patch size and brightness when carotenoids are limiting. If differences in patch size were heritable (as required by Hill's hypothesis), then small patched males would tend to produce sons with bright patches and the sons of large patched males would tend to have dull patches. That is, patch size and brightness would be negatively genetically correlated. When two traits are genetically correlated, selection on one causes a correlated response in the other, the net change in each trait being the sum of their respective direct and correlated responses:

$$\Delta \bar{z}_1 = G_{11}\beta_1 + G_{12}\beta_2$$

where  $\Delta \bar{z}_1$  is the change in the mean value of trait 1 between generations,  $G_{11}$  is the genetic variance of trait 1,  $G_{12}$  is the

genetic covariance between traits 1 and 2, and  $\beta_1$  and  $\beta_2$  are the direct components of the selection gradient for traits 1 and 2, respectively (Arnold, 1987; Lande, 1979). If the genetic covariance ( $G_{12}$ ) is negative, and trait 2 is strongly selected, trait 1 may actually change in a direction opposite to the direction it is selected directly. As applied to house finches inhabiting low carotenoid environments, selection for brighter patches may override the weaker selection for larger patches, thus leading, in time, to the evolution of smaller patches. Hill's results are therefore consistent with all three classes of mate choice models. In the absence of a trade-off between patch size and brightness, his results are compatible with no model of sexual selection (unless costs or preferences vary geographically, in which case all models may apply).

The house finch example illustrates a general problem with inferring past selection from reconstructed phylogenies. Changes in the trait of interest may be opposite to the direction the trait was selected directly.

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## Evolutionary inference from patterns of female preference and male display

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In his critique, Grether (1995) challenges conclusions from my comparative study of the evolution of ornamental color display among populations of the house finch (*Carpodacus mexicanus*, Hill, 1994a). Populations and subspecies of house finches vary in both the mean brightness of male plumage coloration and in the extent of ventral carotenoid pigmentation (Hill, 1993). Variation in plumage coloration is a function of access to carotenoid pigments at the time of molt while variation in patch size among populations reflects fixed genetic differences (Hill, 1992, 1993, 1994b). In my study, I compared the mate preferences of females from various populations relative to both the brightness and extent of male ornamental coloration. I found that, regardless of the appearance of males in their own populations, females from all populations preferred potential mates with the largest and brightest patches of color. Moreover, by forcing females to choose between the size and brightness of carotenoid ornaments, I showed that plumage brightness is the primary criterion in mate choice and that extent of pigmentation is a secondary criterion.

I also used a cladistic analysis to construct a hypothesis of the evolutionary relationships of the various subspecies of house finches and the two other North American members of the genus *Carpodacus*: the purple finch (*C. purpureus*) and Cassin's finch (*C. cassinii*). The evolutionary relationships of these taxa suggested that small patches of ornamental coloration evolved from a larger-patched ancestral state (Hill, 1994a). In other words, the extent of the ornamental coloration has been reduced in some lineages of house finches despite females in these lineages preferring larger patches.

I used these observations to evaluate current hypotheses for the evolution of ornamental traits. These models of sexual selection have been described in detail elsewhere, most recently and thoroughly by Andersson (1994). I suggested that a reversal in trait elaboration (large patch to small patch) with no change in preference by females is not consistent with sensory bias or species isolating models of sexual selection or with general predictions of the runaway model of sexual selection. Grether challenges my rejection of sensory bias and runaway models of sexual selection.

Grether's argument focuses on the likelihood of a correlated response by patch size to selection on plumage brightness. In a previous aviary study, I showed that there is a physiological tradeoff between patch size and coloration in male house finches (Hill, 1993): when carotenoid resources are limited, smaller patches concentrate pigment more than larger patches and hence will tend to have brighter pigmentation (Hill, 1993). Grether used this observation and a simple quantitative model to show that male ornament size could have been reduced as a correlated response to selection for increased coloration. The gist of the model is that if females prefer bright coloration, and one way to obtain bright coloration is to shrink patch size, then patch size can shrink in response to selection for brighter coloration. Grether's model is a welcome attempt at formalizing part of the process for the evolution of patch size that I discuss in my paper (Hill, 1994a: 71; see also Hill 1994c). However, Grether's model does not accurately describe the evolution of sexual signals in the house finch.

For Grether's model to work, there must be additive genetic variance in both patch size and plumage brightness. This restriction poses no problem for patch size. In previous research, I found fixed genetic differences in the patch sizes displayed by various subspecies of house finches (Hill, 1993), and likely there is also additive genetic variance for expression of patch size within populations. However, there is no additive genetic component to variation in plumage brightness among male house finches. Variation in the expression of plumage brightness both within and among populations is a function of access to carotenoid pigments at the time of molt (Hill, 1992, 1993), and any given male inherits the potential for all expressions of plumage brightness from extremely drab to extremely bright. Without an additive genetic component to variance in plumage brightness, genetic covariance ( $G_{12}$  in Grether's model) is infinity and the model becomes trivial. Although it does not apply to the house finch example, Grether's model may be applicable in other situations.

Although the lack of additive genetic variance in plumage brightness invalidates models that assume genetic covariation, there can still be a physiological tradeoff between expression of patch size and plumage brightness. When carotenoid pigments are limiting, patch size is reduced to maintain plumage brightness. When carotenoid pigments are more abundant, reduced patch size provides no benefits of increased brightness and becomes a disadvantage in mate choice, so patch size is increased. No genetic covariation of traits is necessary for this process to work. The key point is that trait evolution is shaped by resource abundance (the cost of trait production), not by arbitrary changes in female preference. Moreover, a link between trait expression and individual male condition remains throughout the evolutionary process.

Regardless of the applicability of Grether's model, it is difficult to attribute the observations from my study to a sensory bias process. The sensory bias model posits that sensory perception and a predisposition to respond to certain sensory stimuli pre-adapt organisms to adopt certain traits as criteria in mate choice (Endler, 1992; Ryan and Keddy-Hector, 1992). This model provides a proximate mechanism for all other models of sexual selection, but it lacks any predictive power for explaining trait evolution other than through simple unidirectional change. Invoking sensory bias as a complete explanation for a process in which resource abundance drives trait evolution so as to maintain signal honesty is equivalent to using hormone titer as a complete explanation for patterns of male territoriality and nest attentiveness. Such an argument confuses proximate and ultimate causation. Misapplication of the concept of sensory bias is not so much a problem with Grether's arguments as a misconception in the field in general.

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