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Central Questions in the Domestication of Plants and Animals

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Along with symbolic communication, tool use, and bipedalism, the domestication of plants and animals, together with the associated emergence of agriculture, stands as one of the pivotal thresholds in human evolution. For more than a hundred years researchers have wrestled with the questions of what domestication is, how it is detected, and why it happened. The past decade in particular has witnessed a remarkable acceleration of interest in domestication, thanks to advances in our ability to detect the context, timing, and process of domestication in a wide array of different plant and animal species around the world.[1] This review focuses on overarching issues of defining, documenting, and explaining the domestication of plants and animals, tracing a path through often discordant viewpoints to offer some new perspectives.

DEFINING DOMESTICATION

All approaches to defining domestication in both plants and animals recognize that domestication involves a relationship between humans and target plant or animal populations. There are, however, distinct and often discordant perspectives taken regarding the balance of power in this relationship and its central defining features (Fig. 1). Many approaches to defining domestication, especially those focusing on animals, emphasize the dominant role humans play in assuming "mastery" over all aspects of the reproduction, movement, distribution, nourishment, and protection of domesticates.[2–5] Integral to definitions that place humans in control of the process is the notion of intentionality, that humans with foresight and deliberate intent intervened in the life cycle of target plant and animal populations and assumed responsibility for their care to meet specific and well-defined objectives serving human needs. Also often associated with this emphasis on the human dimension is the notion that domestication involves a fundamental change in socioeconomic organization in which successive generations of domesticates become integrated into human societies as objects of ownership.[3,6]

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Other researchers object to "anthropocentric" approaches to defining domestication that portray domesticates as passive pawns in the process, pointing out that domesticates also reap benefits through vastly enhanced reproductive fitness and expanded ranges.[7] Those operating within an evolutionary biology perspective, in particular, maintain that the relationship between humans and domesticates is no different from other mutualistic relationships in the "natural world" that bring together species like ants and aphids in partnerships of increasing co-dependency.[8] Moreover, as one moves further along the spectrum, from a relatively balanced mutualistic perspective to ones that focus on the domesticate, the role of deliberate human intent declines. The more extreme positions at this end of the spectrum tip the balance in favor of the domesticate, which is seen as manipulating its human partners for its own evolutionary advantage, ensnaring humans in a relationship that may have actually reduced human fitness.[9]

Another axis of variation in definitional approaches to domestication is the relative primary given to genetic and associated morphological change. An emphasis on genetic change and its phenotypic expression is particularly common among researchers focusing on plant domestication, especially the domestication of large-seeded annuals, where human intervention results in fairly rapid genetic changes with easily observed phenotypic expressions.[9,10] Some researchers focusing on animals also see genetic isolation and subsequent quick-onset morphological change as essential attributes of domestication.[11]

The requirement that domesticates show evidence of morphological or even genetic change, however, is not universally accepted. Nor is the basic premise underlying this requirement: that the process of domestication is contingent on reproductive isolation and resultant genetically driven mor-

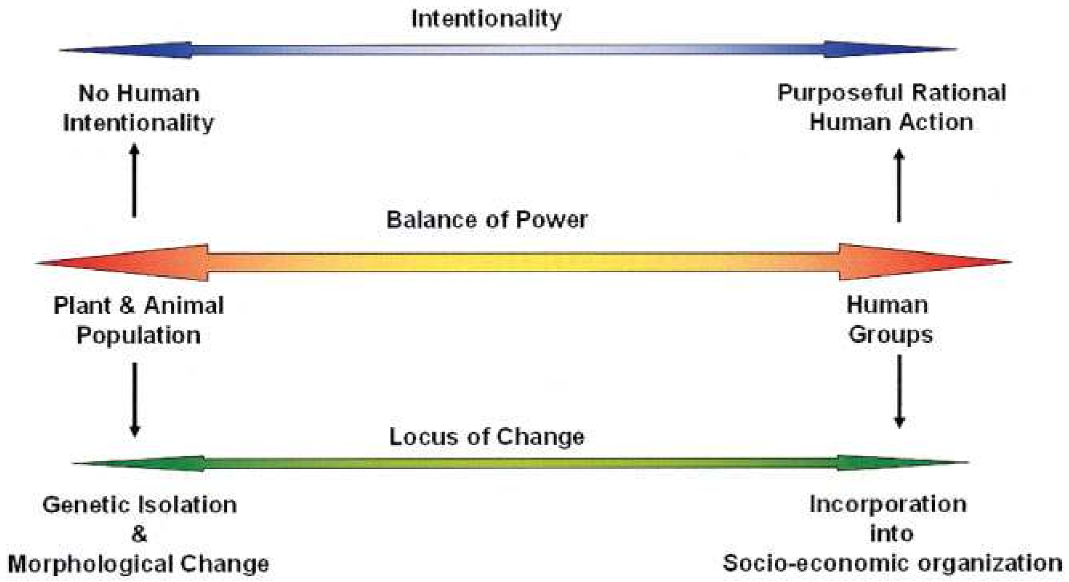


Figure 1. Definitions of domestication tend to fall somewhere along three axes of variation. Definitions that award the balance of power in the domestic relationship to humans tend to stress human intentionality and the social and economic impacts of domestication. Definitions that tip the balance of power in favor of the domesticate tend to discount the role of human intentionality in the process and stress its biological impacts on the domesticate.

phological change. This is particularly true for animals, where morphological change, when it occurs at all, is often both delayed and difficult to tie directly to domestication.[12] As a result, many researchers define animal domestication not in terms of observed genetic or morphological change, but in terms of causal human behavior. According to this view, domestication falls along a continuum of increasing human intervention ranging from predation to genetic engineering[13] in which there are varying degrees of investment in altering an animal's natural behavior (its movement, breeding schedule, or population structure) to suit human needs.[6,14] A similar view is becoming increasingly common in considerations of plant domestication especially perennial plants such as root crops propagated through vegetative cloning or very long-lived tree crops in which genetic and morphological change may be less automatic and more subtle than in annual seed crops.[15] Smith,[16] for example, maintains that for both plants and animals the central defining feature of domestication and the creation of domesticates is the nature of the "ongoing relationship of intervention initiated and sustained by humans." This emphasis on the evolving relationship between humans and plant or animal populations turns attention away from a range of secondary consequences of domestication, such as genetic and morphological change or social notions of property, and properly returns it to a consideration of the new partnership that humans create with target populations.

Domestication does indeed have many features in common with other mutualistic relationships among plants and animals. Both partners in the relationship of domestication clearly derive benefits. Plant and animal partners benefit in increased reproductive fitness and range expansion. Human partners gain increased security and predictability in their access to resources of interest. Both partners respond to this relationship in ways that enhance respective payoffs and further deepen their mutual investment in its continuation. But the mutualism that lies at the heart of the domestication process involving human societies and target plant and animal populations varies in significant ways from other similar relationships found in nature.

In a recent overview of the homologies between human agriculturists and fungus-growing ants, Schultz and coworkers[17] highlight the many parallels between these convergent forms of mutualism while also underscoring key qualitative differences between attine and human agriculture. The codependent relationships between farmer ants and domesticated fungi are the result of a gradual co-evolutionary process based on mutation-induced behavioral and morphological change in both partners. Humans, on the other hand, are capable of modifying their behavioral repertories through "trial and error, observation, and imitation."[17] That ability enables humans to rapidly develop behavioral strategies aimed at meeting consciously recognized needs. The highly developed human ability for cultural transmission of learned behavior, Shultz and coworkers argue, greatly accelerated the adaptive modification of human behavior, shifting the balance of power in the emergent mutualism. Humans quickly assume a dominant role because they are free to choose among genetic variants in the partner population, to manipulate the behavior and life history of symbionts (even to their own detriment), or to terminate the relationship with one partner symbiont and choose another.

This is where intentionality comes into the picture. It is true that humans could not have foreseen the adaptive responses by plant and animal partners to the new selective factors brought into play by the relationship of domestication. Nor did humans likely appreciate the long-term benefits (or the negative consequences) that might accrue from domestication and the subsequent development of agricultural economies. However, ruling out this kind of prescience on the part of humans does not take intentionality out of the picture. While they might not have understood the principles of genetic engineering, humans could appreciate the fact that tending, nurturing, and intervening in the life cycle of certain plants and animals yielded various immediate benefits. On the basis of these returns they could then consciously and deliberately decide to continue to engage in these behaviors, and to elaborate on them, instead of engaging in other strategies.

Intentionality, then, becomes the key factor that distinguishes domestication from other similar mutualistic relationships in nature. The deliberate role humans take in actively pursuing the domestic partnership also distinguishes it from other biological relationships between humans and plants and animal species, such as commensal relationships with mice, sparrows, or weeds that take advantage of new niches created by human habitation. Definitions that try to pigeon-hole domestication as either a cultural or biological process are bound to come up short. Clearly, domestication has a biological component as a mutualistic relationship between humans and plant or animal symbionts. Just as clearly, however, human intentionality sets domestication apart from other forms of mutualism. The uniqueness of the relationship comes from its cultural component and the dominant role humans play in consciously and deliberately perpetuating it to their own advantage.

If the process of domestication is best viewed as a form of mutualism that is asymmetrically enhanced by the human ability to culturally transmit learned behavior, then at what point along this developmental trajectory does the plant or animal partner become a domesticate? Is there a threshold that, once crossed, separates the "wild" from the "domestic"? If so, what does this threshold look like? To some extent, it remains a matter of personal preference to decide just when a domestic subsection of a plant or animal species has been created. Threshold criteria that require total genetic isolation and emergent speciation or complete dependence on humans for survival set a very high bar that many, if not most, widely accepted domesticates would fail to clear. Even somewhat looser standards that involve a lesser degree of genetic modification in the target plant or animal population, or a certain level of human investment in propagating, nurturing, or owning the resource, run the risk of constructing artificial boundaries along what was really a more seamless incremental process.

Ducking the issue by adopting the term "proto-domesticate" also does not help much. This term implies that, if just given enough time and perhaps a little more investment by either partner, full domestic status would be achieved. The actual trajectory of domestication, however, is highly contingent on a wide range of factors, including the ability of the plant or animal to take advantage of the relationship, the strategies and accompanying technologies humans develop to manage the resource, and its changing value vis-à-vis available alternative resources. In some plant and animal species, genetic modification and more focused human investment in the resource may quickly follow. In others there may be a long and very stable relationship involving fairly minimal commitment by either partner. Further, it appears that budding domestic relationships sometimes fail altogether, never moving beyond an initial courtship phase.

It is best to step back and not focus too closely or obsessively on defining the exact demarcation between domestic and wild, and to turn, instead, to a consideration of the full span of the evolving nature of domestic relationships. Different stages in the evolution of this relationship might be characterized by the degree of investment by both partners (Fig. 2). For the plant or animal, this would involve the extent of genetic modification made in response to new selective pressures, the degree of its genetic isolation from populations not involved in the partnership, the nature of subsequent morphological or behavioral change, and its increasing co-dependency on humans. For humans, this might be the level of investment in the production of the resource; that is, in tilling, watering, burning, and land clearance, sowing, and transplanting plants, or in taming, protecting, herding, culling, and selectively breeding animals. It might also include the degree of incorporation of domesticates within the socio-economic organization of the human groups investing in its production.

By expanding the scope of inquiry to encompass the vast "middle ground" between foraging and farming, hunting and herding,[16] we can approach a deeper, more comprehensive, and ultimately more informative appreciation of the range of possibilities open to humans and their plant and animal partners. This expanded territory of investigation includes the stable, long-lived systems of low-level food production involving a mix of both morphologically altered and nonaltered domesticates, as well as "wild" resources, featured in recent books on indigenous resource management in California and the Northwest Coast.[18,19] At the other end of the spectrum are highly structured agricultural economies with complete dependence on domesticates and total investment in their production. Trying to understand the full richness of the various ways in which the domestic partnership may manifest itself in different contexts, we, in turn, stand a much better chance of being able to document and explain domestication.

DOCUMENTING DOMESTICATION

In both plants and animals, this effort requires identifying clear-cut markers that can be explicitly linked to a specific aspect or stage of the unfolding domestication process.[1,20] Different markers may be more effective in detecting different stages of this process. Markers will also vary depending on the biology of the domes-

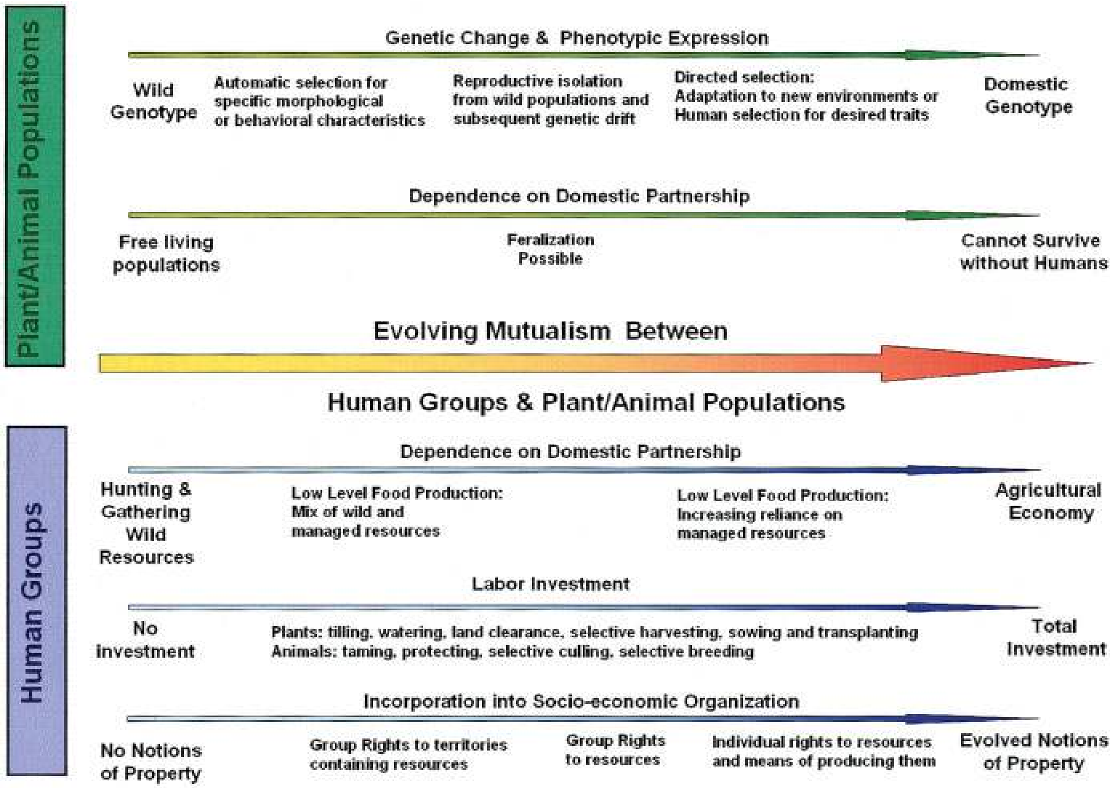


Figure 2. Domestication is best viewed as an evolving of mutualism between humans and populations of plants or animals. The relationship can be characterized along various scales of investment by either the human or the plant or animal partners. All of these scales usually are involved in the process of domestication, though they often operate independently of one another. The degree of change along each scale is contingent on the biology of the species involved, as well as the ecological and cultural circumstances of the human partners. Attempting to distinguish just where and along what scale domestication occurs is not only difficult, but may not be very useful.

ticate and its relationship with humans. There are, in particular, fundamental differences in the selective pressures on plants and animals undergoing domestication, and, as a result, in the corresponding markers used to document plant and animal domestication.

Selective pressures on plants, especially annuals, tend to operate directly on morphological traits that can, in turn, be used as unambiguous markers of domestication.[15] Morphological impacts of the domestication of annuals may come about as largely automatic responses to human planting and harvesting that result in such changes as increased seed size, thinner seed coats, reconfiguration of seed head architecture, or the development of indehiscent seed pods.[15,21,22] Intentional selection for specific morphological attributes in annual plants, such as larger fruit size, appear to happen later in the developing relationship of domestication.[15]

Perennial plants sustained by transplanting root fragments, on the other hand, are not subjected to the same seed-bed pressure and human harvesting selective pressures that result in the morphological markers used to document domestication in annual seed plants.[15] At the same time, however, because there may be more of an opportunity for humans selectively to replant root fragments with desired traits, these plants may respond fairly quickly to deliberate human selection in the development of larger fruits, the loss of chemical defenses against herbivory, or changes in sugars and starches.[23] While many of these crops were grown in tropical areas with poor preservation of plant macro-fossils, the development of breakthrough techniques for the recovery and identification of plant micro-fossils (that is, phytoliths and starch grains) has made it possible to detect these domestication-induced morphological changes in root and other crop plants (Fig. 3).[24,25]

Recent years have seen an increase the use of nonmorphological markers of the intensification of human-plant interactions that may precede clear-cut evidence of morphological change in plants. Evidence of land clearance, modification of natural drainage systems, intentional burning, and changes in the composition of weedy plants in archeological assemblages have all been effectively used to track human modification of landscapes and plant communities as part of the domestication process.[26–28] The occurrence of plant macro- or micro fossils in areas thought to be far outside their natural range has also been interpreted as evidence of human transport and tending of plants.[26,29,30]

There are special challenges to finding markers of animal domestication. This is because the leading-edge pressures on animals undergoing domestication are likely to focus on behavioral attributes rather than on morphological traits.[31] There are a variety of behaviors that probably made certain animal species better candidates for domestication; among them tolerance of penning, a social structure based on dominance hierarchies, sexual precocity, weak alarm systems and, above all, reduced wariness and aggression.[32] Behavioral responses to domestication in animals elaborated on these initial preselection qualifying attributes and include a general reduction in responsiveness to environmental stimuli, reduced activity levels, increased social compatibility, and intensified sexual behavior.[4,33]

Many morphological traits commonly seen in domestic animals are thought to be linked to these behavioral changes. These attributes include piebald coats, lop ears and, of special importance here, reduced brain size and an overall juvenilization of cranial form.[4,33] This latter feature may result in a shortened muzzle, tooth crowding, and reduction in tooth size, traits frequently seen as leading-edge markers of domestication in dogs and pigs.[34,35] Selection for these behavioral traits and their associated morphological effects, however, may not be uniquely restricted to domestication. Similar behavioral traits, such as reduced wariness and timidity, are also selected for in animals such as rats and sparrows that develop commensal relationships with humans. These animals also show changes in pelage coloration and brain size.[4] It is possible, then, that the initial modifications in tooth size and cranial form in pigs and dogs, widely seen as markers of domestication, may in fact be attributable to an early commensal relationship between humans and such omnivore species that began their association with humans as camp-follower scavengers.[31]

Other genetically driven morphological changes in animals undergoing domestication come about when humans begin deliberately selecting breeding partners. Changes in the size and shape of horns in animals like goats and sheep, for example, are directly tied to the relaxation of selective pressures for and, quite likely, active selection against large horns once humans assume control over breeding.[36] Other morphological changes may ensue when animals are moved into new territories, either through founder effects, random genetic drift, or directed adaptation to new environmental conditions. Later still, and probably much later in animals than in plants, deliberate human selection for attributes that enhance meat, fiber, milk yields, or labor potential may result in still other morphological markers that might be used to detect intensification in the human-animal relationship.

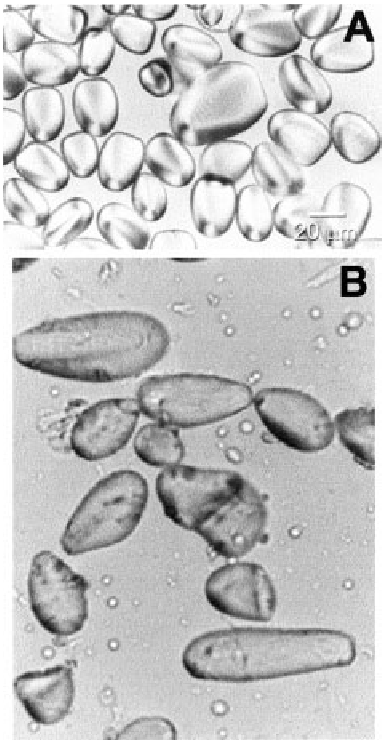


Figure 3. Starch grains from wild and domestic yams, *Dioscorea* sp. A. Granules from modern domestic yams (*D. trifida*). B. starch grains from a wild yam (*D. cymosula*) from Panama. Starch grains from wild yam species studied thus far from the Neotropics are distinct in morphology as compared with domestic varieties. As a rule, wild forms are also highly variable within a single tuber, whereas domesticated species have a single morphological type of starch, which may be a result of human selection.

Domestication has also been suggested to have resulted in a marked and rapid reduction in body size, which, until recently, has been widely held to be a definitive marker of initial domestication.[37] This proposed morphological response has been variously attributed to a plastic response to nutritional deficiencies, an adaptive advantage of smaller bodies for animals subjected to impoverished conditions, or deliberate human selection for more tractable individuals.[38–40] But body size in animals is also known to be affected by well-documented factors such as sex, environment, climate, and age, which may be entirely unrelated to domestication and may mask or be mistaken for changes in body size induced by domestication.[12]

Given the looser connection between domestication and morphological change in animals, it is not surprising that considerable attention has been devoted to identifying markers of domestication that do not rely on genetically driven morphological change, but that, instead, reflect human actions directed at managing animals. Demographic markers aimed at detecting the different harvest strategies of hunters and herders were among the first nonmorphological markers used to detect animal domestication.[41] Largely abandoned in the 1980s and 1990s, when most archeozoologists embraced size reduction as a leading-edge marker of animal domestication, demographic markers are seeing a resurgence, thanks in part to the development of methods for constructing high-resolution sex-specific harvest profiles.[12,42] Applying these methods to archeological assemblages has shown that what was once interpreted as evidence of domestication-induced body size reduction in goats (and likely other livestock species) is, instead, a reflection of a change in the demographics of the adult portion of managed herds dominated by females (Fig. 4).[12] Unambiguous changes in morphological traits such as body size or horn form seem to postdate human management of herd animals by hundreds of years and represent later phases in the domestication process.[12,43]

Both the presence of animals outside their presumed natural habitat and a sudden dramatic increase in a previously little-exploited animal have also been used as markers of animal domestication.[41,43,44] But the use of these markers (in both animals and plants) needs to be tempered by acknowledgment of our generally poor understanding of the geographic range of biotic communities in the past and of the paleo-environmental conditions that shaped these ranges. A rapid increase in the abundance of a plant or animal resource in an archeological assemblage might simply signal the intensification of hunting and gathering strategies, not the beginning of food production.

Markers of animal domestication may also be found in plastic, nongenetically driven responses such as bone and tooth pathologies, evidence of pandemic disease, or chemical changes in the composition of bone and tooth enamel used to track changes in nutrition and the seasonal movement of managed animals.[45–48] The presence of corrals, pens, or other traces of animals, such as manure or hoof prints, in human settlements, changes in human settlement patterns, artifacts related to the exploitation of domestic animals (bits or milk churns and storage vessels), and even changes in food distribution patterns have been used with varying effect to build cases for animal domestication.[49] The application of these later plastic responses and cultural markers needs to be tempered by the realization that they may not be manifested in all instances of animal domestication or may result from other pressures unrelated to domestication. Application of such markers is most effective when many of them are brought together to build strong circumstantial cases for domestication.[49]

Advances in methods for extracting and amplifying both modern and ancient DNA is recent years have provided an exciting new window on the genetic changes associated with the domestication of plants and animals.[1,20,50,51] Some of this work has focused on identifying the genes or gene complexes that are specifically selected for or against in the process of domestication, especially of crop plants.[52] However, most genetic studies of domestication look to largely neutral noncoding loci and organellar genomes. These procedures have proven useful in tracing the divergence of domesticates from their wild progenitors; identifying the number and geographic location of domestication events, which now appear to have been multiple for most animal domesticates and many plant crops; and in tracking the dispersal of domesticates and their human partners out of centers of origin.

Figure 4. Goat (*Capra hircus*) first phalanges from Ganj Dareh ca. 10,000 cal B.P. The small bone on the left falls within the size range of such bones from female goats, while the larger specimen on the right is likely from a male. The female phalanx is fully fused, indicating the animal was slaughtered after this bone fused, which in goats is about 13 months of age. The male specimen is unfused, indicated that this animal was younger than 13 months of age when slaughtered. The selective slaughter of young male animals with prolonged survivorship of female animals is symptomatic of human management. (Photo by Carl Hansen)

There are critical differences in the relative rates of evolution in the different genomes of plants and animals that play a major role in the genetic markers used. The relatively rapid rate of evolution in mitochondrial DNA (mtDNA) in animals makes mtDNA particularly well suited to tracking the relatively shallow time depth of divergence between domesticates and their wild progenitors (<10,000 years). This is why most studies of animal domesticates focus on this genome.[51] While it is less variable than mtDNA and evolves much more slowly, low-copy Y-chromosome nuclear DNA provides a window into patrilineal inheritance, which in many animal domesticates is quite different from matrilineal history.[53,54] Variation in noncoding nuclear microsatellite DNA, contributed by both parents, has also proven useful in tracking the divergence of different breeds of animals.[55,56]

While not approaching the rate of evolution of animal mtDNA, loci in the nuculear genome of plants evolve at about the same rate as nDNA loci in mammals. They also evolve about four times faster than loci in the choloroplast genome and twelve times faster than plant mtDNA. Consequently, genetic studies of plant domestication tend to focus on nDNA, especially on highly polymorphic microsatellites that provide sufficient intraspecific variation to document the domestication process.[50,57–59] The nuclear genome in plants has proven especially useful in tracking down the various ancestral genomes contributing to the complicated genetic heritage of hybrids and polyploid crop plants. These common conditions in plant crops generally are not found among animal domesticates.[50,60]

Most genetic approaches to documenting domestication are based on modern domesticates and likely wild progenitor species. But the window they provide on the origin and early dispersal of domesticates is unavoidably clouded by thousands of years of selective breeding, hybridization, and introgression between wild and domestic populations. Ancient DNA (aDNA), on the other hand, has the potential to shed more direct light on the process of genetic divergence of domesticates. Due to the greater preservation of DNA encased in animal bone and the suitability of high-copy mtDNA in animals for tracking shallow time depth divergences, aDNA studies of animal domesticates have been particularly successful, especially those tracing the more recent dispersal of domestic animals through temperate environments.[61–64] Although it is more difficult to extract enough low-copy nDNA from uncharred archeological plant remains to provide meaningful results, some stunning results have recently been obtained in the use of aDNA to track the origin and dispersal of domestic plants.[65,66]

In the excitement over the possible contributions of genetic analysis to the documentation of plant and animal domestication, it is important not to lose sight of the fact that there is more to domestication than genetic change. The real power of these new tools for tracking the trajectory of domestication can be realized only when genetic analyses are more fully integrated into broader archeological analyses. Genetic studies represent one, albeit very powerful, line among many parallel and mutually illuminating lines of evidence, which, when considered together, provide a fine-grained view of unfolding domestic partnerships (Box 1).

EXPLAINING DOMESTICATION

Efforts to explain domestication and the origins of agriculture tend to cycle among a relatively limited number of forcing factors championed as primary and often universal levers of change. These forcing factors can be generally grouped under three banners: environmental change, demographically induced resource pressure, and changes in social organization and ideology.

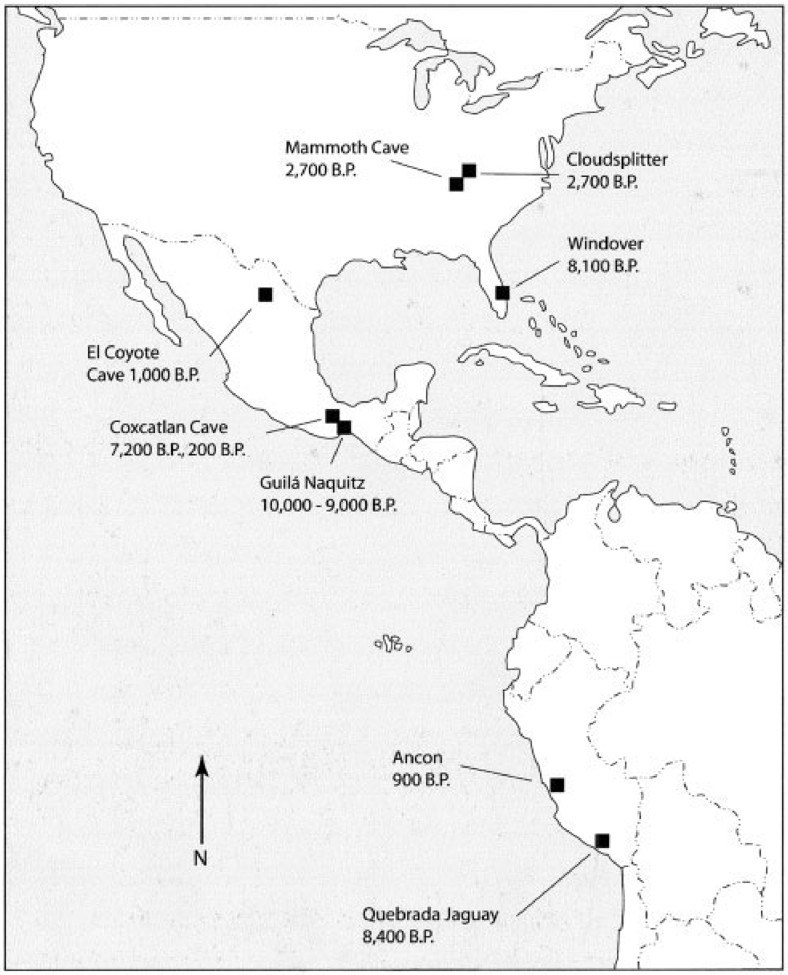
Explanations focusing on environmental change can be traced to V. Gordon Childe, who credited post-Pleistocene aridification with bringing humans together with plants and animals around water sources in positions of “enforced juxtaposition” that promoted “symbiosis between man and beast,” resulting in domestication.[67] While climate models were largely out of favor in the 1960s through 1980s, recent advances in paleo-environmental reconstruction have resulted in its rehabilitation as a primary player in agricultural origins. In particular, the now well-documented brief return to Ice Age conditions at about 13,000 cal. B.P., known as the Younger Dryas, is increasingly featured as having played a key role in agricultural origins,[68] with domestication coming about either during this climatic downturn as a way of coping with environmental degradation[69,70] or after it as a response to the following climatic amelioration and stabilization.[71] One recent climate based model of agricultural origins even maintains that agriculture was a “compulsory” development of climatic stabilization and rise in ambient CO^2 following the final pulse of Ice Age climate in the Younger Dryas.[72]

Explanatory frameworks founded on notions of population dynamics and resultant resource pressures can be traced back to Binford’s Edge-Zone Hypothesis of the late 1960s.[73] According to this theory, agricultural origins were the result of resource pressure in marginal zones caused by emigration from more optimal zones experiencing high rates of population growth. Mark Cohen’s[74] subsequent “food-crisis” model held that runaway population growth worldwide, not just in marginal zones, forced people around the planet to abandon more nutritious hunting and gathering strategies and assume the burden of tending to domesticated plants and animals. Binford’s[75] recent return to the topic down-plays the role of population growth, resource pressure, and emigration, and instead highlights population packing, in particular a threshold limit of 9.098 people per 100 km^2 as the “universal conditioner of change in . . . subsistence strategies” and the *deus ex machina* of agricultural origins.

Although explicitly rejecting universal normative explanations of domestication and agricultural origins, those operating under the general rubric of human behavioral ecology (HBE) also feature resource pressure as a primary causal component.[76] A basic axiom of HBE models is that humans will always opt for strategies that optimize immediate returns from high-ranking resources, with the relative rank of a resource determined by kilocalorie return over pursuit and handling costs.[77] Food production violates these central principals. First of all, farming involves a rise to prominence of low-rank plant resources, while herding requires deferring the rewards from high-rank animal resources.[78,79] Moreover, farming and herding are often seen as carrying higher production and processing costs than do hunting and gathering.[80] A recent review highlights different paradigms within HBE that might be helpful in understanding the transition from foraging to farming, such as concepts of constrained optimization, marginal value, opportunity costs, discounting, and risk-sensitivity.[76] Diet-breadth models that include avenues for plant resources of lower profitability to elevate their rank through changes in density or extraction return hold particular promise here. However, even allowing for such advances up the resource-rank ladder, HBE models generally predict that plant resources will largely be ignored so long as animal protein, a more highly ranked resources, is sufficiently abundant.[78] By necessity, then, strict adherence to the basic axiomatic tenets of HBE casts the transition to food production in terms of rather bleak cost-benefit trade-offs. Following HBE principles, agriculture comes about when people, faced with pressure on resources, whether caused by fluctuating climates, population growth, or packing, are forced to focus on resources and extraction strategies that under other circumstances would be considered far from optimal.

Other theorists deny that external factors like climate change, population growth, or resource pressure have any causative role in this transition. Instead, they look to forces within the human character, especially a supposedly innate compulsion for self-aggrandizement, as primary forcing factors in the domestication of plants and animals and the transition to agriculture.[81] Perhaps the best known and most influential of these socially based explanatory approaches is that promulgated by Brian Hayden.[82,83] In contrast to a backdrop of scarcity and stress central to other models, Hayden conjures up a more Eden-like setting for the origin of plant and animal domestication, claiming that agriculture only develops in contexts of plenty, where an abundance of resources ignites a basic human predisposition for acquisition and social competition. In such settings certain particularly successful “accumulators” were able to marshal high-prestige food items and enhance their own social advantage through such mechanisms as compet-

Box 1. Gourds, Dogs, and the Peopling of the Americas



Location of archeological sites with directly dated bottle gourd fragments studied by Erickson and coworkers.[66]

The recent integration of archeological and genetic research on both the bottle gourd (*Lagenaria siceraria*) and the dog (*Canis familiaris*) has substantially clarified our understanding of the initial domestication of these two very early domesticates, as well as their late Pleistocene radiation from Asia across Beringia into the New World.[20]

The bottle gourd, indigenous to Africa and long valued as a container crop rather than as a food source, has consistently been recovered in archeological association with the earliest evidence of New World domesticated plants in many regions of the Americas. The prevalent consensus has been that *L. siceraria* was carried by ocean currents as a wild plant from Africa to South America. However, a morphological analysis comparing archeological rind fragments from sites in the Americas (Fig. 1) with recently described wild *L. siceraria* fruits from Zimbabwe showed that the much thicker archeological rinds represent domesticated plants.[66] Direct dates of these fragments indicate that domestic bottle gourd was present in the Americas by at least 10,000 years ago. Moreover, DNA recovered from nine archeological rind fragments predating the arrival of Europeans were identical to the modern Asian reference group, indicating that domesticated bottle gourds were carried to the New World during the late Pleistocene from Asia, not Africa. Although it is possible that the bottle gourd could have been carried from Asia to the Americas by the north Pacific current, it is more likely this early domesticate accompanied Paleoindian colonists as they crossed Beringia into the New World.

A parallel genetic study points to an Old World origin of the domestic dog and suggests that at least five founding dog lineages invaded North America with humans as they colonized the New World.[63] The earliest archeological evidence of domesticated dogs in the Old World, dating to ca. 13,000–17,000 B.P., comes from widely dispersed sites extending from the Near East across Eastern Europe. Although the earliest domesticated bottle gourd in the Old World dates to 8,000–9,000 B.P. in China and Japan, it is reasonable, given its arrival in central Mexico by 10,000 B.P., to estimate that it was initially domesticated in the same general time frame as the dog, ca 13,000 B.P. or earlier. Together, these studies indicate that Paleoindians entered the New World with the world's two earliest domestic species, dogs and bottle gourds, and that initial domesticates served utilitarian functions, but not as sources of food.

itive feasting. Domestic resources were especially attractive since they were more amenable to ownership and their supply could be both manipulated and appropriated. This model predicts, then, that domesticates were not, at least initially, ubiquitous dietary staples, but were, instead, more likely to be rare and desirable limited-access delicacies, of little nutritional value, used by avaricious accumulators to both display and enhance their social power.

Another stress-free theory, this one championed by Jacques Cauvin,[84] also sets the stage for agricultural origins in a time of plenty and denies economic necessity a primary catalytic role. But Cauvin looks even more inward into the human psyche for the root cause of this transition. According to Cauvin, domestication is a direct consequence of a conceptual shift in mankind's mental template from one that saw humans as part of nature to one that cast humans in a dominant position, now free to manipulate and transform nature to their liking. This profound and irreversible transformation in the way that humans saw themselves in relation to nature, codified in religious ideology, found expression in concrete ways: in art, household and community structure, and the domestication of plants and animals. A similar notion can be found in Hodder's[85] emphasis on the role of symbols and metaphors of human dominance over nature made concrete in the form of the house, as the *domus* of domestication and the crucible of community.[85]

Increasing sophistication in approaches to defining and documenting domestication make it ever more difficult to support explanatory frameworks based on any single forcing factor. This is particularly true for the Near East, where we have, arguably, the most complete record of the initial domestication of many plant and animal species.

Climate clearly played its part in agricultural origins here. Increases in rainfall and temperature following the Last Glacial Maximum at about 15,000 cal. B.P. undoubtedly contributed to the adoption of increasingly less mobile, more territorially focused strategies centered on intensive exploitation of plant resources rebounding out of glacial refugia,[70] where they had been used by humans since the Upper Paleolithic.[86,87] A subsequent pulse of cold, arid Ice Age conditions during the Younger Dryas, ca. 13,000 to 11,600 cal. B.P., was met with more mobile strategies in the Southern Levant[88,89] and, quite possibly, the initial domestication of cereal crops and pulses in well-watered oasis localities in the Northern Levant.[70] Ameliorating climates following the Younger Dryas saw the domestication of other crop plants in the Southern Levant.[86] Animal domestication seems to have come about sometime later on in the Central and Eastern Fertile Crescent.[12] A brief warming and drying climatic pulse at about 9,000 cal. B.P. coincided with the collapse of early agricultural communities in more arid parts of the Southern Levant and their proliferation throughout the rest of the Near East.[88] So while climate change played a role in domestication and agricultural origins in this region, it did not do so in the simple stimulus-response way implied by many models that award environment prime-mover status. Instead, climate change alternately helped push and pull people along a pathway toward domestication and agriculture, providing both opportunities and challenges that people across the region met in various ways depending on highly localized circumstances.

The transition from foraging to farming in the Near East clearly saw significant changes in mobility, population growth, and nucleation. But the record from the region does not support the exponential population growth and attendant impoverishment of natural resources called for in Cohen's[90] doomsday model. In the absence of settlement-pattern data robust enough to demonstrate that his population-packing Rubicon (9.098 people per 100 km^2) had been crossed, Binford pointed to the clear reduction in mobility, intensification in plant resource use and development of storage technology during the postglacial era in the Near East as proxy evidence of packing.[75] This troubling circularity of using the proposed results of packing as evidence of packing is found in many such demographic models.[91] While population clearly increased, the admittedly incomplete settlement-pattern data do not support the level of population packing that Binford grants exclusive causality for increasing sedentism, intensification of resource use and, ultimately, domestication. It is also hard to make a case that the initial focus on rebounding populations of cereals, pulses, and nut trees after the Glacial maximum was caused by widespread depletion in higher ranking animal resources, as is required by most HBE models.[89]

Rather than being forced to settle down and focus on less desirable resources, it seems more likely that people took advantage of newly abundant high-yield plant resources and associated herbivores in ways that enabled them to increase the size and duration of community nucleation beyond that possible under Ice Age conditions. It is also possible that when people were faced with localized pressures on resources resulting from more sedentary ways of living, an interest in preserving the bonds of community provided an important incentive for the development of strategies that helped promote the yield and predictability of these resources. Moreover, these same social considerations also probably helped guide the subsequent responses to region-wide pressures caused by the climatic squeeze of the Younger Dryas and the stabilization of climate that followed.

Yet while it is possible to award social factors a more active role in the origins of agriculture in the Near East, the record from the region clearly does not support Brian Hayden's[82,83] competitive feasting model. Even those with the loosest tether to reality would have a hard time seeing cereals, the earliest and most important domesticates in the region, as anything but widely available staple resources. And while there is some evidence for feasting on large numbers of animals,[92] no credible case can be made for Hayden's[83] blanket assertion that meat was consumed only within controlled ritual contexts. Moreover, all of the indicators of status differentiation and unequal appropriation of social and economic prestige that Hayden sees as material manifestations of his greedy accumulators have since been more convincingly cast by Kuijt[93] and others as evidence of mechanisms for maintaining an equalitarian status quo in the face of mounting social tensions incurred when larger groups stay together for longer periods of time.[93]

Kuijt maintains, however, that domestication played little role in these social developments, either as a cause or a consequence.[94] He bases this conclusion on the fact that morphologically altered domesticates appear in the archeological record of the Levant

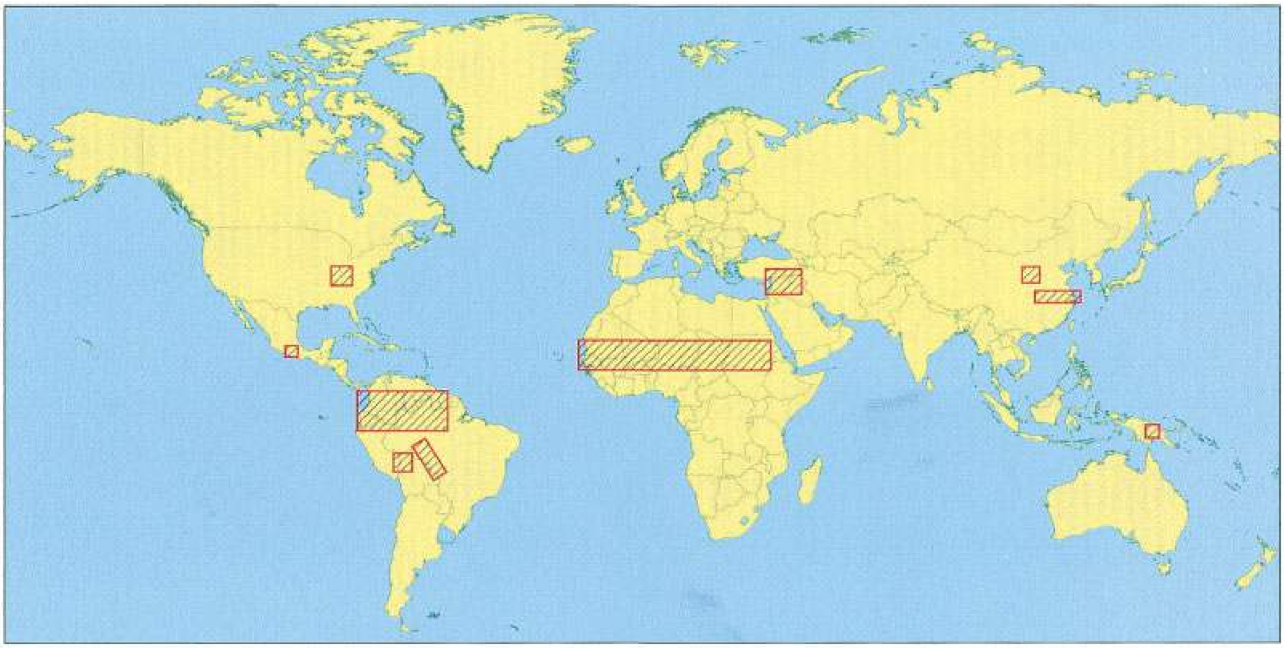


Figure 5. Boxes indicate the general location of centers of independent plant or animal domestication. Currently, at least ten such centers are recognized around the world, making research on the origins of agriculture a truly world-wide enterprise. Future research will, no doubt, discover others.

several thousand years after the first signs of leveling mechanisms for promoting social cohesion in the Natufian and at least a thousand years before their ultimate collapse and the emergence of social inequality in the Late Pre-Pottery Neolithic. Like others who use the appearance of morphological domesticates as a threshold moment in their causal scenarios,[84] Kuijt makes the common mistake of conflating morphological change with domestication. Once the artificial boundary crossing of morphological change is removed and focus is more properly placed on the evolving relationship between humans and plants and animals, then a more complex and ultimately more satisfying picture emerges of the synchronous and mutual reinforcing social and economic forces that shaped the Neolithic Near East.

The partnership between humans and resurgent plant and animal resources that began the domestication process after the Last Glacial Maximum provided the measure of resource security and predictability needed to establish nucleated sedentary communities bound together by an ethos of balanced reciprocity and increasingly elaborate rules of social order and altered world views. By the same token, the goal of maintaining community was probably a factor contributing to the subsequent intensification of evolving domestication relationships, with their attendant impacts on both the human and the plant and animal partners. The domestication process, in turn, created resources that were more amenable to ownership and restricted access, ultimately contributing to the overthrow of the egalitarian communities they initially helped foster and maintain.

Thus, rather than a single forcing mechanism, it seems more likely that the trajectory of plant and animal domestication in the Near East and the emergence of agriculture was shaped by various broad-scale factors, such as climate change, economic goals, and social opportunities and constraints, interacting with highly local, contingent factors, such as the density and diversity of available resources, the history of human occupation, and the agency of individuals coping with their environment, each other, and their universe. While the entire region was engaged in this process, the pace and the direction it took varied depending on the distinctive mix of these factors in the Southern and Northern Levant, the Central and Eastern Fertile Crescent.

A similar range of factors operating at the same time in other places on the planet took very different courses (Fig. 5). In Mexico, for example, squash, corn, and beans, apparently domesticated in different places and at different times, were minor components of mobile foraging strategies for millennia before the adoption of sedentism and the development of agricultural economies.[95] In both eastern North America and Japan, small-seeded locally domesticated annuals were blended into the diverse economic round of stable, sedentary low-level food producers for thousands of years before the introduction of domestic crop plants, maize in eastern North America and rice in Japan. Previously used in small numbers, these plants formed the foundation for the emergence of more fully agricultural economies and increasingly stratified societies.[95,96]

Thus, the story of domestication and agricultural origins consists of a series of complex regional puzzles shaped in unique ways by a dynamic multi-scalar range of macro- and micro-forces. Attempts at explanation that champion any one of these factors and deny the importance of others will not, in the long run, contribute to understanding agricultural origins either as a general process or as it played out in particular instances.

CONCLUSIONS

As this review demonstrates, central questions about the definition, documentation, and explanation of domestication are not easily answered. Domestication cannot be simply defined as either a biological or a cultural phenomenon, but rather needs to be seen as a form of biological mutualism transformed by the highly developed human capacity to effect behavioral change through learning and cultural transmission. Definitional approaches to domestication are most effective, then, when they focus on the evolving relationship between humans and target plant or animal populations as a nexus between biology and culture, not on the manifestations or consequences of such relationships. Genetic and related morphological changes in domesticates are not defining features of domestication, but are instead artifacts of evolving relationships that vary in their intensity and pace of development. Notions of ownership and restructuring of social relations are similarly best viewed as possible results of domestication, not as central to its definition. Nor are the clear-cut thresholds that define when wild resources become domesticated ones. Rather than looking for definitive either-or boundary conditions in defining domesticates, it is much more profitable, if more challenging, to look at the whole span of evolving domestic relationships as they operate over various scales of investment on the part of both human and plant or animal partners.

There are also no easy, universally applicable ways to document domestication. Instead, documenting domestication requires a clear understanding of the species-specific linkage between a proposed marker of domestication and the stage of the unfolding domestication process it is held to mark. It also requires recognizing that markers vary depending on the biology of the species involved and the cultural context of human populations engaged in the domestication process. Above all, effective documentation means not letting the availability of new scientific techniques lead the search for new markers without first thinking about how the process of domestication might manifest itself in whatever these techniques are designed to measure.

So, too, causal scenarios that narrowly focus on single, universally applicable prime-mover levers of change will never provide satisfying answers to the critical “why” questions about the origins of domestication and subsequent agricultural emergence. It is easy when dealing with complex and extended processes to draw artificial thresholds that help make the case for the primacy of whatever variable one is sponsoring as the cause of events that follow, whether it be climate change, population increase, or social and ideological transformations. Yet we have gained too sophisticated an understanding of the process of domestication and the means of detecting it to support the kind of drive-by theorizing that selectively chooses accommodating bits of information from individual regional scenarios to support a favored epistemology *de jour*. Advances in answering “why” questions about domestication and agricultural origins can only be gained through close-grained understanding of complex multi-scalar regional puzzles and assessment of the commonality and the differences in the way the pieces of these different puzzles fit together.[16,97]

There are, then, no easy answers to central questions about domestication and agricultural origins. It is no wonder that for more than 100 years this area of inquiry has held the attention of archeologists working worldwide and representing all of archeology’s many and rapidly increasing subdisciplines. It is a research domain that carries broad currency with scholars based in biological and physical sciences, social sciences, and humanities. It is a topic that captures the imagination of a public interested in how the familiar world around them came to be. It is a problem that truly matters. With an enhanced understanding of the nature of the problem and an expanding array of powerful tools for studying it, there has never been a time of greater promise for pursuing challenging questions about the origin and diffusion of domesticates and agricultural economies in virtually all areas of the globe.

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