Quick guide

Domestic pigeons

Michael D. Shapiro and Eric T. Domyan

"That man is fortunate who finds in his breast an inexplicable love for them [pigeons]…When fortune frowns and when the cares of a harsh or disordered world seem almost too heavy to bear…then the pigeon lover finds in his birds a solace and consolation impossible to describe."
— Levi, *The Pigeon,* p 34

What are domestic pigeons?
While several of the approximately 300 species of pigeons and doves (family Columbidae) are kept as pets, the term domestic pigeon usually refers to breeds of *Columba livia*, the rock pigeon. Pigeon breeding is a popular hobby worldwide, and over 350 different breeds are currently recognized. Their ubiquitous association with humans over the millennia pervades literature, visual arts, and religious symbolism, and they have also served as steadfast messengers during war and peacetime.

As with dogs, chickens, and other domesticated animals, the huge variety of domestic pigeons represents a large-scale selection experiment that started thousands of years ago. Domestication involves intensive directional selection for particular phenotypes, followed by stabilizing or purifying selection; similar evolutionary processes operate during selective sweeps and sexual selection in natural populations. In pigeons, these processes have produced arguably the greatest phenotypic diversity within any single avian species.

Some pigeon breeds are under intensive selection for flight characteristics: racing homers can navigate to their home lofts after being released from hundreds of miles away; the tippler can remain continuously aloft for more than 20 hours; and tumblers and rollers perform backward somersaults in flight. Others are bred for vocal traits and striking morphological differences (Figure 1). For example, facial morphology in pigeons ranges from the tiny beak of the African owl to the massive, recurved beak of the Scandaroon (Figure 1A,B); many breeds have elaborate feather ornaments, such as the Jacobin breed favored by Queen Victoria (Figure 1D); and extremes in body mass among breeds differ by an order of magnitude.

When and where were they domesticated? By genetic measures, domestic breeds are only weakly differentiated. This could be partly due to crosses among breeds to 'improve' traits such as plumage pigmentation and pattern, or to transfer traits among breeds. The precise number and timing of domestication events could be forever obscured by this widespread hybridization and introgression.

Rock pigeons are native to Europe, North Africa, the Middle East, and South Asia, and they were probably domesticated at several times and places. Archeological evidence points to human use of pigeons as a food source as early as the Pleistocene (~10,000 years ago) in the Fertile Crescent, though whether this entailed domestication is not known. Ancient Egyptians began using pigeons for ceremonial and culinary purposes at least 4000 years ago, and later as harbingers of the progress of the Nile's annual flood. Ancestors of some modern breeds such as the resplendent fantails (Figure 1E) and enormous, amusingly-named runts were probably developed at least 860 and 2000 years ago, respectively.

The temporal origins of many other fancy breeds are lost to antiquity, but the ancient geographic centers of domestic pigeon diversity appear to be the Middle East and South Asia (modern India and Pakistan). Moreover, birds were exchanged between these two regions in the 16th Century (and probably earlier), providing ample opportunity for hybridization among breeds. Writings from the 16th century and earlier discuss derived morphological and behavioral traits and breeds that persist today. In Europe, the popularity of the pigeon hobby rose markedly in the 17th Century, and artistic depictions of some domestic breeds from this era already closely resemble modern forms.

What are homing pigeons and how do they navigate? The rock pigeon's innate ability to navigate to its home loft over unfamiliar terrain has long fascinated humans, and pigeons have served as message bearers for millennia. For example, Julius Caesar used pigeons to communicate to Rome his victory over Gaul, and the pigeon's role in military communication persisted well into the 20th Century.

Figure 1. Diversity among breeds of domestic pigeons (*Columba livia*).
Variation among pigeon breeds is often of the magnitude observed among different species of birds, including beak size extremes of the (A) African owl and (B) Scandaroon; (C) the head crest of the Old German owl and (D) hood of the Jacobin; (E) supernumerary and elevated tail feathers of the fantail; and (F) scales versus (G) feathers on the lower leg and foot of the Brunner pouter and English pouter, respectively. (Photos in (A–D) modified from Stringham *et al.* (2012); original images in (A) and (D) courtesy of Thomas Hellmann.)

The modern racing homer breed is a surprisingly recent creation, however, and was generated independently and contemporaneously in Belgium and England in the early 1800s by the hybridization of several different breeds, followed by interbreeding of these two racing strains.

Today, pigeon racing is a popular sport worldwide, and prize purses of thousands of dollars are common. Racing is serious business: the top price paid for an individual racing pigeon was £207,000 ($328,000) in 2012! Generations of intense selection have enhanced the homing ability of racing strains: domestics get lost less often and show a greater drive to return home than their free-living counterparts, particularly over long distances. The hippocampus, an important part of the vertebrate brain for spatial learning and memory, is larger in racing homers than in wild rock pigeons, though the respective contributions of fixed genetic differences and phenotypic plasticity to this phenomenon are not completely understood.

Experiments suggest that pigeons rely on the position of the sun, direction and intensity of the geomagnetic field, and olfactory cues when far away from home, switching to visual landmark navigation as they near the home loft. Magnetoreceptive cells, long thought to reside in the beak, were recently demonstrated to reside in the inner ear lagena, and signal to neurons in the vestibular brainstem. Interestingly, these neurons are capable of responding to the direction, polarity, and intensity of a magnetic field, and these factors vary predictably based on geographic location. While the relative importance of each homing cue to navigation is not entirely clear, pigeons probably use information opportunistically depending on environmental conditions.

What are feral pigeons? The current geographic range of the rock pigeon extends to all continents except Antarctica. Outside the native range — and even many places within it — rock pigeons are feral. That is, they are free-living descendants of escaped domestics, and some Old World feral populations are probably thousands of years old. Rock pigeons first became feral in North America over 400 years ago, and ongoing natural selection has resulted in their close morphological resemblance to the wild rock pigeons of the Old World. Molecular evidence suggests that the racing homer, a breed that has regular opportunities to fly outside the loft and potentially escape, is a major genetic contributor to some North American feral populations.

Why did Darwin value domestic pigeons? The rock pigeon is generally held in low regard by most ornithologists, but this species has a special place in the history of evolutionary biology. Charles Darwin was a pigeon aficionado and used this dramatic example of diversity within a species to convey his ideas about natural selection in *The Origin of Species*. He recognized the fundamental similarities between artificial and natural selection, and took a special interest in the extreme variation among pigeons that evolved from a common 'blue'-colored wild type. "Believing that it is always best to study some special group, I have, after deliberation, taken up domestic pigeons," he wrote in *The Origin*. He chose pigeons as an exemplar of diversity under domestication in a later volume, *The Variation of Animals and Plants Under Domestication*, noting, "I have selected this case, because…the materials are better than in any other; and one case fully described will in fact illustrate all others." Darwin asserted that based on external morphology alone, some domestic pigeon breeds were as distinct as different genera of wild pigeons and doves. Yet he also observed that even highly divergent domestic breeds could be crossed to produce viable offspring, and thus they belonged to the same species.

What do we know about the genetic basis of variation among pigeons? Several key features make pigeons a promising model for avian and vertebrate evolutionary genetics. First, some traits that vary among pigeon breeds also vary among numerous natural species of birds, providing a model for understanding genetic mechanisms that control variation in the wild. Second, classical experiments by academic geneticists and hobbyists alike suggest the genetic architecture for many traits is relatively simple, thereby increasing the likelihood of identifying genes responsible for differences among breeds. Finally, variation in several traits shows similar trends in distantly related breeds, making it possible to test whether the same or different genes underlie similar phenotypes in different breeds, a topic of longstanding interest in studies of biodiversity in domesticated and natural populations.

A reference genome sequence of the rock pigeon was recently assembled, thereby facilitating exploration of the molecular origins of diversity within and among breeds. For example, by sequencing the genomes of breeds with (Figure 1C,D) and without (Figure 1A,B) crests of reversed feathers on their heads, we found that breeds with crests shared the same coding mutation in the *Ephrin receptor B2* (*EphB2*) gene. The genomic data also suggested that the head crest mutation evolved just once and spread to a variety of breeds through either hybridization, repeated selection on a mutation that was already present in a wild rock pigeon population, or perhaps both.

Will the finding that the same, simple genetic basis underlies similar derived traits in different pigeon breeds hold true for additional traits? Classical genetic experiments suggest this might sometimes — but not always — be the case, and genomic resources now permit rigorous testing of this question from a molecular perspective. The tremendous amount of phenotypic diversity in this species, coupled with tractability in genetics, genomics, and developmental biology, makes the domestic pigeon a powerful model for understanding trait evolution and development in vertebrates.

Where can I find out more?

Darwin, C.R. (1868). The Variation of Animals and Plants Under Domestication, Volume 1, (London: John Murray).

Hansell, J. (1998). The Pigeon in History. (Bath, U.K.: Millstream Books).

Levi, W.M. (1986). The Pigeon, Second Revised Edition, (Sumter, S.C.: Levi Publishing Co.).

Secord, J.A. (1981). Nature's fancy: Charles Darwin and the breeding of pigeons. ISIS *72*, 163–186.

Shapiro, M.D., Kronenberg, Z., Li, C., Domyan, E.T., Pan, H., Campbell, M., Tan, H., Huff, C.D., Hu, H., Vickrey, A.I., *et al*. (2013). Genomic diversity and evolution of the head crest in the rock pigeon. Science, Epub ahead of print, Jan 31.

Stringham, S.A., Mulroy, E.A., Xing, J., Record, D., Guernsey, M.W., Aldenhoven, J.T., Osborne, E.J., and Shapiro, M.D. (2012). Divergence, convergence, and the ancestry of feral populations in the domestic rock pigeon. Curr. Biol. *22*, 302–308.

Department of Biology, University of Utah, Salt Lake City, UT 84112, USA.
E-mail: shapiro@biology.utah.edu