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Biological Sciences: Anthropology

Title: Evaluating the roles of directed breeding and gene-flow in animal domestication

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Abstract

Domestication has resulted in profound phenotypic and behavioral changes and significant modification of animal endocrine and reproductive systems. Since the nineteenth century scholars have emphasized the roles of intentional breeding of domestic animals and genetic isolation of captive animals from wild relatives during domestication. Recent research has drawn attention to variability in the pathways to domestication, but assumptions about genetic isolation and intentional breeding are still fundamental to thinking about domestication processes. This analysis of ethnoarchaeological, archaeological, and genetic data suggests that intentional breeding was probably largely absent from the early phases of animal domestication and that long-term gene flow between wild and domestic stocks has been much more common than previously assumed. As a result, domestication histories were longer and more complex than often thought. These findings challenge assumptions about severe genetic bottlenecks during domestication, expectations regarding monophyletic origins, and interpretations and instances of multiple domestications. They also raise new questions regarding ways in which behavioral and phenotypic domestication traits were developed and maintained.

Significance Statement

Directed breeding and genetic isolation of captive animals from wild relatives have long been considered fundamental to animal domestication. This evaluation of anthropological and genetic evidence suggests that directed breeding was probably largely absent from the early phases of domestication and that long-term gene flow between wild and domestic stocks was much more common than often assumed. Our findings indicate long and complex domestication histories that challenge assumptions about the significance of severe genetic bottlenecks during domestication, instances of multiple domestications and the ways in which domestication traits were maintained.

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Domestication resulted in a diverse array of phenotypic and behavioral changes to animals including decreased flight responses, increased sociality, earlier reproduction and modification of endocrine and metabolic systems (1-4). Darwin's (5) seminal research was heavily influenced by European animal breeding practices during the nineteenth century, which led subsequent scholars studying animal domestication to prioritize the central roles of human intentionality, directed or controlled breeding of individuals, and genetic isolation of captive herds from wild relatives (6). This anthropocentric legacy is evident in various widely used definitions of domestication that continue to emphasize human control of breeding and animal care (6-8). Clutton-Brock's (6) influential research emphasized the long-term microevolutionary nature of domestication, yet argued that domestication "*was complete when the new population is permanently isolated from the wild species and its breeding, organization of territory, and food supply is under total human control*". However, a growing body of evidence presented and discussed here, shows that neither reproductive isolation nor intentional breeding of individuals were as significant for early animal domestication as traditionally thought. Archaeological, genetic and ethnohistorical data instead indicate long-term gene flow between managed and wild populations, weak directional selection resulting from culling and castration and long and complex domestication histories. These findings challenge assumptions about severe genetic bottlenecks during domestication and interpretations of genetic variability in terms of multiple instances of domestication. They also raise questions about ways in which domestication traits were maintained.

Research on dog and pig domestication over the last several decades has drawn attention to the roles of likely non-human drivers in the domestication process, especially regarding opportunities for wild animals to exploit food resources in increasingly modified human environments (9, 10). Early domestication is now widely viewed as a mutualistic relationship resulting from diverse human relations with animals (3). Commensal pathways to domestication were also likely followed by animals that were attracted to food in human niches such as wolves, wild cats and possibly wild boar. Prey pathways provided other trajectories to domestication for animals relied upon for meat, such as goats, sheep and cattle (11). More directed routes to domestication have been proposed for animals such as donkeys that may have been domesticated by herders (3). Despite these new emphases on diversity in human-animal relations and increasingly significant roles for unintentional processes during domestication, most models still rely on human-directed breeding over generations (3, 12, 13) and reproductive isolation to delineate later phases of domestication (14). The creation of separate breeding populations of animals that are wholly isolated from their wild progenitors persists as a fundamental assumption of classic speciation-based models (14, 15).

To date, there has been little discussion of how variabilities in the biology and behavior of captive animals, human environments, human management regimes, and subsequent migration and dispersal of domestic animals affected directed breeding and gene flow between domestic and wild populations. These processes are explored here through a combination of biological data, archaeological genetic and ethnographic

evidence. We focus on large ungulates including equids, camelids, yaks, pigs, sheep, goats, and cattle. The domestication history and the combination of high gene flow and low directed selection in donkeys and the quality of genetic evidence for gene flow in pigs make these especially clear examples, which we discuss in detail (Table 1).

Management and gene flow

Equids, camelids and yaks*. Humans have relied heavily on donkeys, horses, Bactrian camels, dromedaries, llamas, alpacas, and yaks for transport, food, fiber and ritual practices over the millennia. These animals are physiologically well adapted to extreme environments and are thus important for mobile herders who rely on animals for survival in cold steppe, desert, and mountainous regions. With the exception of horses and yaks, transport animals are territorial and challenging to manage. They are also large bodied with correspondingly slow gestation and herd growth rates, which do not permit high levels of culling. These biological influences on human management mean herders value the adaptations of wild relatives of their domestic animals, manage animals lightly, cull at low levels, and grow herds through capture of more wild animals. Consequently, transport animals reflect low levels of directed selection and high levels of gene flow. Directed selection refers to selection resulting from intentional human management including breeding, culling or castration of selected animals.

Herders have relied on donkeys throughout the millennia almost exclusively for transport. As a result of their desert adaptations, lack of sociality, long gestation rates, and use by mobile herders for long distance movement, donkeys provide an especially clear case of an animal that has been subject to low levels of management and little directed breeding. Donkeys have never been cut off from gene flow with wild and feral relatives, at least within their wild range. By definitions that focus on reproductive isolation (6, 7) they could, perhaps, not even be considered a domestic animal. Although consideration of the donkey's long-term role as a beast of burden has precluded serious discussion of this point; donkeys—much like cats—have often been treated as exceptions to the accepted rules for domestic animals.

Ancient populations of desert-adapted, African wild asses were the ancestors of domestic donkeys (16, 17) (Table 1). African pastoralists today rely on donkeys for transport and not for food. Animals are rarely if ever slaughtered, and drought and disease are the principal causes of mortality in household herds. Herders value individual animals for strength and hardiness (18) and they castrate difficult males but prefer un-castrated males for transport-use. This results in multiple breeding males and little directed selection (18). Donkeys are rarely herded because lack of sociality makes them difficult to manage (18). Moreover, males and females range widely in search of mates, and as a result donkey-owners do little to manage reproduction. Slow herd growth due to long gestation periods and the value placed on the size, strength and hardiness of donkeys used for transport led historic pastoralists (and Romans in North Africa) to capture feral donkeys and African wild asses, and to encourage inter-breeding with wild males (19-21) (Table 1).

Modern pastoral use of donkeys presents a picture of weak directed selection principally resulting from castration and strong environmental selection. In the context of domestication, "environmental selection" refers to unconscious or natural selection resulting from mortality due to the effects of events such as drought, disease and predation on managed animals in human settlements or in humanly influenced landscapes (15). In regions where wild asses still exist, continued gene flow results from managed and inadvertent breeding of domestic donkeys with wild asses. These aspects of the present are relevant to understanding past processes (22) because they reflect consistent mechanisms, biology and transport use.

Archaeological and genetic data support conclusions that donkeys were domesticated in arid environments, bred with a variety of wild populations, and were used for transport and trade over long distances. Morphological data suggest lack of strong directed selection and continued gene flow from the wild over a period of several thousand years. The presence of two divergent mitochondrial lineages in donkeys has been interpreted as evidence for more than one domestication, though this pattern is equally consistent with recurrent recruitment of genetically divergent wild females into domestic herds (16, 17). Archaeological evidence for specialized hunting of territorial desert asses goes back *ca.* 16,000 years in northeast Africa (18). However, desert assemblages are rare and evidence is lacking, though, for the critical period of their likely earliest management 9000-6500 B.P.[†] A reduction in the size of some asses, often accepted as indicative of domestication, is first documented at Maadi in Egypt *ca* 6000 B.P. (23)(Fig. 1). A thousand years later, despite expectations for significantly smaller animals, metacarpals from equids ritually buried at Abydos still fall within the size range of wild asses (19). Nevertheless, pathologies indicative of loading demonstrate that these morphologically wild animals were used for transport (19). Size decrease appears slow and inconsistent through time, with variability within and between archaeological sites indicating a non-linear process of phenotypic change.

Herder reliance on donkeys for transport, the behavior of donkeys and the long-term presence of wild asses near the Nile suggest that weak directed selection, continued recruitment of animals from the wild, and gene flow with wild asses contributed significantly to phenotypic variability among Predynastic and Early Dynastic donkeys in Egypt over at least a 2500 year period. The value that donkey herders placed on strength is demonstrated by donkey-onager and subsequent donkey-horse hybrids (mules) bred in the ancient Near East (6, 24). Uncontrolled breeding among village donkeys and along trade routes also contributed to gene flow between founder populations and mitigated genetic drift (17, 18).

Archaeological evidence, ethnographic observations and genetic data suggest herd management has always been *laissez faire* and characterized by intentional and unintentional inter-breeding with wild asses and feral donkeys, as well as by environmental selection for animals that survived in pastoral settlements (Table 2, Table S4). Together these processes resulted in a prolonged and complicated process of domestication for donkeys.

Ethnographic and archaeological data for horses, Bactrian camels, dromedaries, llamas, alpacas and yaks provide further insights into biological and human social factors

affecting selective breeding and gene flow during the domestication of animals heavily used for transport. Extinct *Equus ferus* from central Asia was the wild ancestor of domestic horses (Table 1.). Evidence for bitting, milking, corralling, and size decrease documents domestication by horse-hunters at Botai in Kazakhstan *ca.* 5500 B.P. (25, 26). As with other species, mitochondrial DNA lineages have been interpreted in terms of multiple domestications (25, 27). Genetic modeling now suggests domestication in a restricted region with incorporation of many different wild lineages into domestic stocks after domestication (28). Horse herds grow slowly and are subject to die-offs in severe storms, so the hardiness of wild horses is advantageous to herders. Accordingly, it has been argued that difficulties in maintaining domestic horse herd sizes during pastoral migrations led directly to restocking through the capture of wild females (25, 28).

Another transport animal subject to long-term gene flow is the Bactrian camel. Evidence is sparse, but these animals are thought to have been domesticated in cold desert regions of Central Asia (Table 1). The presence of Bactrian camels found outside their likely wild range suggests domestication *ca.* 6000-4000 B.P. (29), with a geographically restricted domestication indicated by genetic data (30). Extinction of their closest wild relatives (30) is thought to have resulted from both hunting and introgression with domestic camels (31). Historically herders have relied heavily on the strength of domestic Bactrian-dromedary crosses (32). Possibilities for increased strength and resilience may also have led nomads to encourage breeding of early domestic and wild camels, with chance admixture also more likely occurring within their natural range. The domestication of a related camelid—the dromedary—also indicates both intentional and chance breeding of domestic and wild camels. Dromedaries are adapted to hot deserts and thought to have been domesticated in Arabia (33). However, their wild ancestor is now extinct (34)(Fig. 1). Increased frequencies of dromedaries at archaeological sites suggest domestication *ca.* 4000 B.P. (34, 35). Ethnographic data show that herders select bulls based on size, color, family milk yields and environmental adaptations (36). Culling takes place at low levels and principally affects males, therefore directed selection is low. In contrast, high environmental selection on domestic camel herds is indicated by camelid genetics (30, 33). As shown by Bactrian-dromedary crosses, strength and hardiness were important to ancient herders and admixture is thought to have played a role in wild camelid extinctions.

There is also strong evidence for wild-domestic admixture and weak directed selection among South American camelids, guanaco, vicuña, llama and alpaca, which are all adapted to the cold, high altitude environments of the Andes (Table 1). Zooarchaeological research suggests multiple processes of domestication by hunters and possibly early cultivators in the central and south central Andes *ca*. 6000-4000 B.P. (37, 38). Archaeological and ethnographic data indicate that, although initially used for meat, through time herders relied more on larger llamas for transport and managed alpacas for fiber production. In the Lake Titicaca basin, the zooarchaeological record documents increasingly intensified and controlled herding, continued hunting, and gene flow among camelids 3500-900 BP. Evidence for continuous morphological variation implies long-term cross-breeding within and between wild and domestic camelids during this period (39).

An extremely complex history of interbreeding, which has even blurred the taxonomy of these species, is indicated by the occurrence of maternal mitochondrial DNA (mtDNA) haplotypes from vicuñas and guanacos in both domesticated llamas and alpacas. Recent research (also using mtDNA) documents early divergences within the guanaco clade—interpreted as evidence for multiple centers of llama domestication (40). However, the nature of connections amongst early herders is not well known and these genetic and morphological patterns could, once again, simply reflect recurrent recruitment of individuals from diverse wild populations. Adaptations of wild ancestors to extreme environmental conditions may have contributed to intentional breeding of wild and domestic camelids. Due to the unpredictability of animals surviving extreme weather events and disease, contemporary herders prefer diverse herds, retaining rather than culling individuals with a wide variety of characters (41). In the southern Andes there are records of wild guanacos being tamed and hybridized with llamas (42). Chance breeding of wild and domestic animals also still occurs when llamas and alpacas graze unsupervised in the same pastures and most hybrid offspring are fertile (42). Given prolonged inter-specific and intra-specific gene flow among Andean camelids, the possibility of ancient chimera species is likely.

Low levels of selection and high levels of gene flow among transport animals are also indicated by ethnographic data for yak management on the Tibetan plateau, where limited archaeological data suggest its domestication by sheep-herders some 5000-4000 B.P. (43) (Table 1). Since wild yaks are adapted to high altitude environments (31) and are resilient to low levels of oxygen, high solar radiation and extreme cold (44), human reliance on them for transport and food allowed herders to survive year-round on the high plateau. Genetics shows two mtDNA lineages in domestic yaks (45), which have been used to infer two separate domestications (43). However, as in other cases already discussed, it is as likely that diverse wild yak lineages were recurrently recruited into domestic herds (45). Ethnographic data, once again, reveal that breeding of wild and domestic animals is encouraged, since domestic yaks are subject to frequent mortality during winter storms. Crosses have strong flight responses, but are desired by herders because of their adaptation to the harsh plateau environment, size, and superior ability to protect herds from wolves (43, 46). Wild bulls move to lower elevations to mate with *dri* (female domestic yaks), where both encouraged and accidental breeding occurs (43, 46). Castration and limited culling are the only forms of directed breeding (46). Environmental selection on herded animals in pastoral camps and landscapes is strong (46).

These cases involving animals from extreme environments that are primarily used for transport show relatively low levels of directed selection resulting from limited culling and castration, but strong environmental selection within the human niche. They also demonstrate practical difficulties for mobile herders of breeding selected animals and maintaining genetic isolation from wild relatives. These findings show the potential advantages of gene flow between wild and domestic animals: it increases hardiness and resistance of animals used for transport in extreme environments. Given the unique domestication history of transport animals, it could be argued that this scenario is unlikely to hold more broadly. However, current evidence suggests that gene flow

between domestic and wild populations is far from unique to animals used from transport, but also may well be true for most domestic animal taxa—particularly those economically important ones kept for meat and secondary products such as meat and wool.

Pigs. Research into the domestication of wild boar across the Old World provides some of the most comprehensive evidence to date for ancient patterns of outcrossing and gene flow during and after initial domestication, as well as significant variability in these processes within Eurasia (Table 1, Table S1). Although, like many other animals, pigs had multifaceted economic and social relations with people, they were principally relied upon for meat. Wild boar are social animals, adapted to temperate or subtropical climates. Pigs are multiparous, with rapid gestation and herd growth rates leading to culling at much higher levels than equids, camelids or bovines and consequently to higher levels of selection. Unlike animals principally used for transport, intentional interbreeding of pigs with wild relatives confers no productive advantage. Gene flow is most likely to result from wild-capture as a herd-building strategy or from chance breeding of domestic pigs with wild relatives.

Zooarchaeological research on pig domestication indicates a long and complex process with early shifts in management and morphology occurring over thousands of years. This process is comparable in length to that previously outlined for donkeys and possibly involved two different, but related stages: initial commensalism followed by direct human involvement/control and resultant selection (10). Morphometric studies at early Neolithic sites dating to 9500-8600 B.P. as far apart as eastern Anatolia (10) and central China (47) indicate at least two separate independent domestications for *Sus scrofa.*

Genetic research over the last decade on both ancient and modern *Sus* has revealed a minimum of six phylogeographically distinct wild boar mtDNA lineages present in domestic pig populations across the Old World, as well as evidence for outcrossing of domestic pigs and wild boar. From this emerges a complex picture of initial domestication, dispersal, recruitment of local wild boar, genetic turnover and replacement (48, 49). Clear evidence exists for the introduction to Europe of *Sus scrofa*—of Near Eastern (mtDNA) origin—and its subsequent westward spread across Europe with early Neolithic farmers. Replacement of these Near Eastern lineages by European mtDNA haplotypes followed, first in Europe and then (during the late Bronze Age/Early Iron Age) eastwards across Anatolia to Armenia. At least three geographically distinct wild pig mtDNA lineages were recruited into domestic swineherds during the early Neolithic of Western Eurasia, which then involved turnover/replacement of introduced and indigenous Near Eastern *Sus scrofa* populations by European lineages.

The story for pig domestication in East and Southeast Asia is quite different from that of S.W. Asia and Europe. Mitochondrial DNA from both ancient and modern *Sus scrofa* show that few modern domestic pig lineages share mtDNA with those first domesticated in the early Neolithic. Most wild boar lineages that exist in China today were never incorporated into domestic herds nor exterminated as a result of hunting or introgression with feral pigs (50). This may suggest close control (even penning) from an

early stage. Just as further west, however, agriculturalists moving into S.E. Asia also incorporated local wild boar lineages into their domestic stock either deliberately, or accidentally. As a result ancient mainland, Island S.E. Asian, New Guinea and remote Oceanic domestic pigs do not share their maternal ancestry with the earliest central Chinese domestic pigs, but with lineages recruited from other S.E. Asian wild boar populations (48, 51-53).

In this and most other cases that we discuss, such conclusions are based upon analyses of mtDNA. This neutral marker informs only about the maternal line, which can itself be rapidly replaced during the hybridization process between incoming domestic and local wild stock (52). These data do not reveal the extent of inter-breeding between male wild boar and domestic pig herds. However, recent combined analyses of mitochondrial DNA, coat-color markers and tooth shape (54) of domestic pigs in Ertebolle contexts in Northern Germany provide evidence for outcrossing (intentional or otherwise) of domestic early pigs with wild boar. The nuclear genome is now the principal research focus for ancient DNA research because it retains such introgression signatures over longer evolutionary timescales (52).

These Eurasian datasets for *Sus scrofa* reveal definitive evidence of significant introgression and gene flow between wild boar and domestic pig populations indicating a rather different domestication process than traditionally purported. This involved initial domestication of a limited number of individuals from discrete local populations, leading to a degree of genetic isolation. However, extensive and mobile husbandry practices, along with subsequent migration/dispersal of domestic pig herds, led to inevitable introgression of new local wild boar lineages, which rapidly replaced 'founding' lineages. Whether this was a deliberate strategy or an accidental by-product of early Neolithic swine herding/husbandry strategies is impossible to conclude from the biomolecular evidence alone.

However, historical and modern-day ethnographic observations of traditional pig keeping in, for example, the Mediterranean, point to the common practice of rather loose and extensive management of domestic pigs, along with long-distance mobility patterns linked with the search for summer and winter feeding (55). Even more closely managed pig rearing in Europe, such as the pannage/mast systems of medieval times, saw swineherds managing free-roaming pigs in extensive woodland – the natural habitat of the endemic wild boar. Such traditional pig husbandry were likely to have been the norm at least across Europe millennia earlier than the historical period. In such circumstances, it is unlikely that outcrossing of domestic pigs with wild boar was uncommon.

Sheep, goat and cattle. Unlike pigs, Old World bovids - sheep, goats and cattle - were widely used for meat, milk and fiber. They provide an interesting contrast to equids, camelids, yaks and pigs in their biology and relationship with humans, and insights into the widespread nature of evidence for gene flow. Ancient populations of *Capra aegagrus* and *Ovis aries*, are the S.W. Asian ancestors of domestic goat and sheep (Table 1). Age and sex profiles document very early culling of managed herds of both species by settled hunter-gatherers and early cultivators in eastern Anatolia and the Zagros

mountains *ca.* 11,000-10,000 years ago (56, 57)(Table 1), with goats already displaying morphological changes by *ca* 9400-8900 B.P. (11, 58). Compared to pigs, sheep and goat produce only one or two offspring at a time, which alters the dynamics of herd management and culling. Traditional pastoralists today manage sheep and goats principally for growth, relying on female dominated herds with male-offtake sustained up to 8-16% a year(59). Herders' decisions regarding males spared for breeding or new stock acquisition (male or female) are informed by family histories of growth potential, color, milk production and resilience (60-62). Nevertheless, directed selection remains weak, because it acts primarily upon males.

The discovery of six maternal lineages of wild bezoar in domestic goats once again most likely indicates long-term recruitment of wild females to domestic herds (63). Long-distance pastoral movements of flocks through the Zagros provided continual opportunities for unintentional admixture within the natural range of sheep and goats. This has led to arguments that morphological change, traditionally associated with domestication, did not occur in ancient goats until gene flow was reduced by the dispersal of managed herds outside the range of their wild relatives (58). Any decline in domestic herd size would have provided incentives for wild-capture. Periodic weather events, drought and disease would have created instability in herd size (59). Such instability is implied in the case of pigs and goats introduced to Cyprus during the mid-eleventh millennium B.P. (13, 64). However, once secondary products such as milk or wool became important, domestic traits such as productivity and docility would have become highly desirable, increasing the influence and intensity of directed selection.

Cattle, native to temperate or semi-arid sub-tropical environments, were principally used for meat, and then at times depended on heavily for milk, traction and ceremonial use. Due to their large size, diverse use, and broad environmental adaptations, relations between humans and cattle differ greatly from those of sheep and goats. Taurine cattle were domesticated in Anatolia 10,500-10,000 B.P. (65-67) and zebu cattle in South Asia by *ca*. 8,000-7500 B.P. (68, 69)(Table 1). The size of cattle, low growth and culling rates, as well as early use for milk (70) and/or traction, once more imply lower levels of directed selection than even those experienced by pigs or sheep and goat. When selecting herd bulls, contemporary African pastoralists consider similar factors to those discussed for camels, sheep and goats (59, 71). However, cattle are seldom culled at higher than 4-8%. Productive females are not culled, multiple bulls are kept, and natural mortality is often higher than that due to culling (72). This results in weak directed selection and strong environmental selection. Slow herd growth promotes gene flow, as does lightly supervised grazing.

Based on ancient DNA and modeling it has been argued that small numbers of wild taurine cattle contributed to initial domestication in Anatolia and that diverse wild populations were not incorporated into domestic herds (73). However, the zooarchaeological record suggests cattle domestication was a protracted process (66). In contrast to pigs, there is no genetic support for interbreeding of domestic taurine cattle with wild cattle as herders moved across Europe (74). The one exception is data from Italy, where ancient mtDNA suggests that female aurochsen may have been recruited into domestic taurine herds. The picture is different for South Asia where high

autosomal diversity indicates repeated crossing of domestic zebu cattle with wild males and females (75). Multiple mitochondrial lineages have been interpreted to represent either two separate domestications or, again, recruitment of wild animals into domestic zebu herds (68). This variability highlights the roles of regional differences in management practices or herd viability in promoting gene flow. The debate over the question of local domestication of cattle in northeast Africa (76) *versus* interbreeding of Near Eastern cattle with African wild cattle indicates the extent to which scholars are grappling with the significant role of gene flow in patterning genetic data.

Despite differences in environments, biology and husbandry practices between taxa, there is strong evidence for gene flow between these domestic artiodacyls (i.e. pigs, sheep, goat or cattle) and their wild relatives in areas of common distribution. Set against the whole history of domestication, complete separation between wild and domestic populations appears to be a relatively late, region-specific phenomenon. Regional variability in gene flow is demonstrated for pigs and cattle, which took several dissimilar domestication "pathways" with different degrees of admixture in western, southern and eastern Eurasia. These findings point to regionally different approaches to management, with animals closely herded or provisioned in some settings or extensively ranging in others. Variability in herd size and viability was also a contributory factor leading to admixture in some—but not all—regions.

Variable pathways to domestication

Since the role of gene flow in the domestication of large herbivores has, until now, largely been considered minor or peripheral to more dominant processes, drivers of gene flow have not been systematically investigated. Ethnographic and ethnoarchaeological data clearly demonstrate that admixture is not simply an occasional or accidental process. Recent and historic herders intentionally captured wild relatives of their domestic animals and encouraged directed breeding between them. Both herders' goals and unintended circumstances influenced the extent of gene flow between wild and domestic animals. At the same time as discounting gene flow as a significant component of early domestication history, the primacy of strong directional selection in the process has often been assumed (15) but never demonstrated. It appears, however, that under most historic and prehistoric management regimes weak directed selection was driven primarily by culling or castration of males surplus to the growth needs of herds. We also see environmental selection in various new human influenced environments as a key factor in domestication history.

These findings have significant implications for our interpretation of the archaeological record, determinations of the timing and location of initial domestication, and interpretations of genetic data on domestication. Trends in the extent of directed selection and in gene flow potentials reinforce many of the distinctions proposed among commensal, prey, and directed pathways to domestication (11, 13)and point to additional selective mechanisms that differentiate them. Culling rates were lower and outcrossing potentials higher for larger transport animals, horses, donkeys, camelids and yaks. Correspondingly, high rates of turnover, culling and

therefore of directed selection characterized sheep, goats, and pigs or more rapidly maturing animals domesticated and managed in less extreme environments.

Inter-breeding among domestic, feral and wild animals, augmented by the opportunities afforded by migrations and trade routes, has created long and complex evolutionary and domestication histories that challenge current expectations regarding genetic isolation and long-held, traditional definitions of domestication. Given differences of degree between domestic and wild animals, some might question whether domestication remains a useful concept? We consider it is essential to treat changing human-animal relations as a continuum, specifying domestication traits that vary with taxon and context—animal-human relationship, place and time—rather than focusing on general expectations or arbitrary boundaries. This is the direction in which recent archaeological research has been moving (11, 13, 77).

Current assumptions regarding severe domestication bottlenecks and monophyletic origins have complicated attempts by zooarchaeologists and geneticists alike to study the domestication histories of animals such as South American camelids (39) or to interpret coalescence data and estimate domestication time-frames for cats (15). Recurrent gene-flow makes wild and domestic animals more similar and the perceived time of divergence more recent. The same assumptions have resulted in in widespread (mis)-interpretation of mitochondrial variability in terms of multiple instances of domestication. Recognition of the extent of long term gene flow within and between wild and domestic animals better reconciles archaeological and genetic data for many species and suggests longer and more complex domestication processes (52). In addition, long-term gene flow further undermines the ability of modern genetic data derived from highly developed modern-day breeds to shed light on the earliest phases of domestication (78).

If gene flow resulting from breeding between wild and domestic animals was more common, rather than the exception, during domestication, it raises many questions regarding the ways in which behavioral and phenotypic domestication traits arose and were maintained. To address these issues, we need better characterization of animal-human relationships through time, including better integration of multiple scales of analysis: from the molecular level, to whole animals, to the social contexts and landscapes within which domestication occurs. Diverse zooarchaeological, chemical and geoarchaeological approaches to documenting changes in herd sizes, penning, milking and feeding strategies, as well as culling and castration across ancient sites, offer promise for eliciting temporal and site-specific data on selection processes and gene flow. We need to know, for example, exactly where and when outcrossing was common or directed selection high before we can begin to evaluate the respective importance of these processes in the domestication of particular species or to understand regional variability.

Other questions, such as the amount of gene flow required to counter directed selection at different levels of culling or natural mortality in human environments are amenable to modeling (79). We identify environmental selection under human management as an important force in animal domestication. This is an area that genomic studies are currently exploring (4). Understanding epigenetic mechanisms, such

as patterns of DNA methylation that cause genes to express themselves differently in human compared to wild settings or under varying management regimes (e.g. under stress), promise to provide new insights into ways in which selection was maintained (80, 81). Finally, landscape genetic studies of how small-scale social and biological processes such as household mobility and exchange or captive animal breeding rates affect movement, interbreeding and gene flow at large scales, have the potential to integrate anthropological, behavioral and genetic data (82).

Instead of assuming strong intentional and directional selection during the early stage of animal domestication, the challenge is to investigate sources of selection more critically bearing in mind the complex interplay of human and environmental selection and the likelihood of long-term gene flow from the wild. These insights on gene flow and unintentional breeding provide new perspectives on early animal domestication, alter current sets of assumptions and questions, and enhance our understanding of domestication as a complex biocultural process.

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† All dates are reported in calibrated years before present.

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Figure legends

Figure 1. Intentional capture and outcrossing of donkeys, wild asses and hybrids A) African donkey with shoulder cross B) Tuareg taming captured Saharan wild ass or feral donkey 1950's (21) C) donkey-Somali wild ass hybrid with cross and striped legs Berbera 1900's. Donkeys were tied outside the village to breed with Somali wild asses (20) D) Somali wild ass with striped legs.
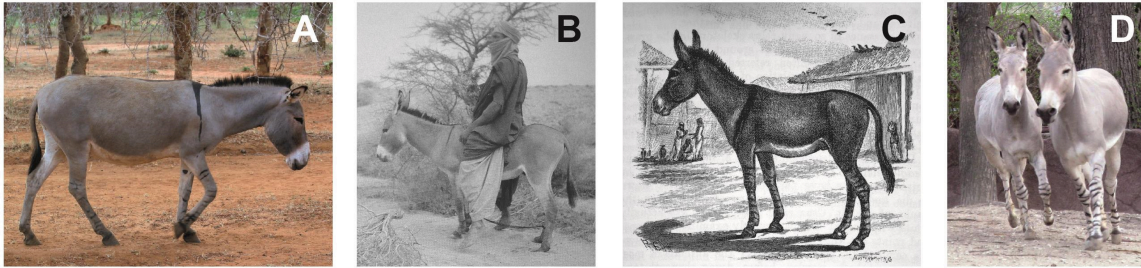
Table 1. Domestic animals, key archaeological sites, and domestication time-ranges. Wild-domestic gene-flow occurred among all taxa. Large transport animals were subject to low culling and high outcrossing potentials.

	Animal Domestication		Sites	References
Donkey,	*Equus asinus*	6,000-3,500 BP	Maadi, Abydos, Uan Muhuggiag	17, 19, 23
Horse,	*Equus caballus*	5,500 BP	Botai	25, 26, 28
Bactrian camel,	*Camelus bactrianus*	6,000-4,000 BP	Anau	29, 30
Dromedary,	*Camelus dromedarius*	4,000-3,000 BP	Shahr-i-Sokhta	33-35
Llama,	*Lama glama*	6,000-4,000 BP	Pikimachay, Tulan, Inca Cueva	37-40, 42
Alpaca,	*Vicugna pacos*	5,000-3,000 BP	Telarmachay	37-40, 42
Pig,	*Sus scrofa*	12,000-8,300 BP	Çayönü Tepesi, Jiahu	10, 47-51, 53
Goat,	*Capra hircus*	11,0000-9,000 BP	Asiab, Ganj Dareh, Ali Kosh	57, 62
Sheep,	*Ovis aries*	12,000-10,500 BP	Cafer Hüyük, Zawi Chemi Shanidar	55-57
Taurine cattle,	*Bos taurus*	10,500-10,000 BP	Dja'de, Çayönü	65, 66
Zebu cattle,	*Bos indicus*	8,000-7,500 BP	Mehrgarh	67, 68
Yak,	*Bos grunniens*	?	Tibetan Plateau	443, 45