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Digest: How the snowshoe hare got its brown coat: Convergent evolution or gene flow?*

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The winter-brown phenotype of snowshoe hares in the Pacific Northwest was acquired through hybridization with black-tailed jackrabbits. Some snowshoe hares in more northern boreal populations exhibit the same phenotype, but how did they acquire it? Jones and colleagues show that the phenotype in the boreal populations is the outcome of convergent evolution, highlighting the importance of understanding the genetic basis of a trait in reconstructing its evolution.

The genetic variation underlying rapid adaptive change can come from a variety of sources, such as *de novo* mutations, standing genetic variation, or introgression (Hedrick 2013). Understanding the genetic basis of a trait allows researchers to reconstruct the evolutionary history of that trait and pinpoint the exact source of genetic variation. The evolution of brown coat color in snowshoe hares (*Lepus americanus*) in the Pacific Northwest, for example, is due to a recessive mutation affecting the pigmentation gene *Agouti*. Homozygous individuals retain their brown coat color in winter—a phenotype known as winter-brown—and survive better in snow-free areas compared to individuals that change to a white coat color in winter (Zimova et al. 2016; Jones et al. 2018). Detailed analyses of this trait revealed that the winter-brown phenotype was likely recently acquired through hybridization with black-tailed jackrabbits (*L. californicus*), an example of adaptive introgression (Jones et al. 2020b).

In this issue, Jones et al. (2020a) focus on another set of snowshoe hare populations. Similar to the hares in the Pacific Northwest, some individuals in more northern boreal populations exhibit the winter-brown phenotype. This observation raises the question whether the boreal populations received the recessive allele through gene flow from the Pacific Northwest, or if the phenotype is the outcome of convergent evolution. Analyses of whole exome data revealed low levels of gene flow between Pacific Northwest and boreal populations. Moreover, a winter-brown individual from the boreal population lacked the recessive allele of the *Agouti* haplotype. Together, these results suggest that the boreal populations acquired the winter-brown phenotype independently. The exact genetic basis of the boreal winter-brown phenotype remains to be determined, but might be due to a loss-of-function mutation in the molecular pathway involving *Agouti*.

This study has important implications for macroevolutionary analyses that attempt to reconstruct trait evolution. Using only phenotypic data will lead to the conclusion that the winter-white phenotype originated only once in the snowshoe hare and was subsequently retained in this species as a polymorphism (Fig. 1A). Taking into account genetic data leads to a different conclusion and reveals unexpected origins of the trait. First, the winter-brown phenotype in the Pacific Northwest populations was likely acquired from black-tailed jackrabbits through introgression (Jones et al. 2018). Second, the winter-brown phenotype in the boreal populations originated independently from the Pacific Northwest populations (Fig. 1B).

Moreover, understanding the genetic basis of a trait can provide insights into phenotypic trait evolution (Ottenburghs 2020).

*This article corresponds to Jones, M. R., L. S. Mills, J. D. Jensen, and J. M. Good. 2020. Convergent evolution of seasonal camouflage in response to reduced snow cover across the snowshoe hare range. *Evolution*. https://doi.org/10.1111/evo.13976

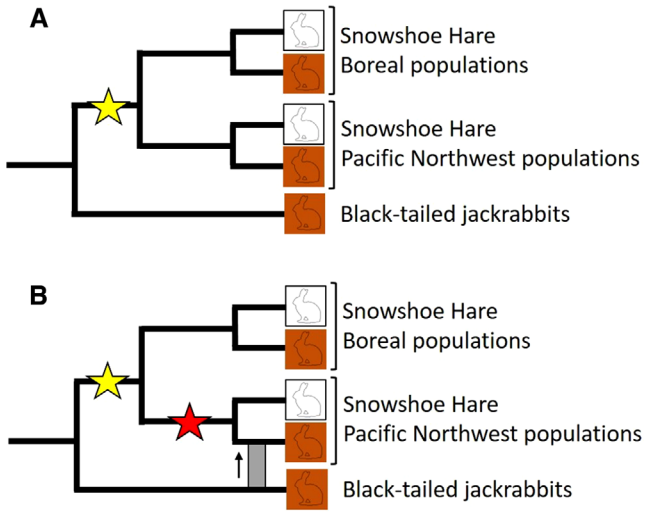

Figure 1. **The evolution of coat color in snowshoe hares. (A) Only using phenotypic data suggests that the winter-white phenotype arose once (yellow star) in snowshoe hares and that the ancestral winter-brown state was retained as a polymorphism. (B) Genetic data revealed that the Northwestern population probably lost the ancestral winter-brown state (red star) and regained the phenotype through hybridization with black-tailed jackrabbits (grey bar).**

For example, this study highlights that loss-of-function mutations are more likely to result in convergent evolution and that traits with a simple genetic basis (e.g., a single mutation) are easily exchanged through introgressive hybridization. Hence, a solid genetic understanding of a trait is advisable when reconstructing its evolutionary history. In other words, before you study the evolutionary history of a trait, first catch your (genetic) hare.

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