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THE DOMESTICATION OF ANIMALS

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Over the past 11,000 years humans have brought a wide variety of animals under domestication. Domestic animals belong to all Linnaean animal classes—mammals, birds, reptiles, amphibians, fish, insects, and even, arguably, bacteria. Raised for food, secondary products, labor, and companionship, domestic animals have become intricately woven into human economy, society, and religion. Animal domestication is an on-going process, as humans, with increasingly sophisticated technology for breeding and rearing animals in captivity, continue to bring more and more species under their control. Understanding the process of animal domestication and its reciprocal impacts on humans and animal domesticates requires a multidisciplinary approach. This paper brings together recent research in archaeology, genetics, and animal sciences in a discussion of the process of domestication, its impact on animal domesticates, and the various pathways humans and their animal partners have followed into domestication.

HUMANS HAVE BROUGHT A WIDE RANGE OF ANIMALS INTO DOMESTIC PARTNERSHIPS over the past 11,000 years—as livestock, working animals, household pets, and companions. The pathways that different animal species followed into domestication are remarkably varied, shaped by the different biological constraints and opportunities of the animals brought into domestication, as well as by the different cultural contexts of their human partners. It is a journey that continues today as humans, with enhanced understanding of the process of domestication and increasingly sophisticated technology for breeding and rearing captive animals, bring an ever-expanding array of animal species, on land and sea, into domestication. Recent years have seen dramatic improvements in our understanding of animal domestication and the varied pathways traveled into domestication. Increasingly fine-grained insights into animal domestication have

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been gained from research grounded in archaeology, genetics, and animal science. This paper brings together information on animal domestication generated by work in these varied fields to explore the universals of animal domestication and to trace the three primary pathways that animals and their human partners have followed, and continue to follow, into domestic partnerships.

DOMESTICATION DEFINED

All definitions of domestication, whether dealing with plants or animals, recognize that domestication involves a relationship between humans and target plant or animal populations (see Zeder 2006a). The primary difference between different definitions of domestication lies in the degree of emphasis placed on either the human or the plant/animal side of the equation. Some definitions, especially those focusing on animal domestication, cast humans as the lead partner in the relationship. Domestication is seen as a process in which humans deliberately and with forethought assume control over the domesticate's movement, feeding, protection, distribution, and, above all, its breeding—directed at achieving specific clearly identified goals (Bökönyi 1989; Clutton-Brock 1994; Ducos 1989; Hale 1969; Reed 1959). Domesticates within this perspective are usually characterized in economic terms as productive capital (e.g., Meadow 1989) or by the way in which they become integrated into the social fabric of human society (Ducos 1978; Ingold 1996; Russell 2002, 2007).

Other definitional approaches, in contrast, portray domestication as a mutualistic relationship in which both partners, human and domesticate, reap benefits. This approach is especially common among researchers focusing on plant domestication (Anderson 1952; Blumer 1996; Harlan et al. 1973; Harris 1996; Smith 2001), though it is also seen among those concentrating on animal domesticates (Budiansky 1992; Morey 1994; O'Connor 1997). Perhaps the farthest extreme on this side of the human/domesticate balance is found in the work of David Rindos (1984), who argued that the relationship between humans and domesticates is no different from other mutualistic relationships in the natural world, drawing close parallels between human relationships with crop plants and those between social insects and a variety of plants and other insect species. In fact, Rindos went so far as to argue against any role of deliberate intent on the part of humans in the domestication process, placing plants in the driver's seat of a relationship that afforded them great evolutionary advantage while reducing the selective fitness of their human partners.

There is, I think, a middle ground between these two polar opposite characterizations of the relationship between humans and domesticates. I believe a strong argument can be made that domestication qualifies as a form of biological mutualism with clear benefits for each partner in the relationship. Although the quality of life of domesticates, especially animal domesticates, is arguably poorer than that of their free-living progenitors, there can be no question that domestication has vastly enhanced the reproductive output of crop plants, livestock, and pets far beyond that of their wild progenitors. Similarly, while a diet

based on domesticates may not have the same nutritional value as that based on wild resources, and although the lifestyle of farmers and herders may not, by some measures, compare all that well with that of hunter-gatherers, domesticates have provided humans with resources that they could more predictably and securely control, move, and redistribute—an advantage that fueled a virtual population explosion of agro-pastoralists and their spread to all corners of the globe.

Although domestication shares many features with mutualistic relationships in nature, there are, nevertheless, critical differences that distinguish domestication from any symbiosis found in nature. Mutualisms in nature involve essentially symmetrical, codependent relationships driven by selection operating on mutation-induced changes (behavioral, morphological, or physiological) in *both* partners (Schultz et al. 2005). Humans, on the other hand, have the capacity to spontaneously modify their behavioral repertoires, to invent new behaviors that better suit certain goals and abandon old ones. Most importantly, humans do not have to rely on sexual reproduction to pass on effective behaviors to the next generation. Instead humans are able to transmit adaptive new behaviors through social learning to their direct descendants, as well as to others in their immediate social group and beyond (Boyd and Richerson 1985; Richerson and Boyd 2005). This capacity for the invention and transmission of learned behavior shifts the balance of power in the symbiosis between humans and emergent domesticates, affording humans the upper hand in the relationship as they choose among individuals in the target plant or animal population that best suit their needs and try out new ways to manipulate the behavior and life history of those individuals in ways that enhance the benefits humans are able to reap from these managed plant and animal resources.

There is, then, an important element of intentionality that is a central distinguishing characteristic of human-mediated domestication (Zeder 2009a, 2009b). Humans could not have foreseen the adaptive responses target plants or animals would make to their manipulations, nor were they, at least initially, working toward developing a domestic crop plant or livestock animal through their efforts. But they were able to evaluate how well their efforts at breeding, nurturing, and selectively harvesting certain individuals within the target plant or animal population met their immediate needs; they could, on the basis of this evaluation, continue, modify, or invent new ways of manipulating responsive individuals in order to further these goals. This essentially Lamarckian aspect of human cultural evolution is the reason why mutualistic relationships between humans and domesticates are fundamentally different from non-human symbiotic relationships. The human capacity for inventing and transmitting new behaviors vastly accelerates the process and transforms the domesticate and the domestic relationship far beyond any mutualism in the natural world.

Following this line of argument, a recognition of both the biological and the cultural components of the process might define domestication as: *a sustained, multigenerational, mutualistic relationship in which humans assume some significant level of control over the reproduction and care of a plant/animal in order to secure a more predictable supply of a resource of interest and by which*

the plant/animal is able to increase its reproductive success over individuals not participating in this relationship, thereby enhancing the fitness of both humans and target domesticates.

The sustained, multigenerational nature of the relationship introduces the plant or animal partner to a number of selective pressures that, over time, transform the genotype of the plant or the animal from that of the free-living wild progenitor to that of its descendent domesticate. When Darwin wrote his seminal work *The Variation of Animals and Plants under Domestication* (1868) he focused on the impact of artificial or directed selection on domesticates as humans deliberately bred plants and animals for specific desired traits. Directed selection certainly plays a major role in determining the genotype of domesticates, especially, as we will see later, in more recent domesticates. But other factors are involved in shaping the transformation from the wild to the domestic genotype that, especially early on in the process, likely played an even larger role in shaping the domestic genotype (Price 1984, 1998, 1999, 2002).

Among the most important of these is the relaxation of selective factors operating on free-living individuals once humans take over the role of provisioning and protecting managed plants and animals and, especially, once they begin to select breeding partners. At this point a whole range of stochastic variation in an organism's behavior or morphology, previously selected against, may find expression. Equally important are new selective factors that arise through this association with humans and human-altered environments—the new seed-bed pressures which select for seeds able to sprout quickly and shade out competitors, for example, or the selection for animals able to cope with the stress of coming into close association with humans and other animals. Reproductive isolation is another major factor shaping the domestic genotype once human-tended plant and animal populations are prevented from interbreeding with free-living ones, as is random genetic drift that occurs with the isolation or movement of small subsets of tended plants and animals from larger populations.

In plants the new selective factors introduced under domestication tend to target genes that control morphology and physiology, whereas in animals the primary focus of selection under domestication tends to be on genes that control behavior (Zeder 2006a, 2006b). This is why the initial and most profound phenotypic changes in plants undergoing domestication are likely to be in morphology—seed size, plant architecture, dispersal mechanisms—or in physiological functions such as the timing of germination or ripening. In animals, in contrast, the initial and sometimes the only impact is on their behavior, with physiological functions (i.e., the timing of estrus cycles, the duration and volume of lactation, and developmental rates) also often affected by the ongoing domestic relationship with humans. Genetically driven morphological change, especially early on in the domestication process, seems to be a later side effect of domestication.

A number of different factors shape when and how these various selective forces kick into action during the domestication and how the emergent domesticate responds to them. These factors include the basic biological constraints of the domesticate (morphological, physiological, and behavioral), the culture context

in which the process takes place, and even accidental happenstance that brings potential domesticates together with receptive human populations at particular times and places. As a result, the pathways various plant and animal species followed into domestication are highly variable. The selective forces and the rate and course of the domestication of the same species of plant or animal under certain cultural and environmental circumstances, for example, may have been very different from those that drove the independent domestication of another population of the same species under different circumstances. Similarly, the same social and economic pressures may set the stage for the domestication of a wide array of diverse species of plants and animals within a single cultural and environmental context.

In addition to experiencing genetically driven changes in the domesticate's phenotype, plants and animals undergoing domestication may also experience a number of plastic responses to the developing relationship. Different nutritional regimes of animals (foddering or early weaning) or different field conditions for plants (irrigation or various crop-rotation schedules) may result in plastic epigenetic changes detectable in the size, development rates, or even chemical components of tended plants and animals that distinguish them from free-living forms.

Domestication also leaves its mark on the human side of the equation. There is growing evidence that humans, like their domestic partners, have experienced reciprocal genotypic responses to domestication (Laland and Brown 2002:101). However, the most significant and distinctive impacts of domestication on humans are cultural. The act of tending plants and animals, whose productive capacity and output can be controlled, has played a major role in reshaping the organization of human societies. Notions of ownership and access to resources are transformed with the shift from free-living to managed plant and animal resources and modes of production are altered. Even the ways in which humans rationalize their existence within the natural world and the larger cosmos are changed.

Research on domestication, whether grounded in archaeology, genetics, or agricultural sciences, requires reference to all of the different vectors that shape this process, on both the domesticate and the human sides of the equation. Documenting the process of domestication, either in antiquity or today, involves understanding how this process causes the various genetic, phenotypic, plastic, and cultural responses used to track its progress. It also requires acknowledging that domestication is a fluid and nonlinear process that may start, stop, reverse course, or go off on unexpected tangents, with no clear or universal threshold that separates the wild from the domestic.

UNIVERSALS OF ANIMAL DOMESTICATION

Behavioral Preadaptations

Certain behavioral characteristics make certain animal taxa, and certain individuals within taxa, better candidates for domestication than others (Figure 1) (Hale 1969; Price 1984, 2002; Zeder 2012a). Grouped into five general categories these behaviors include attributes that determine (1) social structure—especially

Favorable Characteristics	Unfavorable Characteristics
<ol style="list-style-type: none"> 1. Social Structure <ol style="list-style-type: none"> a) Large gregarious social groups b) Hierarchical group structure c) Males affiliated with social group 2. Sexual Behavior <ol style="list-style-type: none"> a) Promiscuous mating system b) Males dominant over females c) Sexual signals provided by movement or posture 3. Parent-Young Interactions <ol style="list-style-type: none"> a) Social bonds created through imprinting b) Female accepts young soon after parturition or hatching c) Precocial young 4. Feeding Behavior & Habitat Choice <ol style="list-style-type: none"> a) Generalist feeder or omnivorous b) Wide environmental tolerance c) Non-shelter-seeking 5. Responses to Humans <ol style="list-style-type: none"> a) Short flight distance from humans b) Low reactivity to humans or sudden changes in environment c) May solicit attention d) Readily habituated 	<ol style="list-style-type: none"> 1. Social Structure <ol style="list-style-type: none"> a) Family groupings b) Territorial structure c) Males in separate groups 2. Sexual Behavior <ol style="list-style-type: none"> a) Monogamous mating system b) Females dominate males/males appease females c) Sexual signals provided by markings or morphology 3. Parent-Young Interactions <ol style="list-style-type: none"> a) Social bonds created on basis of species characteristics b) Female accepts young on basis of species characteristics c) Altricial young 4. Feeding Behavior & Habitat Choice <ol style="list-style-type: none"> a) Specialized dietary preferences or requirements b) Narrow environmental tolerance c) Shelter-seeking 5. Responses to Humans <ol style="list-style-type: none"> a) Extreme wariness and long flight distance b) Easily disturbed by humans or sudden changes in environment c) Independent/avoids attention d) Difficult to habituate

Figure 1. Preadaptive behavioral characteristics in animal domestication (Hale 1969; Price 1984, 2002).

the size and organization of groups; (2) sexual behavior—particularly the degree of selectivity (or lack thereof) in the choice of mating partners and the ease of replacing one preferred partner with another; (3) parent-young interactions—the ease and speed with which the parent bonds with young and the maturity and mobility of the young at birth; (4) feeding behavior and habitat choice—the degree of flexibility in diet and habitat tolerance; and (5) responses to humans and new environments, including flight responses and reactivity to external stimuli.

It is these final sets of behaviors—those dealing with the responses of animals to humans and new environments—that are particularly important in animal domestication. Low reactivity to humans and other external stimuli is a key preadaptation for domestication. These behaviors are also the primary target of the selective pressures experienced by the animal undergoing domestication. The strong selection for reduced wariness and low reactivity is a universal feature that cuts across all animal domestication, including all domesticated mammals—carnivores (Coppinger and Coppinger 2001; Trut 1999), herbivores (Tennesen and Hudson 1981), and rodents (Murphy 1985), as well as domestic birds (Andersson et al. 2001) and fish (Waples 1991), and even domesticated invertebrate species (Marliave et al. 1993; Price 2002:27–29).

Brains and Behavior

The sustained and increasingly intensified selection for lowered reactivity among animal domesticates has resulted in profound changes in brain form and function that are clearly evident in all higher-order vertebrate domesticates. The most dramatic manifestation of the impact of this process is a widely documented reduction in brain size (Figure 2; Ebinger 1995; Ebinger and Röhrs 1995; Kruska 1988, 1996; Plogmann and Kruska 1990; Rehkämper et al. 2008). Of the domestic mammals for which comparative measures of brain size in domestic and wild progenitor forms have been made, pigs seem to have experienced the most profound reduction in the size of the brain. Corrected for body size, the brains of domestic pigs are 33.6% smaller than those of wild boars. Carnivores also seem to have experienced a quite severe reduction in brain size under domestication, with dogs' brains being an estimated 30% smaller than gray wolves', the progenitors of domestic dogs. Herbivore brain-size reduction is less marked, at between about 14% and 24%, while the brains of domestic rodents show proportionately little brain-size reduction when compared with wild forms. As a general rule, the larger the size of the brain to begin with and the greater its degree of "cerebralization" (or folding), the greater the degree of brain-size reduction under domestication (Kruska 1988). This pattern also seems to hold true in birds (Ebinger 1995; Ebinger and Röhrs 1995; Rehkämper et al. 2008), and even in captive reared fish (Marchetti and Nevitt 2003).

The degree of brain-size reduction does not seem to be correlated with the length of time since initial domestication. Domesticates such as sheep, domesticated more than 10,000 years ago, show only a 24% reduction in overall brain size. Ferrets, in contrast, which were domesticated around 2,500 years ago, have experienced a 30% reduction in brain size compared with wild polecats,

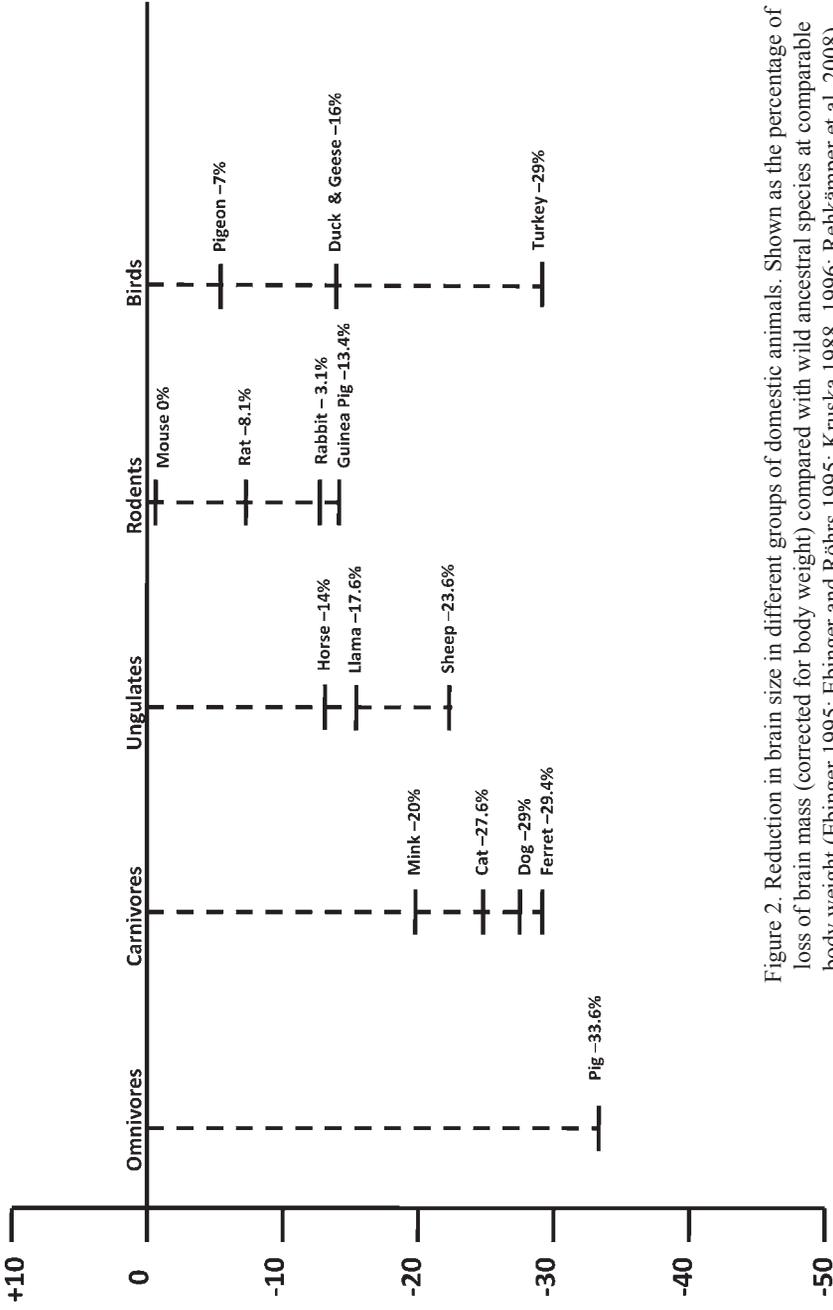


Figure 2. Reduction in brain size in different groups of domestic animals. Shown as the percentage of loss of brain mass (corrected for body weight) compared with wild ancestral species at comparable body weight (Ebinger 1995; Ebinger and Röhrs 1995; Kruska 1988, 1996; Rehämper et al. 2008).

and cage-reared mink, domesticated in the past 100 years, show a 20% reduction in brain size compared with wild mink (Kruska 1996). Silver foxes, selectively bred for tameness over the past 40 years, have experienced a significant reduction in cranial height and width, and by inference in brain size (Trut 1999). The remarkable experiments in domestication of foxes further buttress the hypothesis that brain-size reduction is an early response to the strong selective pressure for tameness and lowered reactivity that is a core, essentially universal, feature of animal domestication.

Not all parts of the brain are equally affected by brain-size reduction, however. There is, in fact, a considerable amount of difference in the degree of reduction seen in different parts of the brain that control different functions among different animal domesticates (Kruska 1988, 1996; Plogmann and Kruska 1990). In pigs, for example, areas of the brain that control olfactory and auditory functions are less reduced than visual structures or motor functions (Plogmann and Kruska 1990); the same holds true in sheep (Kruska 1988). In rats and mink, on the other hand, areas of the brain that control motor functions show a greater degree of reduction than areas of the brain that control visual or olfactory functions (Kruska 1988, 1996). The reduction in the size of parts of the brain that control motor functions in cage-reared mink is nearly 10% greater (at 20%) than in mink raised in open-air enclosures (at 11%) (Kruska 1988, 1996; Price 2002:87)—an indication of the targeted impact of the selection pressures introduced under domestication. Some areas of the brain may experience an increase in size under domestication, as evidenced by the increase in parts of the brain devoted to memory and learning seen among racing and homing pigeons (Rehkämper et al. 2008).

But the most profoundly affected portion of the brain in domestic mammals is the complex structures that belong to the limbic system, which in domestic pigs, dogs, and sheep show a greater than 40% reduction in size compared with their wild progenitors (Kruska 1988). Composed of the hippocampus, the hypothalamus, the pituitary gland, and the amygdala, this portion of the brain regulates endocrine function and the autonomic nervous system, which, in turn, influences behaviors like aggression, wariness, and responses to environmentally induced stress. The dramatic reduction in the size of this portion of the brain in domesticates can be directly linked to an increase in the thresholds for the display of behaviors such as aggression, fear, and flight that result in the overall reduction in reactivity—a cornerstone attribute of domestic animals (Kruska 1988:221; Price 2002:89).

Although some researchers characterize these changes as a “decline of environmental appreciation” (Hemmer 1990) or even more negatively as “regressive evolution” (Röhrs 1985:547), the higher stress threshold of domestic animals is actually a highly adaptive feature (Price 2002:89). Low-threshold stress responses are advantageous in free-ranging animals that need to be alert to sudden changes in their environment that might signal imminent danger. But they are highly maladaptive in a domesticate in which a heightened stress response to humans and other external stimuli can lead to lower reproductive success, decline in health, or even death (Price 2002). The dampening of these responses in domestic animals living in a human-mitigated, controlled environment enables

them to turn their attention from escaping predation to engaging in procreation—thereby increasing their own fitness and making them much more attractive to their human keepers.

Pleiotropic Effects

A number of traits commonly seen in domestic animals are thought to be genetically linked in some way to the intense selection for tameness and reduced wariness in animals undergoing domestication (Price 2002). These linked attributes include changes in the timing of development—usually expressed as a reduction in the rate of development in which the animal passes through fewer development stages than its ancestor so that as an adult it resembles a juvenile form of the ancestor (Goodwin et al. 1997). Pedomorphosis in development, in turn, can result in a neotonization of morphology (often expressed in the juvenilization of skull morphology), in an early onset of sexual maturity (clearly an adaptive trait in a domesticate), or in the retention of more juvenile behaviors in the adult animal (again making the animal a more attractive and tractable domestic companion). Other common morphological attributes in animal domesticates may also be tied to the initial selection for reduced wariness. These features include lop ears, which may be an artifact of neotonization that essentially freezes cartilage in the ears in a more juvenile stage (Trut 1999). Piebald or spotted coat coloration is another of the traits commonly seen in domesticates that may be the result of some linkage in the biochemical pathways of melanins, involved in coat coloration, and neurotransmitters, such as dopamine, that help shape behavior and cognition (Hemmer 1990; Keeler et al. 1968).

Rather than each of these traits arising from site mutations in specific genes, this entire “pleiotropic cascade” of linked traits may arise from the orchestration of gene expression during development caused by mutations in a few key regulatory genes (Jensen 2006). Under such a scenario, mutations in only a few regulatory genes can have a major impact on a network of linked genes, resulting in major phenotypic changes without incurring large allelic differences. A similar mechanism is increasingly thought to control at least some of the responses of plants to domestication (Piperno 2011).

Feralization—Domestication in Reverse

The lasting impact of these behavioral and linked morphological and physiological attributes on domestic animals can be clearly seen in feral domesticates that have reverted to a free-living state. Although feral animals may regain some morphological attributes of wild animals (e.g., feral pigs on the Galapagos seem to have the longer legs and snouts of wild pigs; Kruska and Röhrs 1974), domestication-induced changes in brain size and function in domesticated animals may well be permanent. Feral dogs, cats, goats, donkeys, pigs, and ferrets that have lived outside of an association with humans for generations show little or no sign of regaining the brain mass of their wild progenitors (Birks and Kitchener 1999; Kruska and Röhrs 1974). Even the brains of dingoes, which have lived apart from humans for thousands of years, are the same size as that of a domestic dog

(Schultz 1969). Similarly, although the feralized descendants of sheep brought to Mediterranean islands by Neolithic migrants around 7,000 years ago appear to be morphologically wild, they still retain the smaller brains of their distant domestic ancestors (Groves 1989).

The domestic imprint is especially evident in the behaviors of feral animals. Feral cats, for example, have a generalized diet that includes a wide range of easier-to-catch terrestrial animals—either smaller, less-mobile prey or the young or sick of larger, fleeter animals, with as much as one-fifth of prey obtained near human settlements. Wild cats, in contrast, specialize on particular species and are more likely to include arboreal prey or adults of larger terrestrial prey that may require more hunting skill to capture; they also tend to avoid anthropogenic environments as a source of prey (Biró et al. 2005; Corbett 1979; Gil-Sánchez et al. 1999). Fully feralized dogs that receive no food or shelter from humans and actively avoid human contact are still dependent on the human niche for survival and have not regained the self-sustaining behaviors of their wolf ancestors (Boitania and Cuicci 1995).

Thus, while feral animals may have escaped the bonds of the domestic partnership with humans, they nonetheless retain central morphological and behavioral attributes of this relationship that continue to tie them to humans, even indirectly. It would seem, then, that the imprint of domestication is not only strong and lasting, but likely irreversible.

PATHWAYS TO ANIMAL DOMESTICATION

Beyond the universal features held in common by all domesticated animals, there is remarkable variety in the ways in which animals respond to domestication, as well as in the ways in which domestic animals have become integrated into human society. It might even be argued that each instance of animal domestication is unique, shaped by diverse biological and social contingencies that have pushed and pulled animals and their human partners into domestic relationships. Broadly speaking, however, I think there are three general domestication scenarios—three major pathways that most animal domesticates followed into domestication (Zeder 2012a).

The Commensal Pathway

The first of these general domestication scenarios might be labeled a “commensal pathway.” This pathway is traveled by animals that feed on refuse around human habitats, or by animals that prey on other animals drawn to anthropogenic environments. These animals begin their journey into domestication by establishing a commensal relationship with humans—a relationship in which one partner benefits and the other reaps little if any benefit or harm. At some point in this association with humans and anthropogenic environments, these animals develop closer social or economic bonds with their human hosts, who begin to derive some tangible benefit from the association. This new reciprocity sets the former commensal and its human host on a pathway to a domestic relationship.

The dog is a classic example of a domestic animal that likely traveled a commensal pathway into domestication. It is widely thought that dog domestication began when wolves were drawn to human settlements to scavenge on human refuse (Coppinger and Coppinger 2001; Morey 1994). Rather than dominant alpha wolves, however, the wolves more likely drawn to human settlements were subdominant pack members, less-aggressive animals that may already be less wary around humans and human settlement. The initial commensal stage on this domestication pathway, then, likely serves as a kind of preselection for individuals with lowered flight response and higher stress thresholds—features that make them better candidates for domestication. In this regard, it is interesting to note that one of the earliest morphological manifestations of domestication in dogs is a juvenilization in skull morphology (Morey 1992), which has been attributed to the strong selection for reduced aggression (Trut 1999). The neotonization of skull morphology manifests itself both in changes in the dimensions of the skull (Morey 1992; Trutt 1999, but see Wayne 1986) and in a shortening of snout length which, in turn, results in tooth crowding, reduction in tooth size, and a reduction in the number of teeth in dogs (Turnbull and Reed 1974). This process may have begun during the initial commensal stage of dog domestication, even before humans began to be active partners in the process.

The most compelling evidence for initial dog domestication comes from Late Pleistocene archaeological sites in the Near East dating to about 15,000–14,000 years ago (Dayan 1994; Davis and Valla 1978; Tchernov and Valla 1997; Turnbull and Reed 1974). Canid remains from these sites show clear evidence of snout shortening and tooth crowding (Turnbull and Reed 1974). The placement of young dogs in human burials at one site in the southern Levant suggests, moreover, that a special social bond had been formed between human and dog (Davis and Valla 1978; Tchernov and Valla 1997; Morey 2005).

A recent genetic analysis supports the Near East as an initial center of dog domestication (vonHoldt et al. 2010), overturning an earlier argument for an East Asian origin (Savolainen et al. 2002). This study also identifies potential additional sources of variation in dogs arising from wolf populations in Europe and Asia—a suggestion that is supported by fossil evidence for putative early dogs across Western and Eastern Europe into Central Asia in the Late and Terminal Pleistocene (e.g., Benecke 1987; Chaix 2000; Musil 2000; Pionnier-Capitan et al. 2011; Vigne 2005). If these remains are truly dogs and not simply smaller wolves or some other extinct canid species (Pionnier-Capitan et al. 2011), these early fossil dogs indicate either a rapid spread of dogs out of a single homeland or multiple origins of domestic dogs across Eurasia. Interestingly, these remains coincide with postglacial periods of increased residential permanence, if not year-round sedentism as in the Levant, providing further support for a commensal pathway into domestication. The initial appearance of commensals such as the house mouse, spiny rat, and house sparrow in Levantine settlements at the same time as early dogs (Tchernov 1991) further buttresses the case for a commensal pathway into domestication.

Another commensal domesticate that likely arose in the same context is the cat. As with dogs, genetic evidence also points to a Near Eastern origin

for cat domestication (Driscoll et al. 2007). The presence of the remains of morphologically wild cats among the diverse array of small carnivores in assemblages from the first sedentary settlements in the Near East (Rosenberg et al. 1998; Starkovich and Stiner 2009; Yeshurun et al. 2009) suggests that cats were among a group of commensal animals that took advantage of the prey opportunities afforded by these early settlements. The placement of a cat in a human burial on the island of Cyprus dating to 8,500 years ago suggests that domestic cats were among the managed animals and crop plants brought to this island by Neolithic migrants from the Near East (Vigne et al. 2004, 2011). Unlike dogs, which quickly display morphological features linked to selection for reduced aggression and wariness, cats were very slow to display any archaeologically detectable markers of domestication—an indication, perhaps, of the different pathway these aloof and far less social animals took into domestication and the different kind of partnership with humans that they maintain to this day.

Domesticated fowl also likely followed a commensal pathway into domestication. These birds include chickens, likely domesticated through a process of hybridization between several varieties of wild jungle fowl in Southeast Asia (Eriksson et al. 2008; Kanginakudru et al. 2008; Liu et al. 2006); Muscovy ducks, posited to play a role in controlling insect populations in Central and South American settlements (Angulo 1998); and possibly turkeys, independently domesticated in both Mexico and the U.S. Southwest (Munro 2011; Speller et al. 2009). In each case, the new food sources found in human settlements may have been the lure that brought less wary individuals into initial contact with humans. It is also likely that most early rodent domesticates followed a similar pathway into domestication. This is especially the case with the guinea pig, first domesticated in the highland Andes around 7,000 years ago (Spotorno et al. 2006).

Another possible commensal domesticate is the pig. Archaeological evidence from the Near East suggests that pigs began their relationship with humans as opportunistic scavengers feeding on human refuse in the initial year-round settlements in the more forested parts of the central Fertile Crescent (Ervnyck et al. 2001; Redding 2005). As with dogs, the leading edge indicator of pig domestication is a gradual reduction in molar length, thought to result from the neotenzation of skull morphology (Flannery 1983). Similarly, the early manifestation of these changes in skull morphology in pigs may also be the result of an extended “getting-to-know-you” self-selection phase of a commensal pathway into domestication. Genetic evidence, however, points to multiple independent domestication events across the broad range of this widespread animal (Larson et al. 2005, 2007). It is certainly possible—perhaps even likely—that pigs and humans followed different pathways into domestication in these different instances of pig domestication.

The Prey Pathway

Most major livestock species entered into domestication through what might be called a “prey pathway.” Rather than initiating the relationship, these animals were focal prey species hunted by humans for their meat. Domestication of these prey species was likely initiated when, perhaps as a response to localized pressure

on the supply of the animal, humans began to experiment with hunting strategies designed to increase prey availability. Over time and with responsive species (i.e., those with the behaviors that make them suitable candidates for domestication listed in Figure 1), these game-management strategies developed into herd-management strategies that included the sustained multigenerational control over the animals' movement, feeding, and reproduction characteristic of the domestic relationship.

These conditions seem to have been in place in the central and eastern Fertile Crescent at the end of the Younger Dryas climatic downturn and the beginning of the Early Holocene (Zeder 2011). During this period of climate amelioration and stabilization, beginning about 11,700 years ago, people in this region established year-round settlements supported by broad-spectrum subsistence economies composed of an array of plant and animal resources drawn from a wide range of different ecozones (Zeder 2012b). Shifting prey profiles for animals such as sheep and pigs (which may have wandered between a commensal and a prey pathway in their initial domestication) have been attributed to localized pressure on wild populations in territories surrounding these sedentary encampments (Redding 2005; Zeder 2011, 2012b). We see signs that these prey profiles developed over time into management profiles typical of those employed by modern herders (i.e., culling of young males and delayed slaughter of females until after their peak reproductive years; Zeder 2001, 2005, 2006c, 2008) so that by 10,500 years ago there is good evidence that the relationship between humans and sheep, goats, and pigs was well along the way to full domestication (Peters et al. 2005; Zeder 2011). Shifts in prey profiles of wild cattle indicative of initial management seem to occur somewhat later—ca. 10,000 years ago—in a region to the west and south of the Taurus/Zagros arc that gave rise to caprine and swine domestication (Helmer et al. 2005).

Since this process unfolded within the natural habitat of free-living progenitor species, with likely frequent introgression between free-living and managed animals and restocking of managed herds from wild ones, there is no archaeologically detectable morphological change in these initial managed animals. Documentation of this process, then, is best achieved through the construction of high-resolution sex-specific mortality profiles—a technique that is only now beginning to be more widely used by archaeozoologists working in the region (Helmer 2008; Helmer et al. 2005; Monchot et al. 2005; Zeder 2005, 2006c).

Genetic analysis by Naderi et al. (2008) has identified all six lineages of domestic goat among populations of modern bezoar goats (the progenitor species for domestic goats) from eastern Turkey to central Iran. Rather than being an artifact of modern introgression between wild and domestic herds, the presence of these domestic haplotypes among wild goat populations is instead argued to be an artifact of quite ancient human-mitigated reproductive isolation and translocation that dates back to a period of early human management of wild populations. The authors present further evidence for the movement of two of the major domestic goat lineages out of this natural habitat incubator zone of initial domestication somewhere in southeastern Anatolia—a finding that fits well with recent

archaeological data for early sheep and goat management in this region (Helmer 2008; Peters et al. 2005; Zeder 2011). These results suggest, then, that although a prolonged period of human management of goats within their natural habitat had no archaeologically detectable morphological impact on these animals, it nevertheless left a clear genetic imprint that can still be detected in the essentially feralized descendants of these six founder lineages of domestic goats. Rather than being the result of six independent “domestication events,” the domestication of all of these lineages was more likely part of the same cultural process in which culturally related people in the rugged and highly dissected Taurus/Zagros region brought different wild populations under domestication. Genetic analysis also points to the domestication of multiple lineages of sheep (Bruford and Townsend 2006; Hiendler et al. 2002; Pedrosa et al. 2005), pigs (Larson et al. 2005), and cattle (Bradley and Magee 2006), which, following the example of goats, may also have been brought into domestication within the same cultural context.

Domestication-induced morphological changes in these animals are not archaeologically detectable until the animals leave the habitat where their domestication journey began, cutting off the possibility for introgression and restocking with free-living animals and exposing these managed animals to a range of new selective forces (i.e., genetic drift and pressures of their new environments; Zeder 2011). In bovids, for example, the distinctive changes in horn size and form once thought to be markers of domestication only begin to manifest themselves once managed animals leave the natural habitat where they were initially brought under human control (Bökönyi 1977; Hole et al. 1969; Reed 1983; Zeuner 1955). These changes likely arose from some combination of factors: (1) the relaxation of selective pressures for large horns that allowed for the expression of random mutations previously selected against in free-living animals, (2) selection against the high energetic costs of growing and carrying large heavy horns no longer needed in mate competition, and (3) deliberate, directed selection for more tractable males with smaller horns and less-aggressive natures. These same factors may also be responsible for a shift in the size of domesticated animals. This is not, however, manifested as an overall reduction of body size in both male and female animals (another characteristic once thought an indicator of initial domestication; Meadow 1989; Uerpman 1978, 1979). Instead, the impact of domestication in bovid body size is targeted on males, primarily on the height of males, resulting in a reduction in the degree of sexual dimorphism in domestic animals such as cattle, sheep, goats, and pigs, most strongly expressed in the length of long bones (Zeder 2008).

In addition to livestock species domesticated in the Near East, it is likely that a wide range of other common livestock species followed prey pathways into domestication. These include humped cattle and water buffalo in South Asia (Fuller 2006, 2011; Kumar et al. 2007), the yak in Tibet (Guo et al. 2006; Olsen 1990), and possibly other rather obscure cattle species such as the mithan in South Asia and Bali cattle in Indonesia (Clutton-Brock 1981). The increasingly well resolved archaeological and genetic data for the domestication of South American camelids (llama and alpaca) certainly suggest a prey pathway into domestication

for these animals as well (Mengoni-Gonalons and Yacobaccio 2006; Wheeler et al. 2006). Reindeer may be the most recent, and perhaps the last, species to follow this pathway, serving in many ways as a good model for the initial stages in the domestication of other prey pathway domesticates (Baskin 1974, 2000; Gordon 2003; Ingold 1974; Mirov 1945; Røed et al. 2008, 2011).

The Directed Pathway

The final pathway to domestication is a more deliberate and directed process—a process initiated by humans with the goal of domesticating a free-living animal to obtain a specific resource or set of resources of interest. This “directed pathway” probably only came into being once people were familiar with either commensal or prey-pathway domesticated animals. Animals domesticated through this intention-driven, directed process are likely not to possess many (or possibly even any) of the key behavioral characteristics that pre-adapt certain species to domestication. As a result, the domestication of these animals requires more deliberate effort on the part of humans to work with (or around) behaviors antithetical to domestication, with increasing technological assistance needed for many of the species domesticated in this way.

This is likely the pathway that horses took into domestication. Horses are thought to have been brought into domestication multiple times in the Eurasian steppe by people who concentrated heavily on the hunting of wild horses (Olsen 2006; Vilà et al. 2006), although they did have domestic livestock (especially sheep and goats). Thought to have been initially domesticated to help in hunting their free-living brethren (Levine 1999; Olsen 2006), managed horses also provided humans with a wide array of other resources—including meat, milk, bones for tool manufacture, and long-distance transportation. No known morphological markers can be used to distinguish wild from domestic horses, nor are demographic profiles much use in distinguishing management strategies from prey strategies—especially when dealing with assemblages made up of a mix of wild hunted horses and managed ones. Instead, archaeozoologists tend to turn to multiple lines of circumstantial evidence to monitor this process (Olsen 2006): the presence of quantities of horse manure in human settlements, evidence of corrals, wear patterns on teeth that indicate the use of rope or metal bits, and lipid signatures of horse milk on pots (Outram et al. 2009).

The donkey is another animal likely to have followed a directed pathway into domestication. Archaeological data suggest that donkeys were domesticated as long as 6,000 years ago by Saharan pastoral populations who used them to transport people and belongings across arid regions (Marshall 2000; Marshall and Weissbrod 2011). Recent genetic data point to the domestication of two different lineages of wild ass, the Nubian and the Somali (Beja-Pereira et al. 2004; Kimura et al. 2010; Vilà et al. 2006). The proximity of free-living populations of wild ass and, quite possibly, mating habits of wild asses that made it easier to breed managed females with wild males than to keep intact male donkeys seems to have dramatically delayed the display of any morphological change in early domesticated donkeys (Marshall and Weissbrod 2011). As a result,

archaeozoologists seeking to document the process of donkey domestication, like those documenting horse domestication, have had to rely on indirect markers to detect the presence of domestication in donkeys. Extreme pathologies on the vertebra of Early Dynastic (ca. 5,000-year-old) donkeys buried in a ritual context in Abydos, Egypt, for example, are the only indication that these animals, which cannot be morphologically distinguished from wild asses, were in fact used to transport heavy loads (Rossel et al. 2008).

Old World camels, the two-humped Bactrian camel of Central Asia and the one-humped dromedary of the Arabian Peninsula, are also almost certainly directed domesticates domesticated for a variety of resources, including meat, milk, and, above all, their ability to carry goods and people across arid landscapes by people who already possessed domestic animals. As with horses and donkeys, no clear-cut markers in the morphology or demographic profiles of these animals can be used to distinguish between wild and domestic varieties, so proxy evidence (the presence of dung or fiber from camels; figurative representations) are often the only way one can document this process (Compagnoni and Tosi 1978; Peters and von den Driesch 1997). Some researchers have argued that both species of Old World camels were domesticated in the third millennium BC (Compagnoni and Tosi 1978; Hoch 1979; Masson and Sarianidi 1972)—coinciding with the rise of a flourishing trade network that linked Central and South Asia with the Arabian Peninsula, Mesopotamia, and Africa (Zeder et al. 2006). Counterarguments have been mounted, however, that the domestication of both species came well after these trade routes had been in existence for more than a thousand years (Peters and von den Driesch 1997; Uerpmann and Uerpmann 2002). Future work will have to draw on multiple lines of cultural and biological evidence to resolve this issue.

Another category of animal brought under human control for specific purposes are the “tame captives”—animals such as elephants, cheetahs, and falcons (Clutton-Brock 1981) that have been used to aid in hunting or for their labor. These animals are not bred in captivity, either because of barriers to captive breeding or, as with the elephant, because of their long life spans and slow maturation rates. Instead, young animals are captured and trained to perform the desired tasks (Baker and Manwell 1982). In some ways these animals qualify as domesticates in that they are engaged in a sustained, multigenerational relationship with humans, in which humans assume considerable control over their movement, feeding, and protection to extract specific resources. And yet since they are not bred in captivity, the normal array of selective factors responsible for creating domestic genotypes in other animal domesticates never come into play. Instead of passing on selected domestication traits to each new generation, the process of domestication begins anew with each animal tamed for these purposes. This unusual outlier case of directed animal use raises interesting questions about the nature of the domestic relationship and whether it should be viewed more in terms of the role of the animal in human society or the impact of this use on the evolutionary trajectory of the animal.

All recently domesticated animals fit within this category of directed

domestication. This includes the various carnivore species selectively bred for their fur (e.g., minks and foxes) that have been domesticated in the past 100 to 200 years. It also includes ongoing experiments in domestication with animals such as bison, emu, red deer, Père David's deer, fallow deer, blackbuck, eland, musk ox, and Barbary sheep (Clutton-Brock 1981). The most remarkable and fastest-growing area of ongoing animal domestication, however, focuses on aquatic species. By one account 97% of the nearly 450 managed aquatic species were under human control in the past 100 years, with nearly a quarter of these species domesticated in the past decade or so (Duarte et al. 2007). Clearly this new frontier in animal domestication has staggering implications—not only in terms of its productive potential, but also for the problems it raises in terms of the environmental impact of large fishery operations and the potential evolutionary impact these species have on free-living varieties (Kaiser 1997; Kaiser et al. 2000).

CONCLUSIONS AND QUESTIONS FOR FUTURE RESEARCH

The three different pathways into animal domestication identified here clearly vary in how they are initiated, the direction they take, and the length of time it takes to traverse them (Figure 3). Animals following a commensal pathway into domestication began this journey on their own as the animal seeks out new opportunities in an anthropogenic niche. The strength of the attraction of an animal to this new niche was likely shaped by an assessment of the trade-offs between exploiting these new opportunities and remaining aloof from humans. The strength of the species' avoidance responses to humans was certainly another factor that shaped this pathway, as was the degree to which humans would tolerate the presence of the animal and the benefits they saw in forging a closer relationship with them. Some animals entering into domestication through this route, such as the cat, have arguably never reached the pathway's final destination.

Whereas animals traveling the commensal pathway began the journey on their own initiative, animals entering the domestic partnership through the prey pathway were less willing fellow travelers. As with the commensal route, however, progress down the prey pathway was also likely quite slow as generalized hunting strategies evolved into game management strategies aimed at promoting availability and sustainability of hunting before morphing into selective harvest of managed animals and then to deliberate breeding of target animals for specific resources. Not all animals embarking on this path reached its conclusion. Gazelle may be one such example. While future livestock species such as sheep, goats, pigs, and cattle were primary prey species in the central and eastern parts of the Fertile Crescent, in the western part of this region people were intensively hunting gazelle, the primary ungulate in the southern and northern Levant. And although there is evidence that human hunting pressure may have had an impact on the demographic structure of populations of these fleet-footed animals (Munro 2009), and possibly some indications of tentative steps toward management (Cope 1991; Davis 1983; Henry 1989; but see Sapir-Hen et al. 2009), gazelle have very well

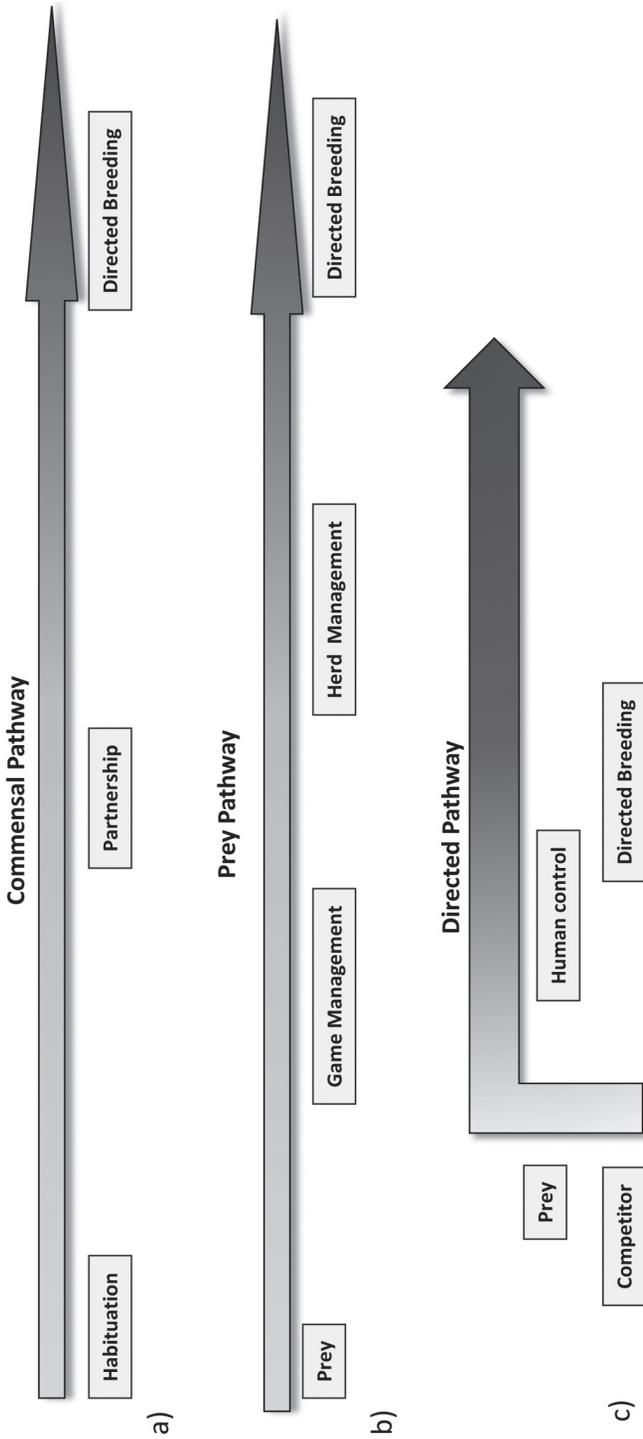


Figure 3. Pathways to domestication: (a) Commensal pathway, (b) Prey pathway, (c) Directed pathway.

developed flight responses and they are difficult to breed in captivity, making them poor candidates for domestication (Clutton-Brock 1981:172).

The final directed domestication pathway is much shorter and follows a more abrupt departure from the free-living animal to an animal under tight human control, often involving deliberate selective breeding to enhance the supply of targeted resources (Figure 3c). Most of these directed domesticates have behavioral or other barriers that may, at least initially, have stood in the way of their domestication. Bringing these animals under human control, then, has required a deep understanding of animal behavior and management and, often, enhanced technology for breeding and tending animals. Entry onto this superhighway of domestication is increasingly dependent on the development of highly specialized techniques for breeding and controlling the animal that, more and more, involves direct manipulation of its genetic makeup.

Thinking of domestication in terms of the different pathways animals and their human partners took raises a number of questions that help set the direction of future research (Zeder 2012a). First, it would be interesting to know if there are differences in the timing and nature of the behavioral, physiological, and morphological responses to the different selective pressures animals experience as they travel these different pathways, and whether there are genetic, morphological, or cultural markers that can be used to reconstruct an animal's course down these different paths. This question, in turn, raises a number of related questions:

1. Are animals that enter into domestication along a commensal pathway, with its long "getting to know you" phase, tamer and more tractable than animals that traveled other pathways?
2. Is the neotonization of cranial form that appears to be a marker of initial domestication in dogs and pigs (but not in animals such as sheep and goats) an artifact of a more prolonged and perhaps intense selection for association with humans?
3. Why is it that animals brought into the relationship through a directed route often do not display much evidence of morphological change, at least in terms of an archaeologically detectable change in skeletal structure?
4. Are there different genetic signatures that can be used to distinguish the behavioral adaptations that grew out of a commensal relationship from those that arose once humans began intervening in the breeding process when game management transitioned into herd management?
5. Does the intensive, focused, artificial selection for specific traits that drives the directed domestication pathway leave a distinctive genetic signature distinguishable from the broader play of selective factors and random events that shape both the commensal and prey pathways?

A second broad area for future research focuses on whether animals that followed these different pathways into domestication have different capacities for feralization. Here one might ask:

1. Are the domestic animals that followed a commensal path more successful as feral animals because they can revert to the behaviors that brought them into the relationship in the first place?
2. How do feral commensals vary from commensal species that never traveled further down the pathway into domestic relationships with humans?

Looking forward, one might ask whether thinking about the processes of animal domestication in this way has anything to offer about on-going efforts at breed improvement or at bringing new species under domestication.

1. Does this deeper understanding of the history of animal domestication have bearing on the development of animal breeding and management strategies that are more productive and/or more humane?
2. What does this understanding contribute to on-going and future efforts at bringing different terrestrial and aquatic animals under domestication?

Finally, we can ask whether this perspective on animal domestication has relevance for the care and welfare of captive animals.

1. Are there lessons to be learned from understanding the different pathways into animal domestication that would help better understand and mitigate the impact of captivity on zoo animals?
2. What are the implications of a deeper understanding of animal domestication, and in particular the route domesticates take into feralization, for efforts directed the conservation, breeding, and restoration of endangered wild species?

Answering these questions will take the combined efforts of researchers working in archaeology, genetics, and animal sciences. As this short review shows, great insights into the process of animal domestication—past and present—have already been gained from work in each of these areas. Future advances in the study of animal domestication will require not only continued work in each of these areas, but a commitment to cross-disciplinary collaborative work that seeks to integrate the information gained in each field into a more coherent and compelling understanding of this enduring and still-evolving area of human-animal interaction.

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