

# Archaeological, genetic evidence expands views of domestication

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One of the markers of domestication is a reduction in size, but archeological evidence indicates size decreases were slow and inconsistent. Donkeys buried 5,000 years ago in an early pharaonic mortuary complex (above) have proportions similar to those of the African wild ass, but the bones of domesticated donkeys found at another, much older site are significantly smaller than those of wild asses. Credit: Stine Rossel/PNAS

Many of our ideas about domestication derive from Charles Darwin, whose ideas in turn were strongly influenced by British animal-breeding practices during the 19th century, a period when landowners vigorously pursued systematic livestock improvement.

It is from Darwin that we inherit the ideas that domestication involved isolation of captive animals from wild species and total human control over breeding and animal care.

But animal management in this industrial setting has been applied too broadly in time and space, said Fiona Marshall, PhD, professor of anthropology at Washington University in St. Louis. It is not representative of the practices of the Neolithic herders who first domesticated animals nor—for that matter—of contemporary herders in nonindustrial societies.

Together with Keith Dobney, PhD, of the University of Aberdeen in Scotland; Tim Denham, PhD, of the Australian National University; and José Capriles, PhD, of the Universidad de Tarapacá in Chile, Marshall wrote a review article that summarizes recent research on the domestication of large herbivores for "The Modern View of Domestication," a special feature of *The Proceedings of the National Academy of Sciences* published April 29.

Recent research on the domestication of donkeys, camelids (which includes dromedaries, Bactrian camels, llamas and alpacas) [pigs](#), cattle, sheep and goats suggests that neither intentional breeding nor genetic isolation were as significant as traditionally thought, the scientists said.

"Our findings show little control of breeding, particularly of domestic females, and indicate long-term gene flow, or interbreeding, between managed and wild animal populations," Marshall said.

Why is it important to get domestication right? "Our livestock is losing genetic diversity even faster than some [wild animals](#), because of [management practices](#) like artificial insemination," Marshall said. "We took only a bit of the diversity from the wild for domestication, and what we're looking at now is lopping it off really fast so we'll be left with little diversity to survive all the climate and disease issues we're facing. It really is a crisis situation.

"If we don't understand what it is we might be about to lose, then we don't count the cost of loss accurately or know how to plan for the future," she said.

## **A walk on the wild side**

For most of history, [artificial selection](#) on large herbivores was probably weak, Marshall said. "Herders could not afford to kill many animals, particularly large-bodied animals with long gestation periods. To keep herd size stable, herders probably culled or castrated males surplus to the growth needs of the herd, allowing all females to breed," she said. These management practices placed only light selection pressure on the herd's gene pool.



Two shorthorn bulls named St. John and Gaudy in this painting by Thomas Freebairn Wilson are products of human control over breeding. The fascination with livestock improvement in 19th-century Britain is reflected in portraits of prize animals like this one -- enough of them to support a trade in itinerant livestock painting. But human control was not so complete throughout most of the history of domestication. Credit: J. Ponsonby

Paradoxically, environmental selection may, in many instances, have been stronger than artificial selection. Early herds were vulnerable to disease, droughts and storms, disasters that would have forced pastoralists to replenish herds from wild populations better adapted to harsh local conditions.

Sometimes domesticated animals were intentionally bred with wild ones, Marshall said. "Wild animals are generally faster, stronger and better adapted to the local conditions than domesticated ones. So, for example,

Beja herders in Northeastern Africa intentionally bred their donkeys with African wild asses in order to produce stronger transport animals."

"And sometimes interbreeding was accidental," she said. "Even today in the Gobi, researchers report that domestic camels sometimes join wild herds after becoming separated from their own. Wild and domestic camels meet at shared oases, and wild males also can become extremely aggressive and may collect domestic females to the dismay of pastoralists."

In the Andes, Capriles said, wild and domestic camelids have interbred in such complex ways that alpacas are maternally related to both wild vicunas and guanacos, and the same is true for llamas.

Artificial selection was probably weakest and gene flow highest in the case of pack animals such as donkeys or camelids. But even in the case of pigs or cattle, interbreeding between domestic and wild animals has created long and complex evolutionary and domestication histories that challenge assumptions regarding genetic isolation and long-held definitions of domestication.

## **The curl in the pigs' tails**

The domestication of pigs is one of these stories. Dobney, Greger Larson, PhD, and their team have shown that pigs were domesticated at least twice, in eastern Anatolia and in central China. Analysis of mitochondrial DNA (DNA in a cell organelle that is inherited from the mother) shows that early herders took pigs with them from Anatolia to western Europe. And analysis of ancient DNA shows that, once in Europe, the [domesticated pigs](#) interbred with the wild boars. These hybridized populations then rapidly replaced the original domesticates, first in Europe and then, later, across Anatolia itself.

In China, the story is somewhat different. There is little evidence that the domestic herds in central China interbred with wild boars. But early agriculturists took their pigs to southeastern Asia and there, deliberately or accidentally, recruited local wild boar lineages into their domestic stock.

All of the New Guinea domestic pigs and those of the islands in the tropical Pacific Ocean carry DNA from those southeast Asian wild boar populations.

The interesting question is why the pigs in central China didn't interbreed with wild boar populations in central China. Dobney suggests that management practices may have made a difference. It is possible that in China where settlements were dense, people started keeping pigs in pens, whereas in Europe, even in medieval times, people took their pigs to forage in the forests, where they might encounter [wild boars](#).

The pig story illustrates how much our understanding of domestication events has changed. The anomaly is the isolated domestic population, not the prolonged interbreeding among domestic and wild animals, which in most domesticated species seems to have continued to recent times.

## **What would Darwin say?**

"The research is really exciting because it is making us completely rethink what it means to be domesticated," Marshall said. "The boundaries between wild and domesticated animals were much more blurred for much longer than we had realized."

"To untangle the history of domestication," Denham said, "scientists will need to bring to bear all of the evidence at their disposal, including archeological and ethnographic evidence, and the analysis of both modern and ancient DNA."

"We must also investigate sources of selection more critically," Marshall said, "bearing in mind the complex interplay of human and environmental selection and the likelihood of long-term gene flow from the wild."

It's probably fortunate the Darwin had clear examples of animal breeding to consider as he thought about evolution. The first chapter of "On the Origin of Species" discusses the domestication of animals such as as pigeons, cattle and dogs, and Darwin then uses artificial selection as a springboard to introduce the theory of natural selection.

It turns out that animal [domestication](#) is more complex, and the role of natural selection more important than Darwin thought. It is also the case that the people who first domesticated animals valued wild ones more than did Darwin's Victorian neighbors.

**More information:** "Current Perspectives and the Future of Domestication Studies," by Greger Larson et al. *PNAS*, To be available at [www.pnas.org/cgi/doi/10.1073/pnas.1323964111](http://www.pnas.org/cgi/doi/10.1073/pnas.1323964111)

Provided by Washington University in St. Louis

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