

EVOLUTION

Parallel Evolution Is in the Genes

Hopi E. Hoekstra and Trevor Price

The pages of any bird guide reveal a spectacular diversity of colors and color patterns. Although color patterns vary within species, often they also distinguish closely related species. Variations in color are thought to have evolved through the interplay of sexual selection and natural selection. What is less obvious—because the birds are on different pages of the guide—is the repeated appearance of similar color patterns among distantly related species (parallel evolution). A list of 9672 of the world’s bird species (1) includes a black-capped chickadee, a black-capped pygmy tyrant, and a black-capped kingfisher as well as 26 other species whose most conspicuous feature—at least prominent enough to prefix their common name—is a black cap. There are 41 black-throated species (in 40 different genera), 8 that are blue-capped, 9 that are orange-breasted, and 29 that are red-billed. There are many such examples of parallel evolution in birds, but the molecular underpinnings of similar plumage patterns among distantly related or unrelated species are still not clear. On page 1870 of this issue, Mundy *et al.* (2) take a step forward in this endeavor with their report of the molecular basis of a similar plumage trait in two very different arctic birds.

Color patterns in birds appear to be evolutionarily labile. Omland and colleagues (3, 4) studied 44 different plumage patches that vary among the 45 taxa of New World orioles. Using both mitochondrial and nuclear genes, they constructed a well-supported phylogeny and found evidence for multiple gains or losses of 42 of the 44 plumage patches. For example, the presence of black melanin pigment on the lesser wing coverts is present in six different species, and each of these species probably gained this black patch independently. Within this group there are spectacular examples of parallel evolution of complex plumage patterns (see the figure).

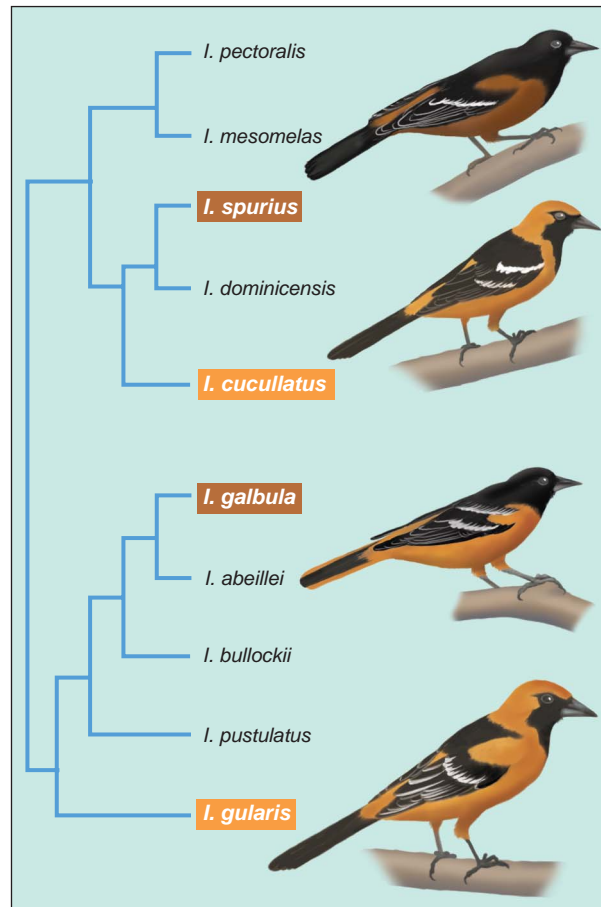
What explains the reappearance of the same traits in diverse lineages? In one

view, color-pattern evolution is driven by the presence of specific selection pressures. For example, both the position and color of various patches of different species of manakins are related to the color of the background and the degree of light in the environment in which the species display their colors during mating (5). Endler and Théry (5) argued that given full knowledge of the selection pressures in the environment, one could accurately predict the color and location of plumage

patches for any given species. In another view, fully developed by West-Eberhard in a recent book (6), the parallel evolution of similar plumage traits in different bird species is due to the limited number of developmental possibilities: Being brightly colored may be sexy, but the specific bright colors and patterns are limited by developmental constraints and the mutations that drive color variations. Of course, the reality probably lies somewhere between these two extremes. The difficulty is how to figure out the relative contributions of selection and limited variation to the appearance of any particular trait.

The report by Mundy and colleagues (2) ushers in a new era in this endeavor. These investigators searched for the genes

causing a simple color pattern polymorphism in two distantly related birds. In both the snow goose and the Arctic skua, individuals vary in the amount of melanin in their plumage and these variations influence mate choice. More than 100 genes that affect the amount and distribution of melanin in the pelts of laboratory mice have been identified; presumably a similar diversity of genes influences melanin production in birds. Remarkably, however, a single amino acid difference in the first candidate gene Mundy *et al.* examined, *melanocortin-1 receptor (Mclr)*, correlates perfectly with color variation in each species. Perhaps most interesting is the observation that different amino acid mutations in *Mclr* are associated with the similar phenotypes observed in snow geese and Arctic skuas. In other words, the convergent phenotypes in these unrelated taxa have arisen independently but through changes in the same gene. Studies of a number of other bird and mammalian species have also found naturally occurring color variation to be mediated by polymorphisms at this locus (7). Mundy *et al.* also propose



Convergence in oriole plumage patterns. The pair of species at the top, *Icterus spurius* (the orchard oriole) and *I. cucullatus* (the hooded oriole), and the pair at the bottom, *I. galbula* (the Baltimore oriole) and *I. gularis* (the altamira oriole), are each other’s closest relatives despite having dissimilar plumage patterns. *I. spurius* and *I. galbula* have similar plumage patterns, as do *I. cucullatus* and *I. gularis*. Within the oriole group, there are many such examples of similar plumage patterns among different species due to parallel evolution. Phylogenetic relationships are based on an analysis of nuclear sequences by Allen and Omland (4).

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that a fixed amino acid difference in *Mclr* in another species, the great skua, accounts for its generally dark plumage. The repeated implication of this same gene suggests that there may be a more limited number of genetic mechanisms to produce dark plumage in natural populations than is suggested by genetic studies of lab mice.

The melanocortin-1 receptor (MC1R) resides in the membrane of specialized cells known as melanocytes, which are the site of melanin synthesis in birds and mammals. Circulating melanocyte-stimulating hormone (MSH) binds to MC1R, turning on the cell's melanin-making machinery. In lab mice, mutations in *Mclr* that result in melanism are due to either hyperactivation or constitutive activation of *Mclr*, without the need for MSH. About 15 *Mclr* mutations, most of which are single amino acid changes, are associated with darkened or melanic coloration in a variety of vertebrates. These mutations are dominant or partially dominant—as is the case in snow geese and skuas—and thus are readily available to selection. Therefore, a single mutation in *Mclr* leads to a visible phenotype on which selection acts with no known antagonistic effects, making *Mclr* a particularly good target for evolutionary change.

In both the snow goose and the Arctic skua, the plumage differences are subject to sexual selection. In both, dark plumage is the derived trait. With the gene in hand, it is now possible to estimate roughly when the dark form appeared by comparing the genetic variation in the derived versus ancestral alleles with sequence differences in the same gene between species whose divergence is dated in the fossil record. For both the snow goose and the Arctic skua, Mundy *et al.* arrive at a late Pleistocene date. In other words, the polymorphism in both species may be several hundred thousand years old. The maintenance of the polymorphism over such a long time span has many implications for ecological geneticists studying patterns of sexual and natural selection in contemporary populations. Armed with genes, we can begin to look at not only the age of the phenotype but also the distribution of *Mclr* allele frequencies across populations, and we can even estimate the strength of sexual selection acting on the dark phenotype in ways that would not be possible without understanding the genetic basis of the color polymorphism.

The independent evolution of melanism in the Arctic skua and the snow goose,

while attributable to the appearance of mutations at the same gene, has not been perfectly parallel. Heterozygous snow geese show a restricted pattern of melanization, whereas heterozygous arctic skuas are generally intermediate in color. Perhaps the selection of a modifying mutation has altered the distribution of melanins in the two species. Alternatively, the genetic backgrounds in which the *Mclr* mutations appeared may be different. Field studies of selection, coupled with characterization of the melanin pathways in each species, will eventually enable a closer tracing of the roles of selection and mutation in generating the similarities and differences between the species. Further down the road, we should be able to dissect the genetic basis of more complicated color patterns like those of the orioles.

References

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CLIMATE

Society and Sea Level Rise

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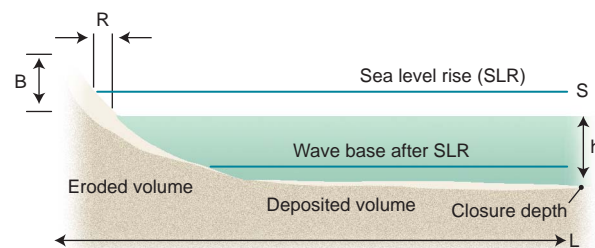
Most of the world's shorelines are in a state of erosion. The only major exceptions are areas of high sediment supply, such as along the rims of active delta lobes and regions of glacial outwash. Many developed nations have experienced a four-decade rush to the shore, with concomitant beachfront development and exponentially increasing total values for beachfront real estate, infrastructure, and buildings. That this unprecedented accelerating coastal development has unfortunately coincided with a century of accelerating global sea level rise (SLR) means that the prediction of the future rate of shoreline retreat has become a major societal priority.

SLR is caused by a number of eustatic and tectonic factors. Eustatic rise from oceanic heating expansion and glacial melting is assumed to be one of the major

fallouts from global warming that will have important impacts on our society. Sea level is rising along mid-latitude coastal plain coastlines at typical rates of 30 to 40 cm per century. Large variations in this SLR rate are found in regions dominated by deltas, areas that are currently or were formerly glaciated, and areas exhibiting tectonic activity. Two important unknowns stand in the way of useful predictions of future shoreline positions: (i) What is the fu-

ture of SLR? (ii) What is the relationship between SLR and shoreline retreat? Here, we are primarily concerned with the latter.

Shoreline retreat (also called shoreline erosion) on unconsolidated shorelines is directly caused by physical shoreline processes, usually storms, over short time scales. Long-term rates of shoreline retreat are related to variations in the supply of sand to a beach, its geologic setting, and SLR. In general, the world's shorelines would not be in a ubiquitous state of erosion without SLR. Typical retreat rates along coastal plain coasts range from 30 cm to 1 m per year. It is generally not possible to isolate the impact of SLR on shoreline retreat, but it is assumed to be impor-



Swept away. (Left) The Bruun rule of shoreline erosion is a simple mathematical relationship with few variables (defined in the equation). The rule states that as the sea level rises, the shoreface profile moves up and back while maintaining its original shape. Sand is removed from the upper part of the profile and deposited on the lower profile. (Right) A house on the beach after a winter storm at South Nags Head, North Carolina. This building is on a stretch of beach that is retreating at nearly 2 m per year.

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