

INSIGHTS

PERSPECTIVES

EVOLUTIONARY GENETICS

Of dogs and men

Ancient genomes reveal the common history of human and dog

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25 YEARS

Joe & Clair Carnegie / Libyan Soup

By Pavlos Pavlidis¹ and Mehmet Somel²

“**B**ut Argos passed into the darkness of death, now that he had fulfilled his destiny of faith and seen his master once more after twenty years.” This quote from *The Odyssey* vividly illustrates the bond between dog and human. These two species, separated by 90 million years of evolutionary history, have spent much of their recent past in each other’s service. This interaction has remodeled both species’ environments and has modified the phenotypic and genetic composition of dog populations. On page XXXX of this issue, Bergström *et al.* (1) use 27 ancient dog genomes from across Eurasia, going back 11,000 years, to resolve whether dog domestication happened once or multiple

times, whether dog dispersals and adaptations were coupled to those of humans, and how dogs interacted with their wild sisters, the wolves.

Dogs likely evolved from a wolf population that self-domesticated, scavenging for leftovers from Paleolithic hunter-gatherers in Eurasia (2, 3). However, the exact timing and geographic location where the dog lineage started remain unknown, owing to the scarcity of Paleolithic dogs in the archaeological record. Analyses of genetic data suggest that dog-wolf divergence took place ~25,000 to 40,000 years ago (4, 5), providing an earliest possible date for dog domestication.

Consistent with previous analyses (2–5), Bergström and colleagues support a scenario where dogs were domesticated 20,000 years ago, around the Last Glacial Maximum

(LGM). If so, the domestication of dogs predated other Neolithic domestications—such as sheep, pig, and cattle—and may have even facilitated them. Interestingly, many of these later domestications happened independently in multiple local wild populations. For example, there is evidence that pigs were domesticated in both Anatolia and China (6). For dogs, however, the story is different. Dogs and modern-day Eurasian gray wolves appear as monophyletic groups; that is, any dog is genetically closer to another dog than to a wolf, and vice versa (7). Monophyly supports a single origin of dogs from a possibly extinct wolf lineage. Although this remspec-

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A hunter and dog are depicted in rock art that dates between 5000 to 2000 BC. It is located in Wadi Tashwinet, Tadrart Acacus, Libyan Sahara, Libya.

ulative, Bergström and colleagues show that by 11,000 years ago dog lineages had already diversified and spread worldwide. But how did they spread? Even though human movement may have contributed to this expansion, LGM human migrations were probably not extensive enough to explain these patterns. Instead, dogs could have been exchanged between forager groups, or may have spread autonomously in a semi-feral state.

Bergström *et al.* show that during the next 10,000 years, diversified dog lineages interbred frequently over wide geographical areas. Further, they directly compare quantitative measures of population history of humans and of dogs. They show that the genetic relations between human populations largely match the genetic relations between proximal dog populations in Eurasia and the Americas, suggesting that movement patterns are correlated between dog and human. For instance, about half of the ancestry of European dogs originates from Paleolithic West Eurasia, and the other half from Southwest Asia; similarly, modern-day Europeans are a mixture between pre-Neolithic hunter-gatherers and Neolithic farmers from Anatolia. However, as shown by Bergström and colleagues, dogs have not always faithfully followed humans, resulting in cases of decoupling between dog history and human history. For instance, comparing Neolithic and Chalcolithic Iran, they find that people have remained, but indigenous dogs have been replaced by Levantine dogs. Conversely, in Neolithic Germany and Ireland, incoming farmers of Anatolian descent appear to have adopted dogs from local foragers.

In addition to sharing dispersal paths, dogs and humans have traced parallel paths of evolutionary adaptation. Variation in the copy number of genes encoding amylase, the enzyme required for breaking down starch, is such an example of convergent evolution. Humans carry extra salivary amylase copies compared to chimpanzees (8, 9), owing to high starch consumption that perhaps began before farming (10). Likewise, most dogs, compared to wolves, carry extra pancreatic amylase (*AMY2B*) copies, possibly facilitating starch digestion in their new environment (11). Bergström and colleagues show that early dogs already carried extra amylase copies compared to wolves, but amylase copy numbers further expanded following the increasing reliance on starch-rich agricultural diets in prehistoric Eurasia over the past 7000 years. Similarly, a recent

study on Arctic sled dogs reported genetic signatures of adaptation in their fatty acid metabolism genes (12), analogous to their Inuit masters who carry adaptive changes in the same metabolic pathways—a likely response to the high-fat Arctic diet (13).

After their split, dogs and wolves have continued to occasionally interbreed. For instance, it was shown that a black coat color allele passed from dogs to wolves in North America (14). Bergström *et al.* also confirm regional wolf-dog admixture. They show that Iberian wolves are genetically closer to European dogs than to Asian dogs, whereas Mongolian wolves are closer to Asian dogs. But did gene flow occur from wolf to dog, from dog to wolf, or both ways? Bergström *et al.* reason that in the case of wolf-to-dog gene flow, all wolves should be more similar to those wolf-like dogs than to non-admixed dogs. However, they do not find such a pattern. Specifically, a wolf from Xinjiang, China, was identified as equally distant from all dogs, past and present, suggesting mainly unidirectional gene flow from dog to wolf. This intriguing finding could be linked with wolf or dog behaviors (e.g., going feral) or asymmetry in population sizes. There might also be selection against such hybrids, perhaps as a result of their unbiddable or suboptimal behavior (12). Studying and dating the distribution of introgression signatures across wolf genomes would be interesting. If population size asymmetry is the reason, then we might expect admixture to intensify after agriculture began. Studying signatures of sex bias in dog-to-wolf gene flow could also provide insight into the behavioral background of the process. We further anticipate that successful genetic analyses of early dog-like fossils from Eurasia may help to resolve the long-standing debate surrounding the origins of dog domestication. ■

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NOISE POLLUTION

The quiet spring of 2020

Anthropogenic noise has no legacy effects on bird song

By Wouter Halfwerk

Sounds of the past can be easily forgotten, especially when soundscapes change gradually over long periods of time. This past spring, many people got a chance to experience how the outside world sounded in the 1950s. Global transport came to a halt as human activities decreased abruptly (either voluntarily or under direct order for lockdown) to stem the spread of coronavirus disease 2019 (COVID-19). With fewer people driving cars and hardly any airplanes traversing the skies, the amount of background noise across whole continents dropped substantially. On page xxxx of this issue, Derryberry *et al.* (1) report the impact of the COVID-19 shutdown on animal behavior—namely, the songs of white-crowned sparrows. The findings suggest that mitigation measures against noise pollution could yield immediate beneficial effects on urban wildlife.

Derryberry *et al.* observed white-crowned sparrows in the San Francisco Bay Area. The males of this species have a beautiful, crystal-clear song, that starts with a long whistle, followed by a series of fast, down-swept notes. Males use their song to keep territorial intruders at bay (2, 3). In urban areas, with high amounts of anthropogenic background noise, males normally sing louder songs compared to their rural counterparts (4). Although increasing song amplitude (making songs louder) is an effective communication strategy to overcome the masking impact of urban noise (5), it is often traded against other song components such as reduced song complexity. In the case of Bay Area white-crowned sparrows, increasing song amplitude comes at the cost of reduced trill performance (4).

Derryberry *et al.* recorded white-crowned sparrow males during the shutdown in March and April of 2020 in San Francisco as well as in nearby rural areas. The authors measured background noise data from their recordings and used toll data since the opening of the Golden Gate Bridge in 1937 to extrapolate traffic data. During the lockdown period,