

From wild animals to domestic pets, an evolutionary view of domestication

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Abstract

Artificial selection is the selection of advantageous natural variation for human ends and is the mechanism by which most domestic species evolved. Most domesticates have their origin in one of a few historic centers of domestication as farm animals. Two notable exceptions are cats and dogs. Wolf domestication was initiated late in the Mesolithic when humans were nomadic hunter-gatherers. Those wolves less afraid of humans scavenged nomadic hunting camps and over time developed utility, initially as guards warning of approaching animals or other nomadic bands and soon thereafter as hunters, an attribute tuned by artificial selection. The first domestic cats had limited utility and initiated their domestication among the earliest agricultural Neolithic settlements in the Near East. Wildcat domestication occurred through a self-selective process in which behavioral reproductive isolation evolved as a correlated character of assortative mating coupled to habitat choice for urban environments. Eurasian wildcats initiated domestication and their evolution to companion animals was initially a process of natural, rather than artificial, selection over time driven during their sympatry with forbear wildcats.

Darwin famously first described natural selection in 1859 with his classic monograph *On the Origin of Species*. Sexual selection was addressed in *Descent of Man, and Selection Related to Sex* in 1871. In between those two, in 1868, Darwin published a 2-volume work, *The Variation of Animals and Plants Under Domestication*, in which he expands upon a third distinct stream of evolutionary mechanism—artificial selection—that he first had outlined in *Origin*.

Natural vs. Artificial Selection

Artificial selection is unique in that, as the name suggests, it is wholly unnatural. That insight seems at first trivial, but reflection reveals just how extraordinary and fundamental artificial selection (manifest as domestication) has been to human success as a species. It was no more than 12,000 years ago that humankind began to consciously harness the 4-billion-year evolutionary patrimony of life on Earth. Exploiting the genetic diversity of living plants and animals for our own benefit gave humans a leading role in the evolutionary process for the first time. Agricultural food production

(*sensu lato*, including animal husbandry) has allowed the human population to grow from an estimated 10 million in the Neolithic to 6.9 billion today, and still expanding (1). Today, 4.93 billion hectares are used for agricultural practices, which also account for 70% of all fresh water consumed (2). The world's species are going extinct at a rate 100–1,000 times faster than the historic “background” rate, primarily as a result of habitat loss, which is itself overwhelmingly driven by conversion of natural habitats to agriculture. However, to date no domestic animal has gone extinct (3). The consequences for the planet (as well as for humanity and its domesticates) have been profound, and have included the complete transformation of almost every natural ecosystem on Earth.

Domesticating animals and plants brought surpluses of calories and nutrients and ushered in the Neolithic Revolution. However, the Neolithic Revolution involved more than simple food production; it was also the growth of an agricultural economy encompassing a package of plant and animal utilization that allowed for the development of urban life and a suite of innovations encompassing most of what we today think of as culture (4, 5). Much of modernity is an indirect consequence of artificial selection. The plow has come to symbolize the Neolithic Revolution, but viewing history in the light of evolution we see that it was intelligently designed changes to the genetic composition of natural biota that made the real tools. In some sense, Neolithic farmers were the first geneticists and domestic agriculture was the lever with which they moved the world.

Variation of Animals and Plants Under Domestication

Modern summaries (and this colloquium) arrange the drivers of “descent with modification” into natural, sexual and artificial selection, but Darwin's conceptual organization was somewhat different from our own. He saw sexual selection as a part of natural selection, and artificial selection as a coin with 2 sides, one he called Methodical and the other Unconscious (6). Unconscious selection supposes no conscious wish or expectation to permanently alter a breed, whereas Methodical selection is guided by some predetermined standard as to what is best; intention therefore is the substantial difference (6). This distinction has largely lapsed in today's debate, although Darwin thought it worth discussing.

We perceive today, as did Darwin, that natural selection is the environmentally driven mechanistic process by which more advantageous traits are, on the whole, passed on to succeeding generations more often than less advantageous traits because of differential reproduction of the individuals possessing them. Sexual selection is a natural process of intraspecific competition for mating rights. Artificial selection, generally the motive force behind domestication, is often equated with selective breeding. This often amounts to prezygotic selection (where mates are chosen by humans) versus postzygotic selection (where the most fit progeny reproduce differentially) as in natural selection. Although natural selection plays a considerable role in the evolution of many traits (e.g., disease resistance) during the animal domestication process, sexual selection is effectively trumped by the human-imposed arrangements of matings and often by the human desire for particular secondary sexual characters. Artificial selection is a conscious, if unintentional, process, and therefore is generally considered to be effected only by humans (but see ref. 7).

We suggest that artificial selection has both a “weak” and a “strong” form. In weak artificial selection, selection pressure is applied postzygotically (selectively culling a herd of deer, for example) and natural selection proceeds from this modified genetic baseline. In strong artificial selection, selection is prezygotic, as well as postzygotic (for example, mating male offspring of high yielding dairy cows to high yielding cows). This will result in a dramatic acceleration of evolutionary processes and entailing a much greater level of control over the selected organism.

Darwin's *The Variation of Animals and Plants Under Domestication* (6) offers a litany of facts and examples of artificial selection in action at the hands of plant and animal breeders. Darwin felt that an understanding and appreciation of the depth of artificial selection was fundamental to the acceptance of natural selection. In *Variation*, Darwin wanted to expand on this artificial mechanism of evolution beyond examples in *Origin*, where he describes familiar and tangible results of husbandmen in his argument that selection by the analogous natural means—survival of the fittest—was not just plausible or possible, but probable. Darwin considered any variety, breed or subspecies, no matter how it was derived, as an incipient species, irrespective of the particular selective mechanism driving the group's evolution (6). He sought to illustrate that tremendous changes can be wrought through the “gradual and accumulative force of selection,” but he also emphasized that evolution by selection of any type can only work where variation is present; “The power of selection ... absolutely depends on the variability of organic beings” (6). Thus, genetic differences between domesticates and their wild counterparts substantially reflect the native genetic variation (i.e., standing variation) present in the wild population before any selection (natural or artificial) for tameness, and the secondary effects of isolation (6).

Through the plethora of examples laid out in *Variation*, Darwin was making a case that the consequences of artificial selection are similar in spirit to those of natural selection, but, moreover, that artificial selection (whether methodical or unconscious) was practiced a very long time ago. Darwin further suggested that there had been little need for humans to understand the mechanism of artificial selection, so long as the process operated effectively and produced tangible results.

Domestication Generally

Are domesticated strains separate species (either from one another, or from their wild ancestors)? The answer generally is “no,” under the conceptual framework of the Biological Species Concept (8–12). Breeds typically are interfertile and intercross if given the opportunity. When domesticates are sympatric with populations of the parent wild species (if the latter still persist), gene flow generally can occur. When is an animal truly domesticated? Hard definitions are elusive because domestication is a continuous transition, attributes differ by species, and genes and environment interact to produce selectable characters that may vary with circumstance (13). However, an interconnected and characteristic suite of modifiable traits involving physiology, morphology and behavior are often associated with domestication (13–16). Critically, all domesticates manifest a remarkable tolerance of proximity to (or outright lack of fear of) people. Reproductive cycle changes such as polyestrousness and adaptations to a new (and often poorer) diet are typical (16). Common physical and physiological recurrences among domesticated mammals include: dwarfs and giants, piebald coat color, wavy or curly hair, fewer vertebrae, shorter tails, rolled tails, and floppy ears or other

manifestations of neoteny (the retention of juvenile features into sexual maturity) (17). Behaviorally too, domestication is not a single trait but a suite of traits, comprising elements affecting mood, emotion, agnostic and affiliative behavior, and social communication that all have been modified in some way.

The appreciable metabolic and morphological changes that often accompany behavioral adaptation to the human environment usually lead to a significant dependence on humans for food and shelter. However, domestication should not be conflated with taming. Taming is conditioned behavioral modification of an individual; domestication is permanent genetic modification of a bred lineage that leads to, among other things, a heritable predisposition toward human association. And domestic animals need not be “tame” in the behavioral sense (consider a Spanish fighting bull) and, conversely, wild animals can be quite tame (consider a hand-raised cheetah or tiger). A domestic animal is one whose mate choice is influenced by humans and whose tameness and tolerance of humans is genetically determined. Controlled breeding amounts to prezygotic selection, a critical element to domestication (because captive breeding allows for the strongest, most direct artificial selection). However, an animal merely bred in captivity is not necessarily domesticated. Tigers, gorillas, and polar bears breed readily in captivity but are nevertheless not “domesticated.” Likewise, Asian elephants are wild animals that with taming manifest outward signs of domestication, yet their breeding is not human controlled and thus they are not true domesticates (18).

Neolithic World of the Fertile Crescent

Most of today's domesticates began as food, but all domesticates, including dogs and cats, have one thing in common: They are all tolerant of people. Where, how, and why did this tolerance develop? To understand this phenomenon, we have to step back to a time when humans began living in settled groups.

Accumulated archaeological, cultural and genetic evidence points to the Terminal Pleistocene ($\approx 12,000$ years ago) in the Fertile Crescent (Fig. 1) as the primary locus of domestication for many western domesticates (3, 5, 17, 19–22). Estimated dates for these events range from 15,000 years B.P. for the dog to 8,000 B.P. for cattle (Table 1). The term Fertile Crescent was coined by James Henry Breasted who characterized the region by both ecological and cultural features present at the time of earliest civilization (23). In his conception, the Fertile Crescent extends from the Mesopotamian plains, through the Taurus mountains and along the Mediterranean coast to the Levant, and does not include Egypt (Fig. 1). Here, hunter-gatherers first became sedentary, domesticated plants and animals, developed agriculture, and built urban villages—the suite of cultural innovations and consequences known as the Neolithic Revolution. The Fertile Crescent during the terminal Pleistocene was much different from the thorny, overgrazed scrub that is present today. Gazelle and deer, wild cattle, boar, horses, and goats and sheep flourished through an oak/pistachio parkland (4, 17). Among the hundred or so species of edible seeds, leaves, fruits, and tubers, there were thick natural stands of cereals (barley, einkorn and emmer wheat) and pulses (pea, chickpea, lentil), which provide a rich source of calories and a balance of nutrients. Together with flax (used for fiber) and bitter vetch, these plants would later form a package that became our 8 founder crops (20). For $>100,000$ years, humans had been nomadic hunter-gatherers. However,

because the Fertile Crescent was so bountiful, the inhabitants of the Levant at this time (known archaeologically as Natufians) were able to hunt and gather all they needed with only short forays from base camps; they became a “hunter–gatherer elite” (4). Over time, movable camps evolved into permanent semisubterranean pit–houses where (we suppose) the Natufians stored wild grains for use throughout the year (4).

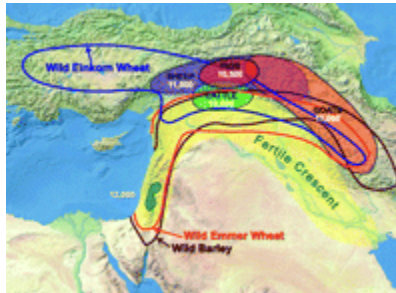


Fig. 1.

Map of the Near East indicating the Fertile Crescent (according to ref. 23). Shaded areas indicate the approximate areas of domestication of pig, cattle, sheep, and goats with dates of initial domestication in calibrated years B.P. (after ref. 3). Colored lines enclose the wild ranges of Einkorn wheat, emmer wheat, and barley (after ref. 21). Green-shaded area in southern Levant indicates the region where all 3 grains were first domesticated 12,000 years B.P.

Between 13,000 and 11,000 B.P. the Natufian hunter–gatherers developed tools such as the sickle and grinding stones to harvest and process wild grains (4). Subsequently (11,000 to 10,300 B.P.), a cold and dry period reduced the available wild plant food and increased the Natufian's dependence on cultivated grasses and legumes (the founder crops mentioned above). This climatic shift, called the Younger Dryas event, may have been the trigger for a change in emphasis away from hunting–gathering and toward true agriculture via improvised cultivation. With a reliable food source, human populations begin to rise, technology for collecting grains further improved, and settlements initially encouraged by naturally abundant food led to larger settlements. Although hunter–gatherers throughout the world had long manipulated plants and animals (for instance by using fire to encourage edible plants or animals that thrive on disturbed land), Neolithic agriculture moved well beyond the raising and harvesting of plants and animals and into an entrenched economic system enforced by labor demands and ecological transformations. Productive land, now the predominant venue for food supply and valued at a premium, would be cultivated and defended year round. This commitment to an agricultural life entailed permanent buildings and facilities for storing surpluses of food, and it created the first farm communities.

Domestication of today's barnyard animals proceeded as a result of pressure by these early hunter–gatherers as they intuitively sought to stabilize their food resources (17, 24, 25). Among the successful domesticates, most were behaviorally preadapted to domestication. Behavioral characteristics considered favorable and unfavorable are presented in Table 2. Barnyard animals descend from herd–living herbivores whose ancestors followed a dominant individual through a territory shared with other herds. Neolithic peoples exploited this dominance hierarchy by, in effect, supplanting the alpha individual and thereby gaining control of the herd. Herd–living animals were

predisposed to tolerate close living quarters, and their temperament allowed them to adapt easily to confinement. They also had a flexible diet (enough to live on what early farmers might provide), grew fast (and thus did not unduly expend farmers' resources), and would freely breed in the presence of people (16, 17, 19). A comparison of the occurrence of preadaptive characters among wild species of the Fertile Crescent is presented in Table 3. The predecessors of today's farm animals were undoubtedly selectively managed in hunts in natural habitats (corresponding to our weak artificial selection) before individuals were taken into captivity and bred (6, 17, 24, 25). Animals that bred well could then be selected (either consciously or unconsciously) for favorable traits (corresponding to our strong artificial selection). Domestication in these cases is a mixture of artificial selection (both weak and strong) for favorable traits and natural selection for adaptation to captivity, with artificial selection being the prime mover.

Domestication of Dogs

The domestication of dogs and cats (today's two most popular companion animals) was a bit different from the barnyard animals. And although Darwin began *Variation* with a discussion of the dog and cat, the two could hardly be more different from each other (or from contemporary barnyard domesticates) in temperament, utility, and evolutionary origin. Farm animals were food items ("walking larders") brought into the human sphere at the transition point from hunting-gathering to agriculture (17). Dogs, the earliest domesticate, proved useful as guards and as hunters for the hunting-gatherers, and perhaps offered necessary lessons for subsequent domestication of other species (26). By contrast, cat domesticates arose much later ($\approx 10,000$ B.P.), after humans built houses, farms, and settlements.

The preponderance of molecular evidence points to an origin of dogs from the wolf, *Canis lupus* (27, 28). The molecular findings are also supported by a large body of archaeological evidence that implicates the Near East as a likely locus of definitive domestication [although dog domestication may have begun in Central Europe as early as the Upper Late Paleolithic (17, 26)]. Wolf domestication is seen as the result of 2 interwoven processes originating $>14,000$ years ago during our hunter-gatherer nomadic period (29). First, a founder group of less-fearful wolves would have been pulled toward nomadic encampments to scavenge kills or perhaps salvage wounded escapees from the hunt. Thereafter, these wolves may have found utility as barking sentinels, warning of human and animal invaders approaching at night (30). Gradually, natural selection and genetic drift resulting from human activities began to differentiate these wolves from the larger autonomous population. Once people had direct interaction with wolves, a subsequent, "cultural process" would have begun. Suitable "preselected" wolf pups taken as pets would have been socialized to humans and unconsciously and unintentionally selected for decreased flight behavior and increased sociality (26), 2 trademarks of tameness. Eventually, people established control over proto-dog mating. From this point forward the wolf in effect became a dog, under constant observation and subject to strong artificial selection for desired traits. Selection for tameness entails morphological and physiological changes through polygenes governing developmental processes and patterns (26, 31), and these provide grist for the mill of further iterations of selection. For wolf domestication, the phases of natural and artificial selection blend one into the other, eventuating in "man's best friend" with doting and obedient behaviors. Although dogs have been prized as household companions for

thousands of years, the wide phenotypic variation of modern dog breeds began more recently (3,000–4,000 B.P.), leading to the ≈ 400 breeds recognized today by the Dog Breeders Associations (32).

Domestication of Cats

The domestication of cats took a different trajectory. Wildcats are improbable candidates for domestication (see Table 3). Like all felids, wildcats are obligate carnivores, meaning they have a limited metabolic ability to digest anything except proteins (33). Cats live a solitary existence and defend exclusive territories (making them more attached to places than to people). Furthermore, cats do not perform directed tasks and their actual utility is debatable, even as mousers (34). [In this latter role, terrier dogs and the ferret (a domesticated polecat) are more suitable.] Accordingly, there is little reason to believe an early agricultural community would have actively sought out and selected the wildcat as a house pet. Rather, the best inference is that wildcats exploiting human environments were simply tolerated by people and, over time and space, they gradually diverged from their “wild” relatives (35, 36). Thus, whereas adaptation in barnyard animals and dogs to human dominion was largely driven by artificial selection, the original domestic cat was a product of natural selection.

A comprehensive genetic examination of the *Felis silvestris* species complex by our group revealed the relationships between domestic cats and their indigenous wild congeners (37). We typed 36 short tandem repeat loci and sequenced 2.6 kb of the mitochondrial genes ND5 and ND6 in ≈ 1000 cats from wild and domestic settings, including representatives of registered-breed and random-bred pet cats from both feral and household environments. Phylogenetic and clustering analyses identified 5 genetically distinctive *F. silvestris* wildcat subspecies (Fig. 2) present in: Europe (*F. silvestris silvestris*, clade I), Southern Africa (*F. silvestris cafra*, clade II), Central Asia (*F. silvestris ornata*, clade III), the Near East (*F. silvestris lybica*, clade IV), and the northern edge of the Tibetan plateau (*F. silvestris bieti*, clade V). Local wildcat populations retained genetic signatures that tied them to their respective regions (Fig. 2A). In contrast, the world's domestic cats carried genotypes that differentiated them from all local wildcats except those from the Near East. Domestic cats show no reduction in genetic diversity compared with the wild subspecies (37), thus giving no indication for a founding genetic bottleneck. Multiple genetic analyses produced concordant results, in each case tracing the maternal origins of cat domestication to at least 5 wildcat lines (A through E, Fig. 2B) originating in the Near East. The domestic cat is referred to as a sixth subspecies, *F. silvestris catus*, although it is clear that domestic cats derive very recently from *F. silvestris lybica* (37).



Fig. 2.

Distribution of *F. Silvestris* microsatellite and mitochondrial genotypes with associated dendrograms. (A) Shaded regions on map reflect the distribution of different STR genotype clades. mtDNA haplotype frequencies are indicated in pie charts specifying the number of specimens carrying each mtDNA haplotype clade. Domestic cats, *F. silvestris catus* are distributed worldwide and overwhelmingly carry clade IV mtDNA haplotypes (beige, see B below). (B) Minimum evolution/neighbor-joining phylogram of 2,604 bp of the ND5 and ND6 gene of 176 mitochondrial haplotypes discerned from 742 specimens sampled across the range of the wildcat (from Europe, Asia, and Africa), Chinese mountain cat, domestic cat, and sand cat. Genetic distance estimators (see ref. 37 for details) provided concordant topologies that specified 6 clusters corresponding to the following subspecies designations: (1) *F. silvestris silvestris* wildcats from Europe (green, Clade I); (2) *F. silvestris cafra* wildcats from Southern Africa (blue, Clade II); (3) *F. silvestris ornata* wildcats from central Asia east of the Caspian Sea (purple, Clade III); (4) *F. silvestris lybica* wildcats from the Near East (beige, Clade IV); (5) *F. silvestris bieti*, Chinese mountain cats (red, Clade V); and (6) *F. margarita*, sand cat (black, Clade VI). The Chinese mountain cat is here referred to as a wildcat subspecies, *F. silvestris bieti*, as supported by data presented in ref. 37. The coalescence-based age of mtDNA ancestral nodes for all *F. silvestris* mtDNA lineages was estimated with the linearized tree method (58). The estimated age for the ancestor of *F. silvestris lybica* and domestic cats (clade IV) is 131,000 years. Other methods of date estimation suggested a range from 107,000 to 155,000 years (37). These estimates are all greater by an order of magnitude than archaeological evidence for cat domestication (39). The persistence within clade IV of 5 well supported mtDNA matriline (A–E) dating back a hundred thousand years before any archaeological record of domestication indicates that domestic cats originated from at least 5 wildcat mtDNA haplotypes. (C) A phenogram (based on short tandem repeat (STR) data) for 851 domestic and wild specimens of *Felis silvestris*. Clade designations as in B.

Cat domestication dates to at least 3,600 B.P., when what are clearly house cats are depicted in tomb paintings of the Egyptian New Kingdom (17, 38). However, the oldest archaeological evidence of cat taming dates to $\approx 9,500$ B.P. in Crete (39) and cat remains have also been dated to 8,700 B.P. from Jericho (19). Given that, a reasonable window for cat domestication is 9,500–3,600 B.P.. However, we estimated a coalescence date of 131,000 years ago for the *catus/lybica* mtDNA clade (37). This date is greater by at least an order of magnitude than any plausible domestication event but can in principle be explained by multiple maternal-lineage recruitments from the wild source population (40). Considering the broadest range of dates for domestication to be from 11,000 to 4,000 B.P., and applying an internally calibrated mutation rate for cat mitochondrial DNA (mtDNA) (41), we expect 0–3 mutations over the 2.6 kb mtDNA surveyed in modern domestic cats (37). We note that $\approx 90\%$ of domestic cats share haplotypes that are 1 nucleotide diverged from each other, a finding that is consistent with these mutations having occurred very recently. Domestic cat mtDNA is therefore expected to have few, if any, widely divergent domestic-specific haplotypes. Our sample, in effect, represents a sampling of the source wildcat population's mitochondrial genetic diversity. In sum, the genetic evidence appears to be most consistent with a single protracted domestication episode, one incorporating multiple wildcat matriline over the broad Near Eastern human cultural

area. We feel this development can best be understood in the context of agricultural development patterns. The following scenario for cat domestication seems likely.

Sympatric Divergence and Plural Mitochondrial Origins

The available archaeological evidence indicates that the process of wildcat domestication began in the Neolithic in the same place and time as the development of year-round settlements and the onset of an agricultural economy (37–39). As far as the local fauna was concerned, these permanent human settlements developed *ex nihilo*. Opportunistic animals apparently ventured into this new urban environment, rich in food year-round and free of most predators, and found fertile new ecological niches to exploit (14, 19). The ability to live around people therefore conferred important advantages to those animals that adapted to it (15). Commensal species such as mice, rats and sparrows that adapted to human village environs (and their trash), probably emerged first. Although the earliest grain cache (of wild, not domestic, grains) in the Near East is dated to 21,000 B.P. (42), the origin of agriculture per se in the region is dated to between 12,500 and 11,250 B.P. (43), and it is from approximately this period that house mice locally appeared (44). Resident populations of peridomestic rodents sustained by trash dumps and stockpiles of grain provided a reliable food source for native wildcats, which then became adapted to an “urban” environment as peridomestic human commensals themselves (45, 46).

Cereal domestication in the Fertile Crescent is characterized by multiple independent domestication of multiple grain species in multiple centers from the southern Levant through Syria to southern Anatolia (47). If cat domestication is largely a sequela of the development of towns (enhanced by the domestication of grains), divergent mitochondrial lineages (A–E in Fig. 2B) may not be unexpected, because recruitment of naturally occurring wildcat mitochondrial lineages would reflect the wide distribution of human settlements. Bearing in mind that a mtDNA gene tree represents only a tiny subset of the species' genetic history (12, 48), and considering domestication as a polygenic trait affecting behavior (31), the polygenic allelic series behind domesticity and mtDNA need not have congruent histories. Over time and space, multiple wildcat matrilineages would have been incorporated into the domestic cat gene pool through the admixture of an initial domesticate with additional wild female conspecifics, thereby spreading genes for the domestic phenotype through the early Fertile Crescent agricultural area. Thus, the relatively profound depth (131,000 years) of the *catus/lybica* clade may be best explained by a protracted wildcat domestication process that spanned thousands of years and extended over much of the Fertile Crescent (Fig. 1). The alternative hypothesis—of multiple independent domestication events—seems unlikely for 2 reasons: First, the vast majority of sampled domestic cats fall into the same mtDNA clade, which also includes *F. silvestris lybica*; and second, the clade lacks biogeographic structure. Individual house cats from any one sampling area may fall into any lineage, and even the most genetically divergent lineages have domestic individuals from the same sampling area. An important validation of this hypothesis awaits the identification of the causal mutations mediating domestic behavior in cats. Finding different mutations for the tame phenotype would suggest the multiple independent invention of domestication in cats, whereas finding the identical mutation(s) in all 5 domestic cat lineages would support a single origin for the gene complex spread by population diffusion.

Taken together, these results provide both phylogenetic and phylogeographic evidence that the divergence of domestic cat from wildcat occurred sympatrically. First, with respect to phylogeny, the monophyly of distinct taxa from the same environment (domestic cat and wild cat from the Near East) (Fig. 2 *B* and *C*) is clearly consistent with sympatric divergence. Second, with respect to a phylogeography, sympatric divergence seems plausible because domestic cat and Near Eastern wildcat are phenotypically divergent (in terms of behavior) yet are more closely related to one another than Near Eastern wildcat are to more phenotypically similar allopatric groups (such as Asiatic wildcat or Southern African wildcat) (Fig. 2*A*). This scenario supposes a model of sympatric habitat–race formation in which habitat–specific beneficial mutations accumulated by assortative mating into a coherent allelic series. Importantly, this model avoids the “selection–recombination antagonism” described by Felsenstein (49), whereby genes required for mating and genes required for assortative mating must be linked, because the same genes that drive habitat choice also drive assortative mating (see ref. 50 for review).

It seems likely that behavioral genes affecting domestication were initially selected by habitat choice of individual wildcats better fit for urban life, and that these genes were later transferred to geographically disparate spots, promoted by a human preference for tameness and perhaps the translocation of these individuals. However, it is also possible that individual component polygenes contributing to domestication derive from different population recruitments as well. Each adaptive locus/allele may have been independently selected in a different Fertile Crescent population and through time these combined, each allele contributing an increasingly additive effect, until their genomic consilience in an irrefutably domestic animal. Domestication in cats could thus be an allelic series of independently selected alleles from throughout the wildcat natural range, but assembled as a composite. In an analogous fashion, modern pig and cattle breeds are routinely “improved” via the introduction of advantageous alleles through cross–breeding distant strains (descended from independent Oriental and European domestications in pigs, and from European and Southeastern Asia in cattle), rather than by independent selection of each trait within each lineage.

Is Wildcat Domestication Complete?

At its most basic, domestication is a dependence on humans for food, shelter, and control of breeding (51). Because 97% or more of the nearly 1 billion domestic cats living today are random–bred house cats, or are feral and intact, the overwhelming preponderance of domestic cats choose their own mates. Only a tiny fraction of cats (mostly those in registered breeds) have mates chosen for them (prezygotic selection). Furthermore, the majority of feral cats obtain what they eat without human assistance. Additionally, the domestic cat varies little morphologically from the wildcat body plan (52, 53), although, as Darwin noted, domestic cats have longer intestines than wildcats, a trait he attributed to a “less strictly carnivorous diet” as a result of feeding on kitchen scraps (6). So an argument can be made that cat domestication is <200 years old and may yet be incomplete (45). Domestic cats have, however, become polyestrous, and their coat colors often depart wildly from the wildcat's striped mackerel tabby. And domestication did socialize the wildcat (cats are the only domesticate that is social under domestication yet solitary in the wild). However, the most noticeable adaptation is the cat's overwhelming tolerance of people, a key attribute of any domesticated animal,

but certainly the primary feature that has made cats the delightful and flourishing profiteers in our homes that they are.

The modern domestic cat is the product of 11 million years of natural selection in a world free of people (54, 55), and 12 thousand years of natural selection in a world increasingly dominated by humanity (54, 55). In 1868, Darwin commented that there are no breeds of cats native to England because of a lack of selective breeding (6, Vol. I, p. 50 and Vol. II, p. 222). The power of artificial selection to produce modern fancy cat breeds has only recently—within the last 200 years—been brought to bear on the accumulated store of wildcat genetic variation (56, 57). But already the pace of change is quickening, and the previously uniform wildcat is found in varieties of hairless and longhair, dwarf and giant, which Darwin himself would have wondered at.

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Footnotes

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References

1. 
 1. Harris DR
 2. Groube L

(1996) in *The Origins and Spread of Agriculture and Pastoralism in Eurasia, The impact of diseases upon the emergence of agriculture*, ed Harris DR (University College London, London), pp 101–129.
2. 

1. World Resources Institute
(2000) *People and ecosystems: The fraying web of life*. Available at http://pdf.wri.org/world_resources_2000-2001_people_and_ecosystems.pdf.
3. ↵
 1. Zeder MA
(2008) *Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact*. *Proc Natl Acad Sci USA* 105:11597-11604.
[Abstract/FREE Full Text](#)
4. ↵
 1. Bar-Yosef O
(1998) *The Natufian Culture in the Levant, Threshold to the Origins of Agriculture*. *Evol Anthropol* 6:159-177.
[CrossRefISI](#)
5. ↵
 1. Vigne J-D,
2. Peters J,
3. Helmer D
4. Peters J,
5. von den Dreisch A,
6. Helmer D
(2005) in *The First Steps of Animal Domestication: New archaeological approaches*, eds Vigne J-D, Peters J, Helmer D (Oxbow Books, Oxford), p 176.
6. ↵
 1. Darwin C
(1890) *The Variation of Animals and Plants Under Domestication* (D. Appleton and company, New York).
7. ↵
 1. Vega FE
2. Schultz TR,
3. Mueller UG,
4. Currie CR,
5. Rehner SA
(2005) in *Insect-Fungal Associations*, ed Vega FE (Oxford Univ Press, New York), pp 149-190.
8. ↵
 1. Mayr E
(1942) *Systematics and the Origin of Species* (Columbia Univ Press, New York).
9. ↵
 1. O'Brien SJ,
2. Mayr E
(1991) *Bureaucratic mischief: Recognizing endangered species and subspecies*. *Science* 251:1187-1188.
[FREE Full Text](#)
10. ↵

1. O'Brien SJ,

2. Mayr E

(1991) *Response. Science* 253:251–252.

[FREE Full Text](#)

11. [↵](#)

1. Dobzhansky TG

(1937) *Genetics and the Origin of Species* (Columbia Univ Press, New York).

12. [↵](#)

1. Avise JC

(2004) *Molecular Markers, Natural History, and Evolution* (Sinauer, Sunderland, MA).

13. [↵](#)

1. Price EO

(1984) *Behavioral aspects of animal domestication. Q Rev Biol* 59:1–32.

[CrossRef](#)

14. [↵](#)

1. Coppinger RP,

2. Smith CK

(1983) *The domestication of evolution. Environ Conserv* 10:283–292.

[ISI](#)

15. [↵](#)

1. Morey DF

(1994) *The early evolution of the domestic dog. Am Sci* 82:336–347.

[ISI](#)

16. [↵](#)

1. Hemmer H

(1990) *Domestication: The Decline of Environmental Appreciation* (Cambridge Univ Press, Cambridge).

17. [↵](#)

1. Clutton-Brock J

(1999) *A Natural History of Domesticated Mammals* (Cambridge Univ Press, Cambridge, UK).

18. [↵](#)

1. Lair RC

(1997) *Gone Astray: The Care and Management of the Asian Elephant in Domesticity* (Regional Office for Asia and the Pacific, Bangkok, Thailand).

19. [↵](#)

1. Zeuner FE

(1963) *A History of Domesticated Animals* (Hutchinson, London).

20. [↵](#)

1. Bellwood

(2007) *First Farmers, the Origins of Agricultural Societies* (Wiley-Blackwell, Hoboken, NJ).

21. [↵](#)

1. Smith BD

(1995) *The Emergence of Agriculture* (W.H. Freeman, New York).

22. [↵](#)

1. Zeder MA,
2. Bradley DG,
3. Emshwiller E,
4. Smith B

(2006) *Documenting Domestication: New Genetic and Archaeological Paradigms* (University of California Press, Berkeley, CA).

23. [↵](#)

1. Breasted JH

(1916) *Ancient Times, a History of the Early World* (Ginn and Co, Chicago).

24. [↵](#)

1. Zeder MA

(2006) *Central questions in the domestication of plants and animals. Evol Anthropol* 15:105–117.

[CrossRefISI](#)

25. [↵](#)

1. Zeder MA,
2. Emshwiller E,
3. Smith BD,
4. Bradley DG

(2006) *Documenting domestication: The intersection of genetics and archaeology. Trends Genet* 22:139–155.

[CrossRefMedlineISI](#)

26. [↵](#)

1. Vigne JD,
2. Peters J,
3. Helmer D
4. Muller W

(2002) in *The First Steps of Animal Domestication*, eds Vigne JD, Peters J, Helmer D (Oxbow Books, Oxford), pp 34–40.

27. [↵](#)

1. Vila C,
2. et al.

(1997) *Multiple and ancient origins of the domestic dog. Science* 276:1687–1689.

[CrossRefMedlineISI](#)

28. [↵](#)

1. Leonard JA,
2. et al.

(2002) *Ancient DNA evidence for Old World origin of New World dogs. Science* 298:1613–1616.

[Abstract/FREE Full Text](#)

29. [↵](#)

1. Serpell J

2. Clutton-Brock J
(1995) in *The Domestic Dog: Its Evolution, Behaviour, and Interactions with People*, ed Serpell J (Cambridge Univ Press), pp 7-20.
30. ↵
1. Lindsay SR
(2000) *Handbook of Applied Dog Behavior and Training* (Iowa State Univ Press, Iowa).
31. ↵
1. Trut LN
(1999) *Early canid domestication: The farm-fox experiment*. *Am Sci* 87:160-169.
[CrossRefISI](#)
32. ↵
1. Fogle B,
2. Morgan T
(2000) *The New Encyclopedia of the Dog* (Dorling Kindersley, New York), 2nd Ed.
33. ↵
1. Bradshaw JWS,
2. Goodwin D,
3. Legrand-Defretin V,
4. Nott HMR
(1996) *Food selection by the domestic cat, an obligate carnivore*. *Comp Biochem Physiol A Comp Physiol* 114:205-209.
[Medline](#)
34. ↵
1. Elton CS
(1953) *The use of cats in farm rat control*. *Br J Anim Behav* 1:151-155.
[CrossRef](#)
35. ↵
1. Wandeler P,
2. Funk SM,
3. Largiadere CR,
4. Gloor S,
5. Breitenmoser U
(2003) *The city-fox phenomenon: Genetic consequences of a recent colonization of urban habitat*. *Mol Ecol* 12:647-656.
[Medline](#)
36. ↵
1. Driscoll CA,
2. Clutton-Brock J,
3. Kitchener AC,
4. O'Brien SJ
(2009) *The taming of the cat*. *Sci Am* 300:68-75.
[MedlineISI](#)
37. ↵
1. Driscoll CA,

2. et al.

(2007) *The Near Eastern origin of cat domestication. Science* 317:519–523.

[Abstract/FREE Full Text](#)

38. ↵

1. Clutton-Brock J

(1993) *Cats, Ancient and Modern* (Harvard Univ Press, Cambridge, MA).

39. ↵

1. Vigne JD,

2. Guilaine J,

3. Debue K,

4. Haye L,

5. Gerard P

(2004) *Early taming of the cat in Cyprus. Science* 304:259.

[FREE Full Text](#)

40. ↵

1. Jones M,

2. Brown T

(2000) *Agricultural origins: The evidence of modern and ancient DNA. Holocene* 10:769–776.

[Abstract/FREE Full Text](#)

41. ↵

1. Lopez JV,

2. Culver M,

3. Stephens JC,

4. Johnson WE,

5. O'Brien SJ

(1997) *Rates of nuclear and cytoplasmic mitochondrial DNA sequence divergence in mammals. Mol Biol Evol* 14:277–286.

[Abstract](#)

42. ↵

1. Tanno K,

2. Willcox G

(2006) *How fast was wild wheat domesticated? Science* 311:1886.

[Abstract/FREE Full Text](#)

43. ↵

1. Hillman G,

2. Hedges R,

3. Moore A,

4. Colledge S,

5. Pettitt P

(2001) *New evidence of Lateglacial cereal cultivation at Abu Hureyra on the Euphrates. The Holocene* 11:383–393.

[Abstract/FREE Full Text](#)

44. ↵

1. Auffray J-C,
2. Tchernov E,
3. Nevo E

(1988) *Origine du commensalisme de la souris domestique (Mus musculus domesticus) vis-à-vis de l'homme*. *CR Acad Sci Paris* 307:517-522.

45. ↵

1. Turner DC,
2. Bateson P
3. Serpell JA

(1990) in *The Domestic Cat, The domestication and history of the cat*, eds Turner DC, Bateson P (Cambridge Univ Press, Cambridge, UK), pp 155-158.

46. ↵

1. Sunquist ME,
2. Sunquist F

(2002) *Wild Cats of the World* (University of Chicago Press, Chicago).

47. ↵

1. Buxo R,
2. Jacomet S,
3. Bitmann F
4. Willcox G

(2005) *13th IWGP Symposium The distribution, natural habitats and availability of wild cereals in relation to their domestication in the Near East: Multiple events, multiple centres*, eds Buxo R, Jacomet S, Bitmann F (Springer, Berlin), pp 534-541.

48. ↵

1. MacHugh DE,
2. Bradley DG

(2001) *Livestock genetic origins: Goats buck the trend*. *Proc Natl Acad Sci USA* 98:5382-5384.

[FREE Full Text](#)

49. ↵

1. Felsenstein J

(1981) *Skepticism towards Santa Rosalia, or why are there so few kinds of animals?* *Evolution* 35:124-138.

[CrossRefISI](#)

50. ↵

1. Via S

(2001) *Sympatric speciation in animals: The ugly duckling grows up*. *Trends Ecol Evol* 16:381-390.

[CrossRefMedline](#)

51. ↵

1. Price EO

(2002) *Animal Domestication and Behavior* (CABI, Wallingford, Oxon, UK).

52. ↵

1. Yamaguchi N,

2. Kitchener AC,
3. Ward JM,
4. Driscoll CA,
5. MacDonald DW

(2004) *Craniological differentiation amongst wild-living cats in Britain and southern Africa: Natural variation or the effects of hybridization?* *Anim Conserv* 7:339–351.

[CrossRef](#)

53. ↵

1. Yamaguchi N,
2. Driscoll CA,
3. Kitchener AC,
4. Ward JM,
5. MacDonald DW

(2004) *Craniological differentiation between European wildcats (*Felis silvestris silvestris*), African wildcats (*F.s. lybica*) and Asian wildcats (*F.s. ornata*): Implications for their evolution and conservation.* *Biol J Linnean Soc* 83:47–63.

[CrossRef](#)

54. ↵

1. Johnson WE,
2. et al.

(2006) *The late Miocene radiation of modern Felidae: A genetic assessment.* *Science* 311:73–77.

[Abstract/FREE Full Text](#)

55. ↵

1. O'Brien SJ,
2. Johnson WE

(2007) *Origins of the World's Cats.* *Sci Am* 297:68–75.

[MedlineISI](#)

56. ↵

1. Fogle B

(2001) *The New Encyclopedia of the Cat* (DK, New York).

57. ↵

1. Stephens G,
2. Yamazaki T

(2001) *Legacy of the Cat: The Ultimate Illustrated Guide* (Chronicle, San Francisco), 2nd Ed.

58. ↵

1. Takezaki N,
2. Rzhetsky A,
3. Nei M

(1995) *Phylogenetic test of the molecular clock and linearized trees.* *Mol Biol Evol* 12:823–833.

[Abstract](#)

59. ↵

1. Hafez ESE

2. Hale EB

(1969) in *The Behaviour of Domestic Animals*, ed Hafez ESE (Bailliere, Tindall and Cassell, London), 2nd Ed, pp 22–42.

60. ↵

1. Clutton-Brock J,

2. Grigson C

3. Garrard AN

(1984) in *Animals and Archaeology: 3. Early Herders and Their Flocks*, eds Clutton-Brock J, Grigson C (BAR International, Oxford), pp 117–132.

61. ↵

1. Diamond JM

(2005) *Guns, Germs, and Steel: The Fates of Human Societies* (Norton, New York).

62. ↵

1. Fraser D,

2. Weary DM,

3. Pajor EA,

4. Milligan BN

(1997) *A scientific conception of animal welfare that reflects ethical concerns. Anim Welfare* 6:187–205.

63. ↵

1. Zeder MA,

2. Bradley DG,

3. Emshwiller E,

4. Smith B

5. Wayne RK,

6. Leonard JA,

7. Vila C

(2006) in *Documenting Documentation: New Genetic and Archaeological Paradigms*, eds Zeder MA, Bradley DG, Emshwiller E, Smith B (Univ of California Press, Los Angeles), pp 279–293.

64. ↵

1. Ericson PGP,

2. Tyrberg T,

3. Kjellberg AS,

4. Jonsson L,

5. Ullen I

(1997) *The earliest record of house sparrows (Passer domesticus) in Norther Europe. J Archaeol Sci* 24:183–190.

CrossRefISI

65. ↵

1. Clutton-Brock J,

2. Grigson C

3. Tchernov E

(1984) in *Animals and Archaeology: 3. Early Herders and their Flocks, Commensal animals and human sedentism in the Middle East*, eds Clutton-Brock J, Grigson C (BAR International, Oxford, England), pp 91-115.

66. ↵

1. Boursot P,
2. et al.

(1996) *Origin and radiation of the house mouse: Mitochondrial DNA phylogeny*. *J Evol Biol* 9:391-415.

[CrossRefISI](#)

67. ↵

1. Krinke G
2. Hedrich HJ

(2000) in *The Laboratory Rat*, ed Krinke G (Academic, San Diego), pp 3-8.

68. ↵

1. Vigne JD,
2. Peters J,
3. Helmer D
4. Fernandez H,
5. Taberlet P,
6. Mashkour M,
7. Vigne J-D,
8. Luikart G

(2005) in *The First Steps of Animal Domestication: New Archaeozoological Approaches*, eds Vigne JD, Peters J, Helmer D (Oxbow Books, Oxford), pp 50-54.

69. ↵

1. Zeder MA,
2. Bradley DG,
3. Emshwiller E,
4. Smith B
5. Luikart G,
6. Fernandez H,
7. Mashkour M,
8. England PR,
9. Taberlet P

(2006) in *Documenting Documentation: New genetic and archaeological paradigms*, eds Zeder MA, Bradley DG, Emshwiller E, Smith B (University of California Press, Los Angeles), pp 294-305.

70. ↵

1. Luikart G,
2. et al.

(2001) *Multiple maternal origins and weak phylogeographic structure in domestic goats*. *Proc Natl Acad Sci USA* 98:5927-5932.

[Abstract/FREE Full Text](#)

71. ↵

1. Vigne JD,
2. Peters J,
3. Helmer D
4. Zeder MA

(2005) in *The First Steps of Animal Domestication: New Archaeozoological Approaches*, eds Vigne JD, Peters J, Helmer D (Oxbow Books, Oxford), pp 125–146.

72. ↵

1. Harris DR
2. Hole F

(1996) in *The Origins and Spread of Agriculture and Pastoralism in Eurasia*, ed Harris DR (University College London, London), pp 263–281.

73. ↵

1. Harris DR
2. Legge T

(1996) in *The Origins and Spread of Agriculture and Pastoralism in Eurasia, The beginning of caprine domestication in Southwest Asia*, ed Harris DR (Univ College London, London), pp 238–262.

74. ↵

1. Zeder MA,
2. Bradley DG,
3. Emshwiller E,
4. Smith BD
5. Bruford MW,
6. Townsend SJ

(2006) in *Documenting Domestication: New Genetic and Archaeological paradigms*, eds Zeder MA, Bradley DG, Emshwiller E, Smith BD (Univ of California Press, Los Angeles), pp 306–316.

75. ↵

1. Zeder MA,
2. Bradley DG,
3. Emshwiller E,
4. Smith BD
5. Bradley DG,
6. Magee DA

(2006) in *Documenting Domestication: New Genetic and Archaeological Paradigms*, eds Zeder MA, Bradley DG, Emshwiller E, Smith BD (Univ of California Press, Los Angeles), pp 317–328.

76. ↵

1. Vigne JD,
2. Peters J,
3. Helmer D
4. Helmer D,
5. Gourichon G,
6. Monchot H,

7. Peters J,
8. Sana Segui M

(2005) in *The First Steps of Animal Domestication: New archaeozoological approaches*, eds Vigne JD, Peters J, Helmer D (Oxbow Books, Oxford), pp 86–95.

77. [↵](#)

1. Clutton-Brock J,
2. Grigson C
3. Buitenhuis H

(1984) in *Animals and Archaeology: 3. Early Herders and their Flocks*, eds Clutton-Brock J, Grigson C (BAR International, Oxford, England), pp 213–221.

78. [↵](#)

1. Baig M,
2. et al.

(2005) *Phylogeography and origin of Indian domestic cattle*. *Curr Sci* 89:38–40.

[ISI](#)

79. [↵](#)

1. Zeder MA,
2. Bradley DG,
3. Emshwiller E,
4. Smith BD
5. Bradley DG

(2006) in *Documenting Domestication: New Genetic and Archaeological Paradigms*, eds Zeder MA, Bradley DG, Emshwiller E, Smith BD (Univeristy of California PRes, Los Angeles, CA), pp 273–278.

80. [↵](#)

1. Harris DR
2. Meadow RH

(1996) in *The Origins and Spread of Agriculture and Pastoralism in Eurasia*, ed Harris DR (Univ College London Press, London), pp 390–412.

81. [↵](#)

1. Vigne JD,
2. Peters J,
3. Helmer D
4. Haber A,
5. Dayan T,
6. Getz N

(2005) in *The First Steps of Animal Domestication: New Archaeozoological Approaches*, eds Vigne JD, Peters J, Helmer D (Oxbow Books, Oxford), pp 80–85.

82. [↵](#)

1. Larson G,
2. et al.

(2005) *Worldwide phylogeography of wild boar reveals multiple centers of pig domestication*. *Science* 307:1618–1621.

[Abstract/FREE Full Text](#)

83. ↵

1. Beja-Pereira A,
2. et al.

(2004) *African origins of the domestic donkey. Science* 304:1781.

[FREE Full Text](#)

84. ↵

1. Bruford MW,
2. Wayne RK

(1993) *Microsatellites and their application to population genetic studies. Curr Opin Genet Dev* 3:939-943.

[CrossRefMedline](#)

85. ↵

1. Zeder MA,
2. Bradley DG,
3. Emshwiller E,
4. Smith BD
5. Vila C,
6. Leonard JA,
7. Beja-Pereira A

(2006) in *Documenting Domestication: New Genetic and Archaeological Paradigms*, eds Zeder MA, Bradley DG, Emshwiller E, Smith BD (Univ of California Press, Los Angeles), pp 342-353.

86. ↵

1. Jansen T,
2. et al.

(2002) *Mitochondrial DNA and the origins of the domestic horse. Proc Natl Acad Sci USA* 99:10905-10910.

[Abstract/FREE Full Text](#)

87. ↵

1. Zeder MA,
2. Bradley DG,
3. Emshwiller E,
4. Smith BD
5. Olsen SL

(2006) in *Documenting Domestication: New genetic and archaeological paradigms*, eds Zeder MA, Bradley DG, Emshwiller E, Smith BD (Univ of California Press, Los Angeles, CA), pp 245-269.

88. ↵

1. Harris DR
2. Kohler-Rollefson I

(1996) in *The Origins and Spread of Agriculture and Pastoralism in Eurasia, The one-humped camel in Asia: Origin, utilization and mechanisms of dispersal*, ed Harris DR (UCL press, London).

89. ↵

1. Clutton-Brock J,
2. Grigson C
3. Wapnish P

(1984) in Animals and Archaeology: 3. Early Herders and their Flocks, eds Clutton-Brock J, Grigson C (BAR International, Oxford), pp 171-200.

90. ل

1. Clutton-Brock J,
2. Grigson C
3. Kohler I

(1984) in Animals and Archaeology: 3. Early Herders and their Flocks, The Dromedary in modern pastoral societies and implications for its progress of domestication, eds Clutton-Brock J, Grigson C (BAR International, Oxford, England), pp 201-206.