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The Evolution of Animal Domestication

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Abstract

The domestication of plants and animals over the past 11,500 years has had a significant effect not just on the domesticated taxa but also on human evolution and on the biosphere as a whole. Decades of research into the geographical and chronological origins of domestic animals have led to a general understanding of the pattern and process of domestication, though a number of significant questions remain unresolved. Here, building upon recent theoretical advances regarding the different pathways animals followed to become domesticated, we present a large-scale synthesis that addresses the global pattern of animal domestication alongside a discussion of the differential evolutionary processes that have shaped domestic animal populations. More specifically, we present a framework for understanding how unconscious selection characterized the earliest steps of animal domestication and the role of introgression and the importance of relaxed and positive selection in shaping modern domestic phenotypes and genomes.

1. INTRODUCTION

The domestication of plants and animals over the past 11,500 years has significantly transformed Earth's biosphere, affecting human population size and altering human evolution. Beginning with the domestication of the dog, animal domestication has taken place over timescales accessible through archaeological evidence and been driven by selection pressures created by both unintentional and deliberate human actions as well as by human-modified environments. Despite its importance in the history of our species, significant questions regarding the timing, location, and evolutionary mechanisms of animal domestication remain. Recent theoretical developments alongside advances in genetic approaches (including the increasing availability of ancient DNA from archaeological animals remains), however, are providing new avenues to explore and understand the dynamics of animal domestication.

Here, we present a large-scale synthesis through a discussion of four separate themes. We begin by discussing how animal domestication took place by considering the process through an evolutionary lens. Using Zeder's (2012) framework of three separate domestication pathways, we present a model for how animals were domesticated in the absence of deliberate human selection by considering the relationship between ecotypes, synanthropes, attraction to human niches, and gene flow. We then discuss the frequency of gene flow between wild and domestic populations and how the genetic patterns that result have often been misconstrued as evidence for independent domestication episodes. In this section, we introduce a new term, introgressive capture, that allows for a reduction of instances in which initial domestication processes are conflated with subsequent gene flow between domestic and wild populations.

Having established how domestication occurred and what we mean by the term, we then present a brief synopsis of the timing and location for the domestication of 32 animal species in the Old and New Worlds. By doing so within the context of the pathway each animal followed into a domestic relationship and their chronological patterning, we demonstrate why the first domestic animals could not have resulted from deliberate, goal-directed human selection. In the final discussion, we consider the relative importance of positive and relaxed selection in shaping the genomes and phenotypes of modern domestic animals. Despite the enormous progress that has been made in understanding animal domestication, key challenges remain, including the need to identify the genes that were responsible for differentiating nascent domestic populations from their wild ancestors.

2. ANIMAL DOMESTICATION AS AN EVOLUTIONARY PROCESS ALONG ALTERNATIVE PATHWAYS

Darwin (1868) was the first to recognize that domestic animals possess a wide variety of similar morphological traits despite the lack of close evolutionary relationships between their wild progenitors. This phenotypic convergence, which includes, for example, variations in coat color and texture, docility, shifts in reproductive timing, alterations in skull shape and tooth crowding, dwarf and giant varieties, and floppy ears, has intrigued scholars for the past 150 years. Though this collection of traits represents an animal equivalent of the domestication syndrome recognized in plants (Harlan 1975), the lack of an obvious connection between them has undermined efforts to explain their individual and collective origins. As a result, it has been easier to envision their initial appearance as the result of deliberate human action.

For example, embodying the notion that domestication resulted as a consequence of goal-directed human intention, Francis Galton (1907) suggested that dogs were domesticated following the capture and nurturing of wolf puppies in human camps. He based this conclusion

on ethnographic research that suggested pet keeping was not unusual among hunter-gatherer groups across the globe. Even if some scientists felt this observation did not constitute a sufficient explanatory mechanism (Serpell 1989), many narratives relied upon human-directed selection to describe the initial appearance of traits that differentiated wild and domestic phenotypes.

In the 1950s, Dmitry Belyaev believed he could explain not only the appearance of the domestication syndrome but also how it could have resulted from a decided lack of both human intentionality and selection pressures focused upon individual traits. Working with a captive population of silver foxes, Belyaev measured their reaction when a hand was placed in their cages. By selecting only the least aggressive individuals to breed, Belyaev demonstrated that selection for tame behavior eventually resulted in the acquisition of numerous other phenotypic traits including piebald coats, drooping ears, upturned tails, shortened snouts, and shifts in developmental timing. Over forty years, Belyaev recreated the domestication syndrome by producing foxes possessing traits that were not only never seen in wild foxes, but also had never been directly selected for (Trut 1999, Trut et al. 2009).

Despite these insights and the demonstration that animal domestication could have begun in the absence of deliberate human forethought and action, the ubiquity of the domestication syndrome suggested the existence of a single domestication process; or at least there was little incentive to consider either differential stages from wild to domestic or the possibility that different animals followed unrelated pathways to reach the same domesticated status. Vigne (2011) recently proposed a multistaged model characterized by a gradually intensifying relationship between humans and animals. In this view, animal domestication proceeded along a continuum from anthropophily to commensalism, to control in the wild, to control of captive animals, to extensive breeding, to intensive breeding, and finally to pets. Although Zeder (2012) also recognized the staged model approach, her insight was recognizing and formally describing three separate pathways that animals followed into a domesticated relationship with humans: a commensal pathway, a prey pathway, and a directed pathway.

2.1. The Commensal Pathway

The commensal pathway does not begin with intentional action on the part of people to bring wild animals (juvenile or otherwise) into their camps. Instead, as people manipulated their immediate surroundings, different populations of wild animals would have been attracted to elements of the human niche, including human food waste and/or smaller animals that were also attracted to the refuse. Those animals most capable of taking advantage of the resources associated with human camps would have been the tamer, less aggressive individuals with shorter fight or flight distances. In general, animal populations that are attracted to and survive at least partly within the sphere of (micro or macro) human habitats are referred to as synanthropes. Though obligate synanthropes, such as human louse and some pigeon populations, exist (Kenward 1997), this term is most often reserved for pest species and is not used to refer to domestic animals. Within the context of Zeder's (2012) model, the leap from a synanthropic population to a domestic one could only have taken place after the animals had progressed from anthropophily to habituation, to commensalism and partnership, at which point the establishment of a reciprocal relationship between animal and human would have laid the foundation for domestication, including captivity and human-controlled breeding.

From this perspective, animal domestication is an axiomatic coevolutionary process in which a population responds to selective pressure while adapting to a novel niche that includes another species with evolving behaviors. The human-directed selection that we associate with modern domestic populations (for commercial traits or fashion) would only have been possible after animal

populations adapted to take advantage of the human environment, a process that took place, at least initially, in the absence of active human instigation. Once animals along the pathway become entrenched within human societies, the phenotypic differences between them and their wild ancestors became sufficiently marked to (at least occasionally) warrant separate taxonomic species names (Gentry et al. 2004). Given the early tenuous links between the nascent synanthropic populations and people, the mechanisms that reduced gene flow between the wild and emerging domestic populations and that allowed the consolidation of genetic and morphological differences between them and people have not been self-evident.

In a recent study, Marshall et al. (2014) demonstrated that for a wide variety of animals, including donkeys, horses, New and Old World camelids, goats, sheep, and pigs, the archaeological and genetic data suggests that long-term bidirectional gene flow between wild and domestic stocks was common, and in at least the case of reindeer, a relatively recent domestication, gene flow continues to the present day (Røed et al. 2008). Thus, the cessation of gene flow between most wild and domestic populations is, at least within the temporal context of animal domestication, a recent phenomenon. The establishment of domestic populations following a commensal route therefore requires a plausible demonstration of two criteria: (a) a mechanism that genetically differentiates the nascent domestic population from its wild progenitor, and (b) evidence that gene flow between the two populations would not break down the differences essential to maintaining a domesticated status.

Speciation in an allopatric context is easily conceived. Geographic barriers limit mating between two populations, thus reducing or preventing the homogenizing effects of gene flow from maintaining a single population. Sympatric speciation requires a reduction of gene flow through a method other than geographic barriers. Numerous mechanisms, including habitat shifts within a single species, have been proposed (Bush 1994), and not only is speciation within populations without the necessity of geographic barriers more accepted (Via 2001) but next-generation sequencing is allowing for the identification of genomic regions that underlie speciation (Feder et al. 2013). The differing selection regimes experienced by populations of one species living in two habitats (one anthropogenic) would promote distinct constellations of adaptations through destabilizing (or disruptive) selection (Trut et al. 2009). It is possible, therefore, that habitat shifts, including a gradual adaptation to human niches, may explain the emergence of domestic animals following the commensal pathway.

As an example, dogs were derived exclusively from gray wolves (Lindblad-Toh et al. 2005) and are the archetypal commensal pathway animal. In addition, they were the first domestic animal and the only animal domesticated before the advent of agriculture (Larson et al. 2012). Gray wolves were once distributed across the Northern Hemisphere, and for this and other reasons it has been difficult to establish where dogs were domesticated or even if multiple populations of wolves were domesticated independently. Wolves competed with humans for similar resources (or preyed upon domestic animals, and they have experienced a long history of persecution as a result). Given that the human populations who domesticated wolves were mobile hunter-gatherers, it is not obvious how dogs evolved or how their domestic nature was not extinguished given that admixture with wild wolves was, and remains, common (Anderson et al. 2009, Vila & Wayne 1999, Vila et al. 2005).

Two recent wolf studies have revealed the presence of significant genetic and morphological differences in sympatric populations (Musiani et al. 2007, Stronen et al. 2014). In North America, a mitochondrial, microsatellite, and Y-chromosome assessment of two wolf populations combined with satellite telemetry data revealed significant genetic and morphological differences between one population that migrated with and preyed upon caribou and another territorial ecotype population that remained in a boreal coniferous forest. Though these two populations spend a period of the year in the same place, and though there was evidence of gene flow between them,

the difference in prey-habitat specialization has been sufficient to maintain genetic and even coloration divergence (Musiani et al. 2007). Arctic foxes have also split into two ecotypes: lemming foxes and coastal foxes, both of which display significant differences in migration, reproductive, and feeding strategies (Dalén et al. 2005). In both of these cases, if the two populations continue to concentrate on different resource strategies for a sufficient period of time, the two ecotypes could evolve sufficient genetic and/or behavioral differences and become classified as separate species.

This is the case for killer whales about whom genetic and behavioral studies have revealed numerous ecotypes on the basis of different feeding strategies (Andrews et al. 2008, Foote et al. 2009). In addition, recent analyses have suggested these differences are significant enough to warrant their elevation from ecotypes to full species (LeDuc et al. 2008, Morin et al. 2010). Wolf ecotypes are not just a modern phenomenon. A recent study identified a population of extinct Pleistocene wolves with unique mitochondrial signatures from eastern Beringia. The skull shape, tooth wear, and isotopic signatures suggested these remains were derived from a population of specialist megafauna hunters and scavengers that went extinct while less specialized wolf ecotypes survived (Leonard et al. 2007). Thus, separate sedentary and migratory ecotypes have recurrently evolved in wolves and in other species.

These examples suggest a plausible scenario for dog domestication in which at least one wolf population became an ecotype suited to the human niche created by hunter-gatherers. Analogous to the modern wolf ecotype that has evolved to track and prey upon caribou, a Pleistocene wolf population could have begun following mobile hunter-gatherers, thus slowly acquiring genetic and phenotypic differences that would have allowed them to more successfully adapt to the human habitat. The ability of modern wolf, arctic fox, and killer whale populations to maintain distinctive population and behavioral attributes despite occasional geographic sympatry demonstrates that it would have been possible for wolves, at the anthropophilic stage of domestication, to establish a synanthropic ecotype. Even if early dogs had occasionally interbred with wolves belonging to different migratory or sedentary ecotypes, the studies above suggest that different ecotypes can maintain their integrity despite significant gene flow (Kraus et al. 2012, Thompson 2005). Thus, despite a potentially long period of acclimatization and a lack of geographic barriers to gene flow, anthropophilic animals could have evolved a synanthropic ecotype characterized by adaptations to the human niche. Having initiated and sustained the divergence, they could have then become domesticated through more intensive human selection.

2.2. The Prey Pathway

Although the early stages of the commensal pathway are necessarily not dependent upon human intentionality, the prey pathway does begin with human action. The primary human motive was not to domesticate, however, but to increase the efficiency of resource management. Animals that followed this path were medium to large herbivores targeted as prey. Thus, they were always wary of humans and would never have been attracted to the waste products generated as part of the human niche. Instead, humans likely altered their hunting strategies to maximize the availability of the prey. In so doing, the selection pressures for traits such as docility would have been significant as people moved from game management to herd management, to more complete control over the animals' diet and reproduction (Zeder 2012).

Importantly, though dogs were domesticated by hunter-gatherers, the conditions for animals following the prey pathway are associated with more settled human communities that cultivated plants and relied upon a broad-spectrum subsistence. By measuring the size, sex ratios, and mortality profiles of zooarchaeological assemblages, archeologists have been able to document changes in the management strategies of hunted sheep, goats, pigs, and cows in the Fertile Crescent starting

in the early Holocene about 11.7 kya. By 10 kya, people were preferentially killing young males of a variety of species and allowing the females to live to produce more offspring (Zeder 2012). A recent demographic and metrical study of cow and pig remains at Sha'ar Hagolan, Israel, demonstrated that both species were severely overhunted before domestication (Marom & Bar-Oz 2013), suggesting that the intensive exploitation led to management strategies adopted throughout the region that ultimately led to the domestication of these populations following the prey pathway.

Intriguingly, this pattern of overhunting before domestication suggests that the prey pathway was as accidental and unintentional as the commensal pathway (Zohary et al. 1998). Each step along the trajectory, from wild prey to game management, to herd management, to directed breeding, may not have been guided by a desire to completely control the animals' life history but instead to increase the supply of a vanishing resource. In this way, animal domestication (e.g., sheep; Stiner et al. 2014) mirrors the process of unintentional entanglement associated with plant domestication as humans first foraged, and then through increased reliance on the resource, became trapped in positive feedback cycles of increasing labor and management of plant species that were evolving in response to human innovations (Fuller et al. 2010a). For animals, as human interference in their life cycles intensified, the evolutionary pressures for a lack of aggression would have led, as Belyaev demonstrated (Trut 1999, Trut et al. 2009), to an acquisition of the same domestication syndrome traits found in the commensal domesticates despite having entered the human niche through completely separate trajectories.

2.3. The Directed Pathway

The only pathway that began with a deliberate objective to domesticate a species is the directed pathway (Zeder 2012). Before these taxa were targeted, humans already possessed and were reliant upon domestic plants and animals. Having the finished products in hand allowed people to imagine domestic versions of wild animals. Thus, though horses, donkeys, and Old World camels were sometimes hunted as prey species, they were each deliberately brought into the human niche for other reasons, such as sources of transport. Even in these cases, domestication was a multigenerational adaptation to human selection pressures, including tameness, and if the suitable evolutionary response was not elicited, domestication was never achieved. For instance, despite the fact that Near Eastern gazelle hunters in the Epipaleolithic practiced a game management strategy to avoid culling reproductive females to promote population persistence (Rowley-Conwy & Layton 2011), neither gazelles (Zeder 2006) nor zebras (Diamond 2002) possess the necessary prerequisites and were never domesticated. Despite the failures, the majority of modern domestic animals have arisen in the past few hundred years because of the directed pathway. These include most small pets, including hamsters, the global population of which derives from a single sibling pair extracted from the Syrian Desert in 1930 and brought into captivity (Fritzsche et al. 2006), and an increasing number of aquatic species (Duarte et al. 2007), many of which have begun to display characteristics consistent with the domestication syndrome (see Section 4).

Though many authors since Darwin (e.g., Driscoll et al. 2009, Serpell 1989, Vigne 2011, Zeuner 1963) have considered domestication through an evolutionary lens, Zeder's (2012) establishment of the commensal, prey, and directed pathways is the first framework that allows for a comprehensive consideration of accidental and intentional selective pressures associated with the context of how separate species entered the human niche. This model allows for hypotheses to be formulated about the individual stages of domestication before deliberate human selective choices. This is essential because, as Marshall et al. (2014) have pointed out, our current conception and definitions of domestication often lack validity owing to an overreliance on modern European relationships with domestic animals. As Vigne has stated, "the concept of (process of)

domestication must be disassociated from that of the domestic animal (Vigne 2011, p. 173).” By considering the specific temporal and chronological patterns of individual animal species within this evolutionary context, we are much closer to revealing and comprehending the nature of the origins of domestication.

3. THE FREQUENCY OF DOMESTICATION AND DIFFERENTIATING DOMESTICATION FROM INTROGRESSIVE CAPTURE

Many early perceptions of domestication assumed that the near universal adoption of agriculture and domesticated animals was the product of demographic diffusion away from a limited number of core zones (MacNeish 1992, Sauer 1952). This perspective has shifted dramatically in recent years as more data has revealed that indigenous plants were domesticated in as many as 20 geographically distinct regions (Fuller 2010, Larson et al. 2014).

A similar narrative has been claimed for animals. Evidence from the zooarchaeological record suggests that most animals were only domesticated once, though pigs were an exception because they were domesticated independently in East Asia (Cucchi et al. 2011) and Anatolia (Otoni et al. 2013). The recent use of genetic sequences derived from modern animal species led numerous authors to conclude that animal domestication was a great deal less rare than previously supposed. These conclusions were primarily based on the affinity between DNA sequences of domestic animals and their wild counterparts and the assumption that branching patterns on phylogenetic trees reflect independent domestication episodes. This rationale has been used to support claims for multiple and independent domestications of genetically and geographically divergent populations of pigs (Larson et al. 2005), goats (Luikart et al. 2001), sheep (Pedrosa et al. 2005), horses (Vila et al. 2001), and cows (Hanotte et al. 2002).

Most of these genetic data sets consisted of sequences derived from the mitochondria, a non-recombining maternally inherited genome that has limited power to either identify or quantify hybridization involving geographically differentiated domestic populations or between wild and domestic populations. This lack of discriminatory power is key because the appearance of divergent mitochondrial haplotypes in domestic populations could result either from an independent domestication process of geographically and genetically divergent wild populations or from introgression of a wild population into domestic stock (Larson & Burger 2013). In the first scenario the process of domestication is common and emerges easily. In the second, domestication is rare, but gene flow between wild and domestic populations is common. Determining which of these two is more likely has significant ramifications for our understanding of the frequency and nature of the process itself.

Developments in sequencing technology have allowed for the nuclear genome to be accessed and analyzed in a population genetics framework, thus overcoming the limitations of mitochondrial data sets. Occasionally combined with modeling approaches (Gerbault et al. 2014), the increased resolution afforded by nuclear sequences has demonstrated that gene flow is common not only between geographically diverse domestic populations of the same species but also between domestic populations and wild species that never independently gave rise to a domestic population.

In pigs, for example, several studies have demonstrated that populations domesticated in one place and then moved to a new region serially acquire the mitochondrial signature of local wild boar populations (Otoni et al. 2013). This pattern, evident in Europe and Asia, suggests persistent admixture between wild populations indigenous to regions outside the core areas where pigs were initially domesticated. The same is true for other taxa. The yellow leg trait possessed by numerous modern commercial breeds was acquired via introgression from the grey junglefowl indigenous to South Asia (Eriksson et al. 2008). African cattle are hybrids that possess both a European

(taurine) mitochondrial signal and an Asian (indicine) Y-chromosome signature (Hanotte et al. 2002). Numerous other bovid species, including bison, yak, banteng, and gaur, also hybridize with ease (Verkaar et al. 2004). In addition, cats (Pierpaoli et al. 2003) and horses (Jordana et al. 1995) have been shown to hybridize with many closely related species, and domestic honey bees have mated with so many different species they now possess genomes more variable than their original wild progenitors (Harpur et al. 2012).

Not surprisingly, hybridization and introgression are also widespread within and between plant species. Neither grapes (Myles et al. 2011) nor apples were domesticated in Europe. Despite this, introgression with local populations following the arrival of the domestic varieties in Europe has been extensive, and European domesticates have lost most of their genetic similarity to their original progenitors (Cornille et al. 2012). Gene flow between domesticated and wild maize has hampered efforts to identify the temporal and geographic patterns of its domestication (van Heerwaarden et al. 2011). The same is true of rice. *Oryza sativa* subsp. *japonica* was domesticated in East Asia before being transported to India, where it hybridized with managed populations that gave rise to subsp. *indica* (Fuller et al. 2010b). Recent genetic studies have even demonstrated widespread introgression from introduced Asian rice (*O. sativa*) into native African rice (*O. glaberrima*) (Nuijten et al. 2009).

The consequence of this admixture propensity is that modern domestic populations can often appear to have much greater genomic affinity to wild populations that were never involved in the original domestication process. This result necessitates a revision of our consideration of the term domestication, and we suggest that it should be reserved solely for the initial process of domestication of a discrete population in time and space. Subsequent admixture between introduced domestic populations and local wild populations that were never domesticated should be referred to as “introgressive capture.” Conflating these two processes muddles our understanding of the original process and can lead to an artificial inflation of the number of times domestication took place (Larson & Burger 2013).

Our ability to extract and sequence DNA preserved in ancient plant and animal remains is increasing at a rapid pace (Shapiro & Hofreiter 2014). Armed with ancient genomes, we will be able to quantify and track hybridization through time (as has recently been shown in human populations (Prüfer et al. 2014), which will allow us, first, to identify those populations that gave rise to modern domesticates and, second, to distinguish those populations from the numerous additional populations (including those now extinct) that contributed genetic material to modern domestic stocks. The power to do so is becoming increasingly important in an interconnected world in which modern domestic populations reflect a legacy of admixture between widely dispersed populations, thus limiting our ability to infer early domestication processes from modern genomes alone.

4. THE CAST OF ANIMAL DOMESTICATES: WHO, WHERE, WHEN, AND VIA WHICH PATHWAY

Although crop cultivation may have begun independently in as many as 20 regions (Fuller 2010), early animal domestication is associated with perhaps only 3 regions (the Near East, central China, and the Andes). In addition, current evidence indicates that early domestication only took place within a subset of the geographical distribution of the wild ancestors, suggesting that animal domestication was relatively rare not only on a global scale but also within the area traversed by the wild species (**Figure 1**). Many more animals were domesticated after the establishment of agricultural societies and often in regions distant from centers of plant domestication. Below we review the current evidence for where and when 35 separate animal domestication episodes took place within the framework of the three pathways (commensal, prey, and directed) discussed above (Zeder 2012).

4.1. Commensal Pathway Taxa

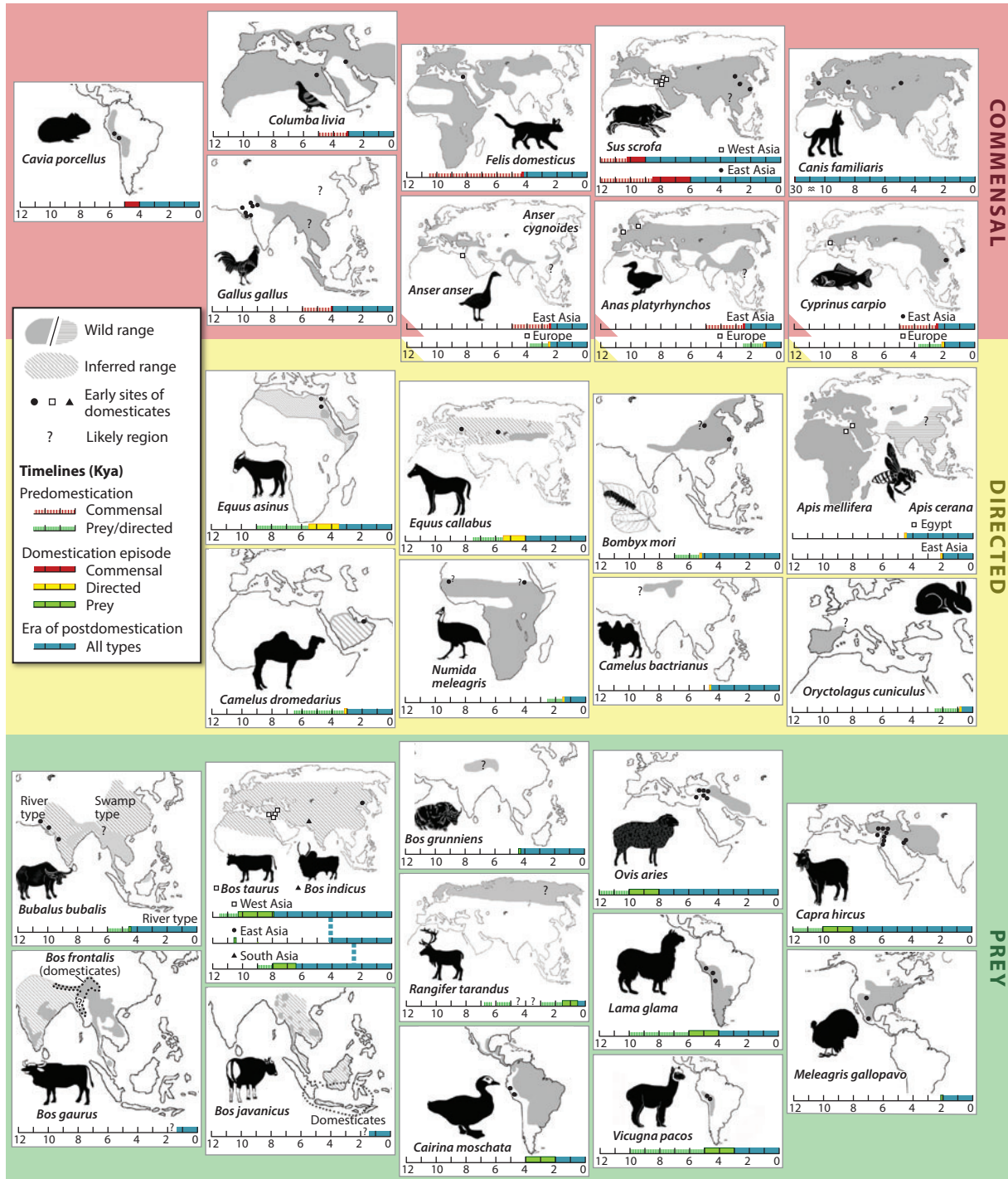
The earliest domestic animals in each independent region all followed the commensal pathway, though the processes did not take place simultaneously. Dogs were first, and though significant questions remain about exactly where, when, and how many times they were domesticated, they were widely established across Eurasia before the end of the Pleistocene, well before cultivation or the domestication of other animals (Larson et al. 2012). Cats also followed the commensal pathway in both Europe, where they were transported to Cyprus by ~11,000 years BP (Vigne et al. 2012), and China (Hu et al. 2014). In both cases, cats were attracted to human communities by pests, including mice that colonized early grain stores of predomestication cultivation (Willcox & Stordeur 2012). Pigeons moved from rocky cliff habitats into permanent towns in the Near East, and though this may have happened in prehistory, clear evidence for pigeon-keeping first appears in written and pictorial records of Mesopotamia and Egypt (Serjeantson 2009). In the Andes, guinea pigs too followed a commensal pathway associated with early sedentism ~5 kya by taking advantage of kitchen waste (Brothwell 1983). Lastly, the widely translocated Polynesian rat, Pacific populations of which have diverged morphologically from those on New Guinea and Southeast Asia, may also have followed a commensal pathway (Motokawa et al. 2004).

The pathway pigs followed is less clear. Though they were hunted, they may also have followed a commensal route because they were able to readily consume human waste and convert it to productive protein. In central China early pigs were associated both with early villages of millet cultivators as well as early sedentary gather-cultivators of wetlands (Cucchi et al. 2011, Flad et al. 2007), whereas in Western Eurasia pigs were associated with early cultivating villages of the oak woodland zone of the northern Fertile Crescent (Vigne et al. 2011). In addition, the prolonged period of gradual morphological change, and changes in culling profiles, suggests an extended era of commensalism and domestication of at least 3,000 years (Ervynck et al. 2002).

Several other taxa followed commensal pathways in eastern Asia, especially in association with early rice cultivation. Globally the most important is the chicken, domesticated from anthropophilic red junglefowl, which was attracted to kitchen scraps, animal dung, and crop-processing waste. Though chickens were thought to have been domesticated as early as 8,000 years BP (West & Zhou 1988), these dates have been questioned because the bones in the original faunal analysis (Chow 1983) were recently shown to derive from pheasants (Deng et al. 2013). Zooarchaeological remains in the Indus Valley, beyond the distribution of wild red junglefowl, suggest that chickens must have been domesticated by at least 4,500–4,000 years BP (Fuller 2006). Duck and goose domestications in East Asia are generally undocumented, though written evidence suggests they were present as domesticates in Central China after 500 BC (Luff 2000). It is possible these species were attracted to rice paddies or grazed the stubble of harvested fields, and the erect habit in some Asian ducks suggests an adaptation to being herded (Serjeantson 2009). Carp similarly lend themselves to being managed within rice agriculture. They were likely domesticated before 2 kya (Nakajima et al. 2010) and consumed alongside other wild freshwater fish by early Yangtze River rice cultivators (Nakajima et al. 2012).

4.2. Prey Pathway Taxa

The larger meat animals more often followed the prey pathway. As described above, these species were likely hunted first, and as people become increasingly sedentary cultivators, more intensive game management strategies were necessary to mitigate the effects of over hunting. In Western Eurasia, sheep, goats, and cattle were likely all domesticated in this manner between 10,500 and 10,000 years BP (Vigne et al. 2011), a period in which cereals and pulses in the same region were also undergoing domestication (Fuller et al. 2011). The fact that sheep, goats, cattle, pigs, and cats were



also translocated to Cyprus suggests that management was well underway, even if morphological traits of domestication are not detectable in the archaeological record before 10,000 years BP (Vigne et al. 2011, 2012). Zebu cattle may have been independently domesticated through the prey pathway in the Indus Valley, where they are associated with early cultivating villages between 9,000 and 7,000 years BP (Fuller 2006, Meadow & Patel 2003). Alternatively, Zebu cows may not have resulted from independent domestication but instead from the introgression of wild Zebu populations into taurine cattle that were transported eastward (Larson & Burger 2013).

A recent study revealed tooth wear patterns consistent with domestication on a 10,500-year-old bovine mandible from North China that possessed a unique mitochondrial genome, thus raising the possibility that people were independently managing wild bovids in East Asia as well (Zhang et al. 2013). The domestication of bovines in Southeast Asia is especially complex. Establishing the timing and geography of the domestication of at least four taxa in the region has been undermined by both the dearth of archaeological evidence and the significant degree of admixture involving each of the bovine species with each other and introduced taurine and indicine cattle (Larson & Burger 2013).

Both the river and swamp species of water buffalo were independently domesticated also following the prey pathway. The zooarchaeological evidence suggests river buffalos were domesticated in the Lower Indus Valley region and in western India by 4,500–4,000 years BP (Fuller 2006, Meadow & Patel 2003). Though commensurate evidence for swamp buffalo is lacking, the wild form remains scattered through tropical Asia, and it was likely domesticated between eastern India and peninsular Southeast Asia before 3,000–2,500 years BP.

Despite claims to the contrary, there is no clear evidence for the domestication of a herded prey animal in Africa. For example, though independent domestication of *Bos africanus* cattle has been suggested (Wendorf & Schild 1994), the archaeozoological evidence is meager. Cattle remains decline relative to other hunted game, and there is no size change until nonnative domesticated sheep and goats arrive about 8,000 years BP (Gautier 2001). This suggests that domesticated cattle were introduced from Western Eurasia alongside sheep and goats and subsequently interbred with Saharan wild populations. There is evidence that in early to middle Holocene Libya barbary sheep were penned and herded (di Lernia 2001), though they were abandoned following the arrival of Western Eurasian sheep and goats in 8,000–7,500 years BP (Garcea 2004).

Reindeer are another example of prey pathway domestication but are an exception because they were domesticated not by sedentary cultivators but by nomadic hunting societies. As a result, archaeological evidence for this domestication is less clear than for other prey pathway domestications. Rock art indicates early attempts at management in Norway from 6,700 to 6,200 years BP (Helskog 2011), and the use of sledge runners has been documented from 6,000 to 5,000 years BP (Grøn 2011). Nevertheless, reindeer herding is thought to have begun 3,000–2,000 years BP (Grøn 2011, Skjenneberg 1984). Written sources refer to Scandinavian herding in ninth-century

Figure 1

A summary of the geography and chronology for 32 ancient animal domestications that took place before 500 kya. Taxa are grouped by commensal, prey, and directed pathways. Each map indicates the wild progenitor ranges inferred using fossil data when available (mostly from Mason 1984), and the locations of domestication are inferred from archaeological evidence. Timelines (in 1,000-year increments before present) summarize the current evidence for predomestication management/anthrophily, domestication, and the duration of postdomestication improvement. For many taxa, it is still only possible to infer the most recent time by which domestication is known to have definitely taken place. Dashed blue lines in the *Bos taurus/indicus* timelines indicate the period of the dispersal of domesticated *B. taurus* and domesticated *B. indicus* into East Asia. This highlights that the early blip of archaeologically inferred indigenous *Bos* herding does not evidently continue into recent times; all recent cattle in East Asia are introduced domesticates from either *B. taurus* or *B. indicus* or their hybrids.

AD, and archaeological data from Scandinavia date clearly domesticated herds to only the past 500 years (Bjørnstad et al. 2012). Interestingly, it was the migratory tundra ecotype that was domesticated and not the more sedentary forest dwelling ecotype (Røed et al. 2008).

In the Americas, llamas, alpacas, turkeys, and Muscovy ducks all followed the prey pathway. Grazers of mid- to high-elevation meadows, llamas and alpacas were initially hunted before being domesticated from 6,000–5,000 years BP (Mengoni Goñalons 2008). Once domesticated, both of these taxa provided wool and were used for transport. Flocks of turkeys were originally hunted on grassland and scrub and were only domesticated in the American Southwest by 2 kya (Thornton et al. 2012). Lastly, Muscovy ducks were likely hunted as they moved into anthropogenic ponds and canals created by human cultivators in southern South America before also being domesticated about 4 kya (Serjeantson 2009).

4.3. Secondary Products Diversification

Subsequent to domestication as sources of meat, many prey pathway animals underwent diversification for additional uses, including textile fibers, milk, and traction as part of the “secondary products revolution” (Sherratt 1983). Each of these adaptations (or improvement traits—see below) occurred as part of postdomestication diversification processes often associated with economic specialization in the context of emerging complex societies. For example, early specialized wool production provided a valued raw material from agriculturally marginal hill zones around Mesopotamia and is associated with urbanization in the region (McCorriston 1997). Water buffalo milk is central to traditional Indian subsistence but absent in China or Southeast Asia, where water buffalo are plough animals. And though milk consumption is evident from ceramic residues in Neolithic Anatolia and Europe (Evershed et al. 2008), evidence for shifts in herd management associated with more specialized milking only appears millennia later (Greenfield 2010). Similarly, the development of egg-laying chickens and ducks is also a secondary diversification. In evolutionary terms these secondary uses represent postdomestication diversification and only regional populations of the domesticated species were involved. Some secondary products, like eggs or milk, are metabolically expensive and, under wild conditions without the aid of human food provision, likely to be limited in production.

4.4. Directed Pathway Taxa

Many more animals were then domesticated (usually postdating the secondary products revolution that led to wool, milk, and cattle traction) following the deliberate directed pathway, and these domestication episodes often occurred in regions peripheral to those where early animal domestication took place. Donkeys were domesticated south of the Fertile Crescent on the fringes of the Nile valley (Marshall & Weissbrod 2011), dromedary camels in the deserts of Arabia (Uerpmann & Uerpmann 2002), and Bactrian camels in the cool deserts of Central Asia (Peters & Driesch 1997). The domestication of these animals, which provided significantly more efficient transport than cattle carts, is entangled with the expansion of trade and agriculture into new regions. The timing of dromedary domestication, for example, coincides with the expansion of oasis cultivation systems facilitated by qanat irrigation systems, starting ca. 3,000 years BP at end of the Bronze Age (Boivin & Fuller 2009). Horses were domesticated in the temperate grasslands of Central Asia by societies that already herded sheep and goats. Horses may have been tamed and ridden (given the evidence from bit wear; Anthony 2009) firstly as an efficient means to hunt wild horse herds as early as 7,000 years BP. Morphological change associated with more intensive breeding only

occurred from 5,500–4,000 years BP, after which horses were used for trade transport, warfare (with the development of chariots), and horse milking (Anthony 2009, Olsen 2006).

Insects also followed the directed pathway. The earliest evidence for Mediterranean honey bee management in artificial hives comes was recently described from a 3,000 year-old context in the Jordan Valley (Bloch et al. 2010), though the history of bee management in Western and Eastern Asia is likely much deeper. Several saturnid moths produce silk cocoons that have been gathered and spun (Good 2011), but only the Chinese silk worm, now largely dependent on human rearing and feeding, was domesticated. Though cocoon remains and textiles have been reported about 6,000 years BP and 5,300–4,300 years BP, respectively, clear evidence for silk worm domestication comes only from written sources about 3,500 years BP (Cameron 2010).

In the western Old World, many more recent domesticated animals also likely followed the directed pathway. Examples of these secondary food animals, generally much smaller than early herded food animals, include rabbits, birds, and fish. Indigenous to the Iberian Peninsula, rabbits were translocated during the Roman period into walled gardens, and domestic breeding populations were established by post-Roman monastic communities in France as a source of meat during lent (Carneiro et al. 2011). The African guineafowl is wild through much of sub-Saharan Africa, but artistic and bone evidence suggests it may have been domesticated less than 2 kya in Mali and Sudan (Serjeantson 2009). In Europe, domesticated geese (derived from the Greylag goose) may have been reared during the Roman era and certainly became an important meat animal in the middle Ages (Serjeantson 2009). Evidence from the Swedish island of Öland suggests that European ducks were only bred from wild mallards about 1,000 AD (Boessneck et al. 1979). In addition, the Romans transplanted carp from the Danube River into Italian ponds, thus initiating an independent domestication of carp (Balon 1995). Importantly, each of these Roman and post-Roman domestication episodes of waterfowl and carp are distinct in timing and pathway from similar animals domesticated alongside early Chinese rice farming.

The global pattern of animal domestication suggests that the first domesticated animals in each region followed either a commensal or prey pathway. Though humans certainly drove the first steps by hunting animals in the prey pathway, neither of these two routes began with the intention to create a domestic animal. The integration of domesticated animals into human societies created a model and a goal that people could envision when considering other animals. Though the total number of animal domesticates doubled in the middle Holocene (8,000–4,000 years BP) (**Figure 2**) several thousand years after the first domestication episodes, the majority of domestic animals on Earth have been domesticated in the past few centuries. In addition to those discussed above, they include numerous small pets (such as hamsters, gerbils, chinchilla, and degus) and hundreds of freshwater and marine species (Duarte et al. 2007). Just as modern breeding practices do not correspond to early human-animal relationships (Marshall et al. 2014), the fact that all recent domesticates were the result of a directed pathway has corrupted our impression of the initial evolutionary process of animal domestication. What is clear is that people could not begin intentionally domesticating animals until they had procured them through entirely unintentional means.

5. THE RELATIVE ROLES OF RELAXED AND POSITIVE SELECTION IN DETERMINING THE ORIGINS OF DOMESTICATION TRAITS

The genetic differentiation of domestic and wild populations can be framed within the context of two key considerations. The first distinguishes between domestication traits, presumed to have been essential at the early stages of domestication, and improvement traits, those that have appeared since the split between wild and domestic populations (Olsen & Wendel 2013). Domestication traits are generally fixed within all domesticates and were selected during the

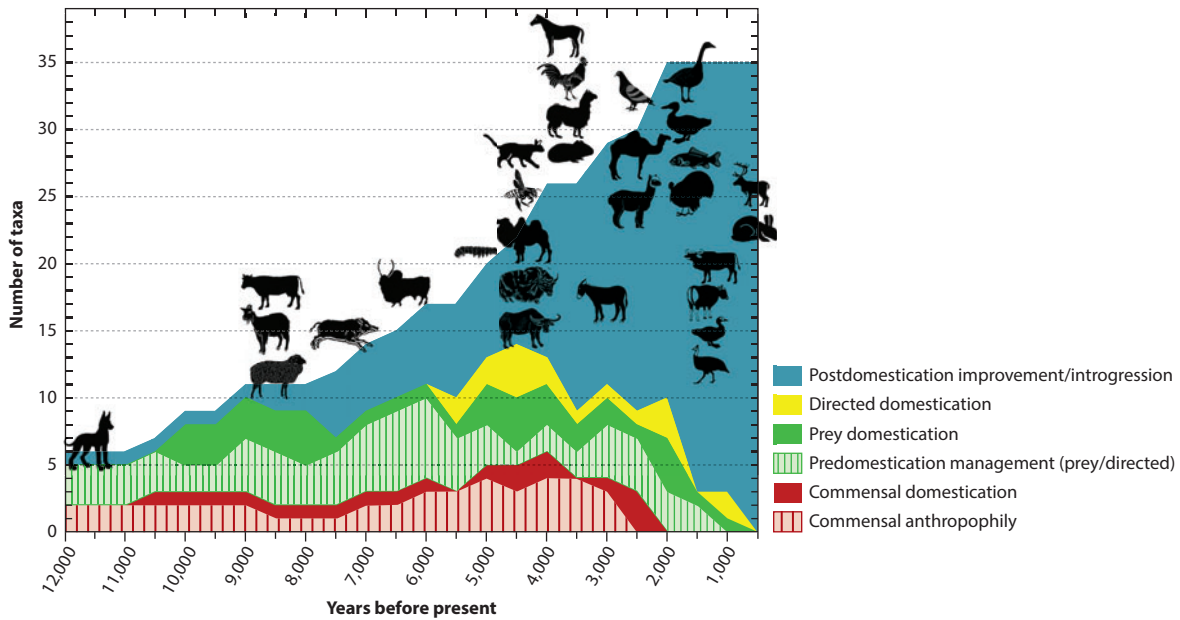


Figure 2

A summary of the timing and increase in animal domestications over the course of the Holocene up to 500 years BP. Domestications are separated by pathways but are grouped as taxa enter the postdomestication improvement phase. Animal icons indicate the approximate period by which animals were domesticated and entered the postdomestication improvement phase.

initial episode of domestication, whereas improvement traits are present only in a proportion of domesticates, though they may be fixed in individual breeds or regional populations. A second issue is whether traits associated with the domestication syndrome resulted from a relaxation of selection as animals exited the wild environment or from positive selection resulting from intentional and unintentional human preference. Recent genomic explorations for the genetic basis of traits associated with the domestication syndrome have shed light on both of these issues.

5.1. Relaxation Versus Positive Selection

A recent study of the coat color gene *MC1R* in wild boar and domestic pigs suggests that both relaxed and positive selection have played important roles in shaping genetic and phenotypic variation (Fang et al. 2009). Sequences from 160 wild and domestic pigs revealed that while wild boar populations in Europe and East Asia possessed seven individual synonymous substitutions, 50 European and Asian domestic pig breeds possessed nine nonsynonymous mutations associated with black, red, and black-and-white-spotted coat colors. This presence of exclusively synonymous mutations in the wild boar indicates that purifying selection for camouflage coat colors experienced by boar in the wild eliminated any individuals carrying mutations that altered the wild-type protein.

The quantity and layered nature of the nonsynonymous mutations found in domestic pigs across the Old World strongly suggested positive selection, evidence for which comes from two observations. First, the existence of the seven synonymous mutations between wild boar populations in East Asia and Europe took place after the split between the two populations 1.6 to 0.8 Mya (Frantz et al. 2013). The nine nonsynonymous mutations present in domestic pigs, in contrast, appeared only after pigs were domesticated independently in Western Eurasia (Ervinck et al.

2002) and East Asia (Cucchi et al. 2011) over the past ~10,000 years. This short time span over which coat color mutations appeared suggests positive selection was responsible for the pattern. A subsequent statistical test of the ratio between the synonymous and nonsynonymous substitutions confirmed a signature of positive selection in domestic breeds (Fang et al. 2009).

Combined, these patterns suggest a phased selective process. First, once domestic pigs began living within a human niche, nonsynonymous mutations appeared because of the mutational process within a relaxed selective regime, thus altering the *MC1R* protein and producing non-camouflage coat colors. These variants would have been eliminated outside of a human setting, but because people valued novel coats, they actively encouraged and positively selected for their proliferation. Evidence for this pattern comes not only from pigs but also from a recent ancient DNA study of 89 horse samples dated from the Late Pleistocene to the Iron Age. The temporal pattern of variation revealed that though predomestic horses lacked variability, coat color variation increased significantly following domestication (Ludwig et al. 2009).

Both dog mitochondrial (Björnerfeldt et al. 2006) and nuclear (Cruz et al. 2008) genomes also possess an overabundance of nonsynonymous changes relative to wolves and coyotes, consistent with a relaxation of selection following domestication. These patterns suggest that once animals are freed from selective pressures associated with living in the wild, they accrue nonsynonymous mutations under a relaxed selective regime, some of which lead to novel phenotypes that people recognize and place a premium upon. By acting on this preference, humans then preferentially and positively select for the same traits that nature actively eliminates.

Coat color change is often considered a domestication trait associated with the early stages of domestication. Because selection for noncamouflaged coats may not have taken place until after humans began controlling the reproductive success of specific animals in their herds, it may instead be an improvement trait. Put another way, knowing what genes are associated with coat colors may not yield insights into those that were central to altering animal phenotypes during the anthropophilic, habituation, or game management stages associated with the commensal and prey pathways.

Piebald and spotted coat colors first emerged in Belyaev's foxes after only 10 generations (Trut et al. 2009). Because he was selecting solely for a lack of aggression, this rapid appearance suggested that the genetic pathways controlling behavior also affected coat colors. To test this, Albert et al. (2009) crossed two populations of rats selected over 60 generations for tameness and for aggression. They typed 201 genetic markers, and though they found a significant quantitative trait locus for tameness and another for white-coat spotting, because the two regions did not overlap there was no genomic evidence for an association between coat color and behavior.

5.2. Domestication Versus Improvement Genes

Although the identification of the genetic basis for a wide variety of traits in domestic dogs and many other domestic animals has increased significantly over the past decade (Karlsson et al. 2007, Rubin et al. 2012), comparatively little progress has been made in revealing traits associated with the key behavioral shifts that facilitated the early phases of animal domestication. This is not the case in plants, in which numerous genes underlying early domestication have been identified (Olsen & Wendel 2013). In fact, just one claim for the discovery of a domestication gene in animals has been made (Rubin et al. 2010). This analysis of wild and domestic chickens revealed a missense mutation in the thyroid stimulating hormone receptor (*TSHR*), a locus possibly linked to seasonal mating behavior. Given that fact, that 264 out of 271 birds representing 36 global populations were homozygous for the sweep allele, the authors concluded that the *TSHR* locus may have played a crucial role during chicken domestication (Rubin et al. 2010) and may be a domestication gene.

A more recent study tested this hypothesis by assessing the variability of this gene in ancient chickens excavated from 12 European archaeological sites dated from 280 BC to the eighteenth century AD (Girdland Flink et al. 2014). A domestication gene crucial for the differentiation of wild and domestic populations should become fixed during the early phases of domestication and remain so to the present. The results of the ancient DNA survey, however, revealed that only 8 of 44 successfully typed individuals were homozygous for the domestic allele, indicating that the ubiquity of *TSHR* in modern chickens took place only in the past 500 years.

Other studies that have revealed the fixation of genetic differences between wild and ancient samples have also conflated modern ubiquity with ancient origins. For instance, the prevalence of a mutation in a gene associated with increased grain size in wheat (*NAM-B1*) was claimed to have been selected for during the early phases of domestication because of its commonality in modern cultivars (Uauy et al. 2006). A subsequent genetic study of nineteenth-century historical seeds, however, revealed significant variation, thereby demonstrating that the fixation of the domestic allele did not occur early in the domestication process but was instead fixed during recent crop improvement (Asplund et al. 2010).

The distinction between domestication and improvement genes remains valuable, but the identification of fixed genetic differences between modern wild and domestic populations cannot automatically be interpreted as evidence for an ancient origin of the mutation. In fact, given the difficulty in finding the genetic basis underlying the behavioral traits that were crucial during early animal domestication, we have yet to begin understanding what genetic shifts occurred as animals entered any of the three pathways. Precisely distinguishing between the relaxation and selective phases of domestication and the genes associated with each remains a high priority for understanding the origins of domestication itself.

6. CONCLUSIONS

Despite the fact that many early animal domestication episodes are genetically and archaeologically poorly documented, a clearer framework for understanding the evolutionary patterns of domesticated animals is emerging. After the initial pulse that occurred during the early Holocene, animals were domesticated with increasing frequency, entangling numerous species into human environments and economies. The beginnings of animal domestication involved a protracted co-evolutionary process with multiple stages along different pathways. Importantly, humans did not intend to domesticate animals by (or at least, they never envisioned a domesticated animal resulting from) either the commensal or prey pathways. In both of these cases, humans became entangled with these species as the relationship between them, and the human role in their survival and reproduction, intensified.

The necessary circumstances appear to have coincided rarely, because few primary animal domestication episodes took place within a limited range of the wild species' distribution. The resulting consequences for economic productivity and increased population sizes and range expansions of both humans and their domestic animal partners are difficult to overstate, though the genetic changes that accompanied the initial animal domestication trajectories remain elusive. Once this process took place, however, gene flow (or introgressive capture) between domestic animals and other populations of wild and domestic species occurred frequently, often significantly affecting the genomes and phenotypes of the domestic animal populations.

Once domestic populations became established, a relaxation of natural selective pressure allowed for the appearance of mutations related to novel traits. By recognizing and selecting for these changes, the genomes of domestic animals became even more differentiated from their wild ancestors. Although some of these traits, such as coat color, were likely linked to fashion, others,

including milk, wool, and egg-laying, were economically motivated. Many of these economic traits and additional novel uses (e.g., as draught animals) were exaptations or rather emergent accidental properties that resulted as the domestication process shifted from unconscious to increasingly conscious selection. Given that domestication is not just a model but rather an authentic evolutionary process in its own right, significantly greater insights into the pattern and process of domestication will be gained by considering the roles of entanglement, emergence, and exaptation in the origin and subsequent history of plant and animal domestication.

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