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Fancy footwork: Darwin's pigeons and the evolution of foot feathers

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Ever since Charles Darwin published *On the Origin of Species*, people have been fascinated with understanding the mechanisms of how species could change over time. Like sitting down with relatives around the dinner table during the holidays, it is sometimes hard for us to look at other species and understand how we could have a common ancestor, yet wind up looking and acting so differently. We know that heritable traits are encoded in DNA, and that changes in DNA (mutations) are responsible for changes in traits. But this raises many questions, such as: how many mutations does it take to evolve a new trait? Which genes are mutated to form a new trait, and how do the mutations affect the gene? And when different species evolve similar traits, did that happen through similar mutations?

Dr. Mike Shapiro's lab at the University of Utah has chosen to investigate these questions using one of Darwin's favorite species, the domestic rock pigeon (*Columba livia*). Domestic pigeons are incredibly diverse, with over 350 recognized breeds worldwide. In this study, we focused on the evolution of one remarkable trait in particular, which is the transformation of foot scales into feathers. Like most bird species, most pigeon breeds are scale-footed, but several breeds grow feathers on their feet, instead. To study this trait, we took several complementary approaches. In one, we mated a scale-footed pigeon to feather-footed one to shuffle the information embedded within their DNA. Such information were then tracked down in order to find which locations of their DNA correlated with the amount of foot- feathering in the descendants. In another, we compared the whole DNA sequences from multiple feather-footed breeds to scale-footed ones to find differences between the two groups. In a third, we identified genes that had different activation levels during leg development between feather-footed and scale-footed pigeon embryos. All of these approaches pointed to the same, surprising conclusion: there were two main DNA mutations largely responsible for foot-feathering, but they weren't simply causing the foot skin to produce feathers instead of scales. Rather, they were partially re- programming the pigeon's *leg* into a *wing*.

During development, certain genes act to "tell" cells to which body part they belong. For instance, during limb development, a gene called *Tbx5* programs the developing forelimb to develop into a wing, while another gene called *Pitx1* programs the developing hindlimb to develop into a leg. These same genes are involved in arm and leg development in humans. Normally, they act in the correct limb, so each limb develops properly. In foot- feathered pigeons, however, one mutation was causing *Tbx5* to be active in both the forelimb and hindlimb, and another mutation was reducing the amount of *Pitx1* activity in the hindlimb. As a result, the leg partially changed its development into a "wing" like one, which resulted in the growth of feathers instead of scales. In addition, these mutations also caused the hindlimb of feather-footed pigeons to develop differences in muscle and skeletal anatomy, too.

Although the vast majority of birds are scale-footed, pigeons aren't the only species that have evolved foot-feathering; some domestic chicken breeds (*Gallus gallus*) have, as well. We performed similar experiments and found that changes in *Tbx5* expression contributed to foot-feathering in chickens, too. This means that both pigeons and chickens independently evolved similar changes in the exact same gene to produce foot-feathering. Even more strikingly, previous research had found that the other "foot-feathering" gene, *Pitx1*, was also involved in the evolution of pelvic spines in a *very*-distantly related organism, the three-spined stickleback fish (*Gasterosteus aculeatus*) *(Shapiro et al., 2004).*

So to revisit the questions posed at the beginning of the article, we see that for foot-feathering in pigeons, two mutations were sufficient to produce a dramatic transformation in the appearance of the leg, that these mutations altered expression of two genes important in programming limb-type identity, and that mutations in these same genes are responsible for hindlimb evolution in other animals, too. As we ponder the shared origins and diverse trajectories that life has taken on this planet, this study shows that sometimes a small number of mutations can have a very big effect!