9 Pathways to Animal Domestication

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Jack Harlan was a polymath. His life-long study of crop evolution combined plant sciences, archaeology, systematics, genetics, and conservation, leaving a legacy of five decades of influential publications that explored all aspects of crop plants – their origins, their dispersal, and their continued and future role in supporting the Earth's burgeoning populations. To Harlan, agriculture was not an invention or the product of a single big idea. Instead, he saw agricultural origins in terms of a long co-evolutionary process involving humans and plants that grew out of "many independent tentatives in many locations that fused over time to produce effective food production systems" (Harlan 1995). Harlan's remarkable body of published work contains only one short encyclopedia entry on the subject of animal domestication (Harlan 1994). He was, in fact, somewhat dismissive of the contribution of animal domesticates to humankind's food supply stating that "(a)nimals are not essential, plants supply over 90% of the food consumed by humans" (Harlan 1995). Jack Harlan would likely agree, however, that understanding livestock evolution requires the same breadth of focus that he brought to the study of crop evolution. Here I follow Harlan's example in a consideration of domestic animals, bringing together information from animal sciences, genetics, and archaeology to explore the multiple pathways leading to animal domestication and the implications of these pathways for current and future relationships between humans and their animal partners.

1 Domestication as a process

All considerations of domestication, whether focusing on crops or livestock, acknowledge that it involves a two-way relationship between humans and target plant or animal populations. There is less unanimity in different conceptual approaches to domestication on whether emphasis should be placed on the human or the plant/animal side of the equation (see Zeder 2006a). Some cast humans as the dominant partner in a relationship in which humans consciously

and with deliberate intent assume "mastery" over all aspects of the production, movement, feeding, and protection of the domesticate (Hale 1969, Ducos 1978, Bökönyi 1989, Clutton-Brock 1994). Others see domestication as a form of biological mutualism in which both partners (humans and domesticate) reap benefits (O'Connor 1997). Some even contend that domesticates manipulated unwitting humans into relationships that gave the domesticate great evolutionary advantage at the expense of human fitness (Rindos 1984, Budiansky 1992, Morey 1994).

I take a more centrist position. I acknowledge that both partners in the domestic relationship reap benefits through their increasing reliance on each other. In this way domestication is indeed quite similar to mutualistic relationships in the natural world like those between farmer ants and "domesticated" fungi or between other ant species and their aphid "herds", the most commonly cited analogies with human plant and animal domestication (Rindos 1984). But the mutualism that lies at the heart of the domestication process differs from these convergent forms of biological mutualism in one important and uniquely human way (Schultz *et al*. 2005, Zeder 2006a, 2009). Mutualistic relationships in nature are the product of extended evolutionary processes driven by selection operating on mutation-induced variation in behavior and morphology *in both partners*, with adaptive changes in behavior and body form passed on to future generations through genetic transmission in the course of sexual reproduction. The co-evolutionary relationships between humans and target domesticates, on the other hand, are largely driven by the human ability to spontaneously invent new behaviors that maximize the return of a desired plant or animal resource and, most importantly, to pass on behaviors that best meet these goals to their offspring and to others through social learning. This capacity for the cultural transmission of learned behavior ramps up the mutualism between humans and emerging domesticates and transforms it beyond anything seen in nature. Both partners still derive mutual benefit, plants and animal partners vastly enhance their reproductive fitness and humans gain a predictable and secure resource base. But the human capacity for social learning puts humans in a dominant role in an increasingly asymmetrical mutualism that moves at a vastly accelerated pace and carries a much broader impact than any such relationship in nature.

The process of domestication unfolds across multiple axes on both the plant/animal and human sides of the equation (Figure 9.1). A primary axis on the plant/animal side involves the phenotypic expression of genetic changes that transforms the plant or animal from its wild phenotype to its domestic phenotype. Progress along this axis is driven by a number of selective and random processes that operate either sequentially or in tandem depending on the domesticate and the nature of its relationship to its human partners (see Price 1984, 1999, 2002). Human-orchestrated directed, or artificial, selection for desired traits is only one of the forces that shape a domesticate's trajectory along this axis. Other forces may play an even more important role in shaping the domestic phenotype,
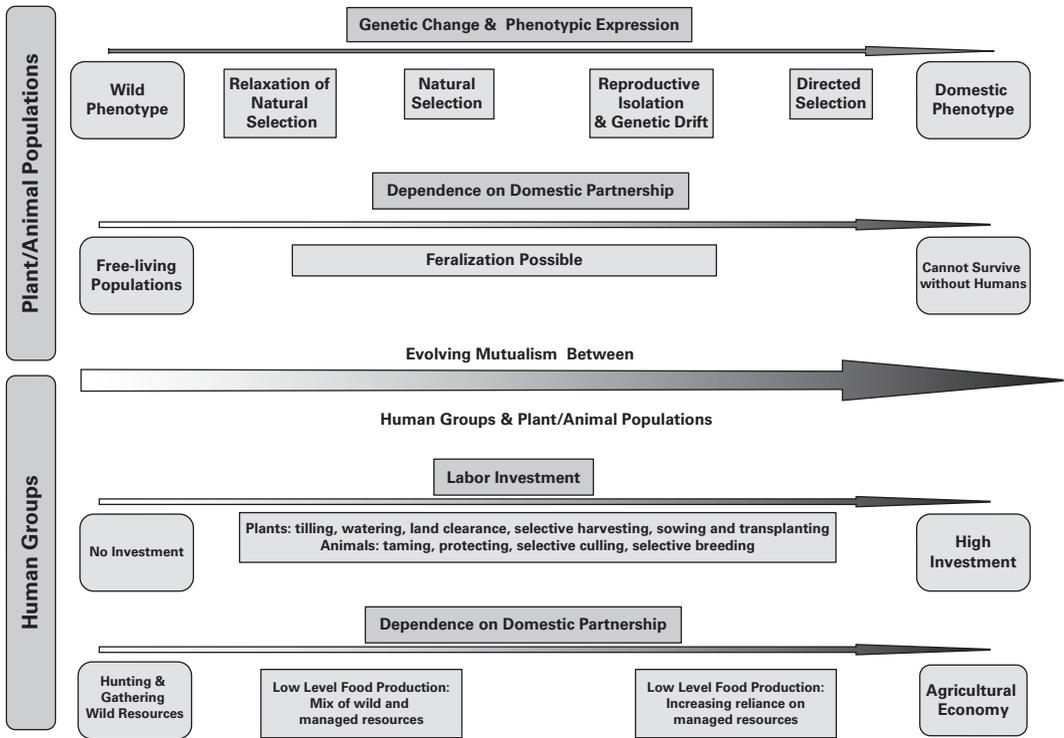
Figure 9.1. Multiple axes of domestication.

especially early on in the domestication process. These include both the relaxation of natural selection once the plant or animal comes under human control and the adaptation to the new selective pressures on the plant or animal as it enters a human environment. Random forces also play a role when, often through human-mitigated movement, small populations of plants and animals are isolated from broader breeding pools, creating "founder" populations that carry a small, more or less random selection of the much broader range of genetic variation of the progenitor population. Another axis on the plant/animal side of the partnership involves their increasing dependence of the domesticate on the relationship with humans. Movement along this axis ranges from free-living populations, to managed ones which can still revert to a wild state, to plants and animals unable to survive outside of the domestic partnership.

The degree of human investment in the plant or animal species forms an important axis on the human side of the domestic partnership. This axis moves from no investment (either because humans ignore the plant or animal entirely or do not engage in any effort to manipulate its availability), to a wide range of increasingly intensive activities aimed at encouraging the supply of a desired plant or animal resource. These behaviors may involve altering the plant or animal's environment, providing nourishment and protection from predation,

or intervening into its reproductive cycle (Harris 1996, Smith 2007a, b). Increasing human dependence on the plant or animal forms another axis on this side of the relationship. In this case, humans move from complete dependence on free-living populations, through various levels of what has been termed "low-level food production" based on a mix of managed and free-living resources, to an agricultural economy in which domesticates make up 40%–60% of human caloric intake (Smith 2001).

All these different axes operate simultaneously during the domestication process. And while every instance of plant or animal domestication involves movement along these axes, not all domesticates travel across these axes at the same pace or direction. Pathways to domestication vary depending on a range of morphological, physiological, and behavioral constraints in the target domesticate, the intensity of human investment, the importance of the resource in the human subsistence economy, and the overall environmental context within which the relationship unfolds. The challenge to those studying domestication, whether in plants or in animals, is to identify ways to trace the variable pathways to domestication and identify the forces that direct humans and domestic partners along these pathways, in the past and the present and into the future.

2   Basics of animal domestication

Although similar co-evolutionary processes drive the domestication of both plants and animals, there are fundamental differences between plants and animals that determine which taxa enter into domestic partnerships with humans and how they respond to the domestication process once underway. Characteristics that make certain plants attractive candidates for domestication center on morphological attributes (i.e., the possession of edible fruits, seeds, or underground storage organs) or growing habits (i.e., a generalized ability to colonize and adapt to open, disturbed habitats). Responses to the ongoing domestication process in plants may take the form of alterations in germination or dispersal mechanisms as plants adapt to the human-mitigated ecosystems, loss of various defenses against herbivory due to the relaxation of selective pressures for defense once humans start tending plants, or changes in fruit size, starch content, and sugar content that may arise as the result of deliberate human selection for desired traits. (Smith 2006).

In animals, on the other hand, candidacy for domestication, the targets of selection under domestication, and the responses to domestication center almost exclusively on behavioral characteristics (Hale 1969, Clutton-Brock 1981, Price 1984, 2002). Physiological and morphological responses to these pressures in animal domesticates are often secondary artifacts of the intense selection on animal behavior (Zeder 2006b). Identifying the behaviors selected for under domestication and the impact of this selection on domestic animals is, then, essential for understanding animal domestication.

Favorable Characteristics	**Unfavorable Characteristics**

1. Social Structure
  a) Large gregatrious social groups
  b) Hierarchical group structure
  c) Males affiliated with social group
2. Sexual Behavior
  a) Promiscuous mating system
  b) Males dominant over females
  c) Sexual signals provided by movement or posture
3. Parent-Young Interactions.
  a) Social bonds created through imprinting
  b) Female accepts young soon after parturition or hatching
  c) Precocial young
4. Responses to Humans.
  a) Short flight distance away from humans
  b) Low reactivity to humans or sudden changes in environment
  c) May solicit attention
  d) Readily habituated
5. Feeding Behavior & Habitat Choice
  a) Generalist feeder or omnivorous
  b) Wide environmental tolerance
  c) Non-shelter seeking
	1. Social Structure
	  a) Family groupings
	  b) Territorial structure
	  c) Males in separate groups
	2. Sexual Behavior
	  a) Monogamous mating system
	  b) Females dominate males/males appease females
	  c) Sexual signals provided by markings or morphology
	3. Parent-Young Interactions
	  a) Social bonds created on basis of species characteristics
	  b) Female accepts young on basis of species characteristics
	  c) Altricial young
	4. Responses to Humans
	  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
	5. Feeding Behavior & Habitat Choice
	  a) Specialized dietary preferences or requirements
	  b) Narrow environmental tolerance
	  c) Shelter seeking

Figure 9.2. Pre-adaptive behavioral characteristics in animal domestication. From Hale 1969, Price 1984, 2002.

2.1   Behavioral characteristics in domestic animals

Attributes thought to be "pre-adaptive" to domestication in animals can be grouped under five general categories of behaviors that affect (1) Group structure, (2) Sexual behavior, (3) Parent–young interactions, (4) Responses to humans, and (5) Flexibility (Figure 9.2), (Hale 1969, Price 1984, 2002). Many of these behaviors make it possible for humans to insert themselves in the animal community – either co-opting leadership of group structure, determining breeding partners and reproductive timing, or assuming a parenting role over young animals soon after birth. Behaviors that affect an animal's response to humans are also critical, with those that determine flight distances and reactivity to external stimuli especially important in this regard. Other pre-adaptive attributes include behaviors that afford the animal more flexibility in meeting dietary and other environmental requirements for survival. In general, the degree to which a species is pre-adapted to domestication is positively correlated with the degree to which its behavior in its natural environment resembles its behavior in its captive environment. Species with the fewest behavioral pre-adaptations to domestication are either never considered as potential domestic partners or, when domesticated, experience the most extensive changes in response to the selective pressures of the domestication process (Price 2002:22).

Once animals embark on the pathway to a domestic partnership with humans, the primary target of the new selective pressures introduced by this developing relationship are those that determine the animal's response to humans and the

human environment. In all domesticated animals, the single most important behavioral response to domestication is reduced wariness and low reactivity to external stimuli (Price 1998:51–2, 2002:18). This is true of all orders of domesticated mammals, including carnivores (Trut 1999, Coppinger and Coppinger 2001), herbivores (Tennessen 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 2002:27–9). And it is the selection for reduced wariness and low reactivity that has the most profound and most universal impact on domestic animals.

2.2   Brains and behavior

The most significant impact of this intense selection for reduced wariness and low reactivity to external stimuli is seen in the size, organization, and function of the brains of domesticated animals. Numerous studies have noted a systematic reduction in the overall size of brains in domestic animals compared with their wild progenitors (Figure 9.3), (Kruska 1988, 1996, Plogmann and Kruska 1990, Ebinger 1995, Ebinger and Röhrs 1995). Within broad classes of domesticated mammals, there is a positive correlation between the degree of encephalization (brain mass above that related to an animal's body mass) and brain size reduction. Mammals with larger brains seem to have experienced the greatest degree of brain size reduction, whereas smaller-brained mammals may experience little or no overall reduction in brain size with domestication (Kruska 1988:217, Figure 9.3). Pigs (*Sus scrofa*) seem to have undergone the greatest degree of brain size reduction of any domesticate (33.6%), followed by various domesticated carnivores in which brain size reduction varies between 20% and 30%. Brain size reduction in domesticated ungulate species ranges from 14% to 24%, while domesticated rodents show the smallest degree of brain size reduction. This same relationship generally holds true among domesticated birds (Röhrs 1985, Ebinger 1995), with the exception of domestic turkeys (*Meleagris gallopavo*) which show a large, almost 30%, reduction in brain size compared with their relatively small-brained wild counterpart – although this large difference may result from the comparison of a possibly non-ancestral wild subspecies with a highly improved modern breed of turkey (Ebinger and Röhrs 1995). Even captive-reared fish like rainbow trout (*Oncorhynchus mykiss*) show significant reduction in brain size compared with wild trout, especially in the areas of the brain linked to aggression, feeding behavior, and reproduction (Marchetti and Nevitt 2003).

The degree of brain size reduction does not seem to be positively correlated with the length of time since original domestication. Sheep (*Ovis aries*), domesticated more than 10,000 years ago, display a 24% reduction in brain size compared with ancestral species (*Ovis orientalis*), whereas ferrets (*Mustela furo*), domesticated for only 2,500 years, show a 30% brain size reduction compared with wild polecats
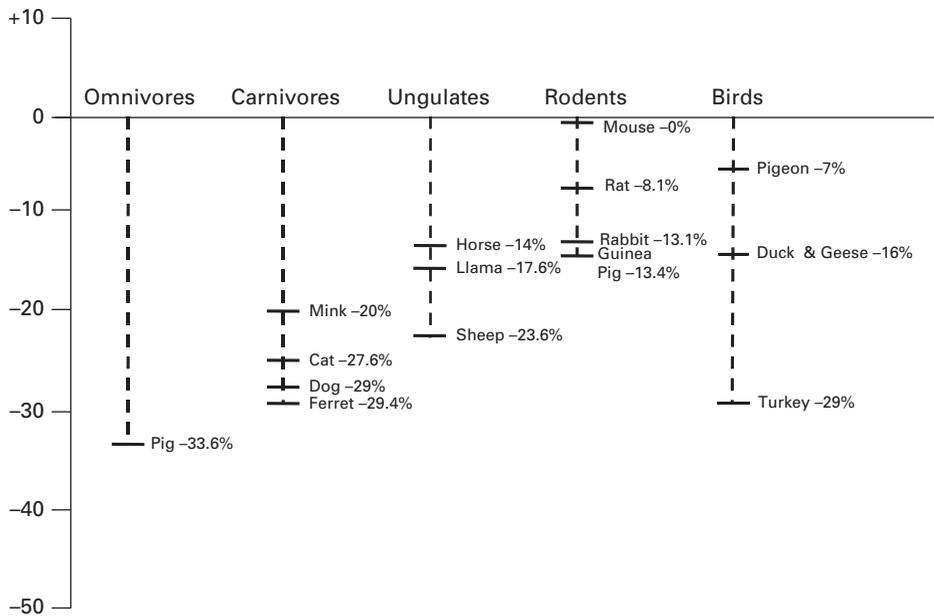
Figure 9.3. Reduction in brain size in different groups of domestic animals. Shown as the percentage of brain mass (corrected for body mass) loss compared to wild ancestral species at comparable body mass. From Kruska 1988, 1996, Ebinger 1995, Ebinger and Röhrs 1995, Rehkämper *et al*. 2008.

(*M. putorius*). Cage-reared ranch mink (*M. vison*) have experienced a 20% reduction in brain size since they were brought under domestication a little over 100 years ago (Kruska 1996). Silver foxes (*Urocyon cinereoargenteus*) selectively bred for tameness experienced a reduction in cranial height and width, and by inference in brain size, after only 40 years of intensive breeding (Trut 1999). It seems likely, then, that reduction of brain size in animals undergoing domestication may have occurred relatively quickly during the early phases of the domestication process and is directly linked to selection for reduced wariness and low reactivity to humans.

Not all parts of the brain are equally affected by the selective pressures introduced by domestication, and there are species-specific differences in the degree of size reduction in different parts of the brain in both domestic mammals (Figures 9.4 and 9.5; Kruska 1988, 1996, Plogmann and Kruska 1990) and in domestic birds (Ebinger 1995, Ebinger and Röhrs 1995). In pigs, for example, brain parts involved in the processing of auditory and olfactory stimuli are less reduced than visual structures, leading Plogmann and Kruska (1990) to conclude that structures controlling critical functions in the ancestral species may be less affected by domestication-induced brain size reduction than less critical functions. Although the telencephalon, which controls higher thought processes and sensory perception, is the region of the brain most profoundly reduced in most domestic mammals, in domestic mink the mesencephalon and the cerebellum, which control
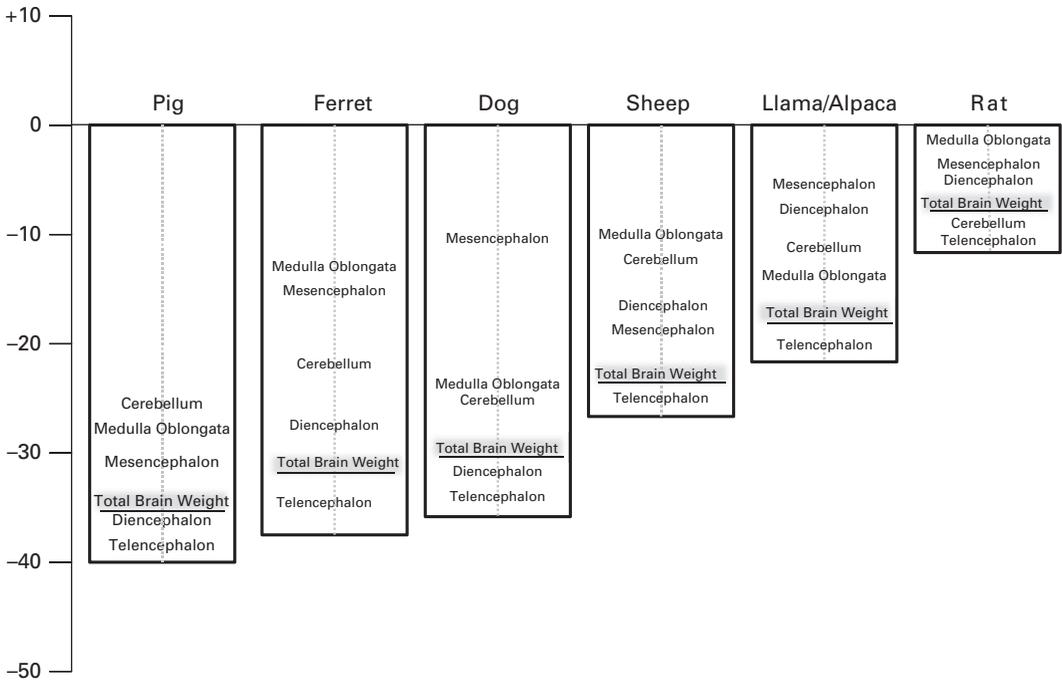
Figure 9.4. Reduction in total brain mass and size of fundamental brain structures in several species of domestic animals. Shown as the percentage of brain mass (corrected for body mass) loss compared to wild ancestral species at comparable body mass. From Kruska 1988.

body movements, show the greatest degree of size reduction – an adaptation, it is proposed, to the spatial restrictions of cage rearing in this highly active mustelid species (Kruska 1996). It is interesting to note in this regard that ranch mink kept in cages have experienced a much more significant overall reduction in brain size (20%) than mink raised in open-air enclosures, in which brain size is only 11% smaller than in wild mink (Kruska 1988, 1996, Price 2002:87). Not all brain size changes in domestic animals are in the direction of smaller size, however. Although net brain volume is reduced in domestic pigeons (*Columba livia*) compared to wild rock doves, the hippocampus, important in memory and learning, is larger, especially among racing and homing pigeons – a likely functional adaptation to homing that requires spatial cognition and sensory integration (Rehkämper *et al*. 2008). As a general rule, phylogenetically younger parts of the brain are more profoundly affected than are "older" structures (Kruska 1988:219). This general pattern is seen by some animal scientists as evidence of "regressive evolution" in domestic animals (Röhrs 1985:547). Others, however, suggest that these structures change more because they are more plastic than more basal brain structures and therefore more responsive to the relaxed need for higher-level brain functioning once humans become buffers between the animal and its environment (Price 2002:89).
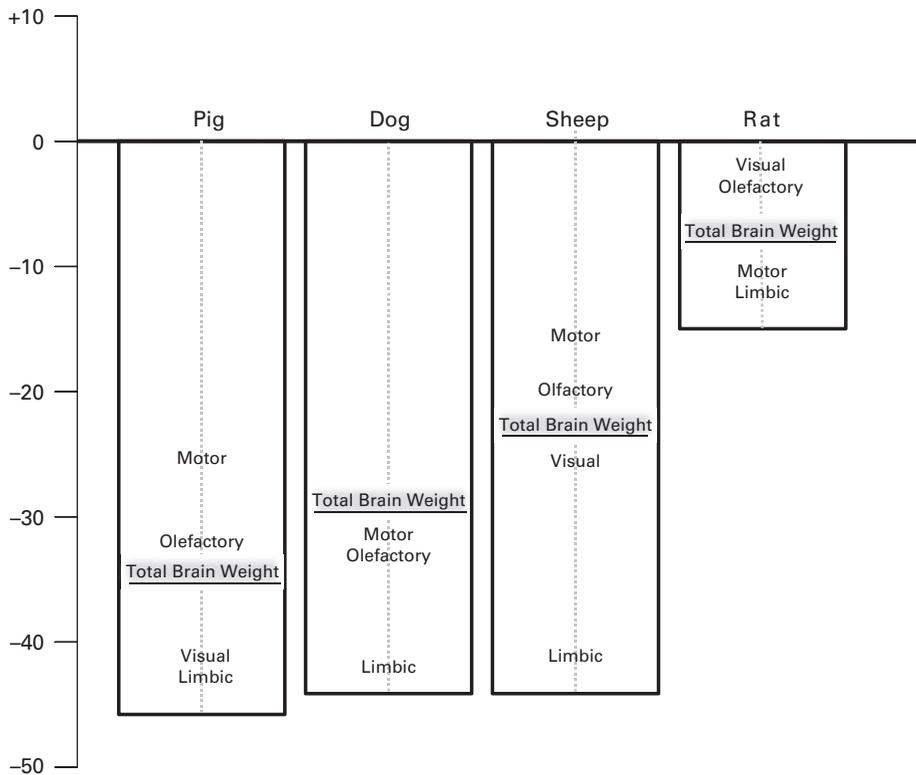
Figure 9.5. Reduction in the volume of brain structures in different functional systems in several species of domestic animals. Shown as the percentage of brain mass (corrected for body mass) loss compared to wild ancestral species at comparable body mass. From Kruska 1988.

The proposed correlation between the degree of reduction and phylogenetic age of brain structures is undercut somewhat by the fact that the region of the telencephalon most profoundly affected by domestication in highly domesticated animals, such as dogs, sheep, and pigs, is the complex set of structures that belong to the limbic system, which are embryologically, and likely phylogenetically, some of the oldest parts of the brain (Figure 9.5). Comprising the hippocampus, the hypothalamus, the pituitary gland, and the amygdala, the limbic system is responsible for controlling emotionally guided behaviors and memory. It operates by influencing the endocrine and the automatic nervous systems that directly control an animal's responses to threats and other external stimuli. The profound reduction in the size of structures within the limbic system in domestic animals can, then, be directly tied to raising the behavioral thresholds for the display of such behaviors as aggression, fear, and flight resulting in an overall reduction of emotional reactivity that is the keystone behavioral attribute of domestic animals (Kruska 1988:221, Price 2002:89).

The linkage between behavior, endocrine function, and domestication is power-fully demonstrated by the work of Künzl and colleagues, which compares behavior and endocrine function in domestic guinea pigs (*Cavia porcellus*) and wild cavies (*Cavia aperea*) (Künzl and Sachser 1999, 2000, Künzl *et al*. 2003). When compared with wild-trapped cavies and their first-generation offspring, domestic guinea pigs show significantly less aggressive behaviors and more socio-positive behaviors toward conspecifics. They are also less attentive to their surroundings, but are more likely to engage in courtship and sexual behaviors. The endocrine responses of wild and domestic cavies are also significantly different. Wild cavies subjected to stressful situations (handling and placement in an unfamiliar cage) register much higher responses in both the pituitary–adrenocortical (PAC) and the sympathetic–adrenomedullary (SAM) systems, major endocrine stress axes that under conditions of long-term hyper-activation can contribute to an animal's injury or death. At the same time, serum testosterone levels in domestic males are significantly higher than in their wild counterparts, a factor no doubt contrib-uting to the greater degree of courtship behavior seen among domestic males. The correlation between higher stress and lower courtship thresholds in domestic guinea pigs reinforces the notion that, rather than having undergone regressive evolution, domestic animals have developed highly successful adaptations to captive environments. Interestingly, captive wild cavies reared in captivity for 30 generations without selective breeding for tameness were found to exhibit the same behavioral and endocrine responses as wild-trapped cavies, suggesting that it takes more than simple captivity to bring about the attenuation of emotional reactivity found in domestic animals (Künzl *et al*. 2003). This finding is reinforced by studies that report similar differences in brain chemistry in silver foxes bred for tameness (Popova *et al*. 1991a) and in Norway rats (*Rattus norvegicus*) selected for reduced aggression to humans (Naumenko *et al*. 1989, Popova *et al*. 1991b).

2.3   Pleiotropic effects of selection for behavioral attributes

Selection for reduced wariness and low reactivity may be pleiotropically linked to other behavioral, physiological, and morphological features commonly found in domestic animals (Price 2002:79). Among these traits are those that relate to alterations in developmental events, or heterochrony, especially a reduction in the rate of change in development known as paedomorphosis. One form of paedomorphosis commonly found in domestic animals is neoteny, in which an animal passes through fewer developmental stages before it reaches adulthood so that as an adult the animal resembles a juvenile stage of its ancestor (Goodwin *et al*. 1997). Neoteny may be manifested in the early onset of sexual maturity or in the retention of both juvenile behaviors and morphology, especially the retention of juvenile cranial morphology. The classic example of domesticates thought to display all these neotenized features is the dog (Coppinger *et al*. 1987, Coppinger and Schneider 1995, Fox 1978, Goodwin *et al*. 1997, Morey 1994). Other

pleiotropically linked effects of selection for reduced aggression may be found in coat color, especially the manifestation of white markings or piebald coloration, with a connection drawn between the melanins involved in coat coloration and the biochemical pathways traveled by neurotransmitters like dopamine that play a role in shaping behavior and cognition (Hemmer 1990:121–30, see also Keeler *et al*. 1968). Features like lop ears and shortened or curled tails, which arise relatively quickly in foxes bred for tameness, may also be part of a linked complex of domestic traits (Trut 1999).

Recent work on gene expression provides a possible explanation for the pleiotropic linkage of seeming disparate behavioral, physiological, and morphological traits in domestic animals. Qualitative-trait-locus (QTL) analysis of second-generation crosses between jungle fowl (*Gallus gallus*) and white leghorn chickens (*Gallus domesticus*) successfully identified loci containing alleles that differentially affect the expression of the phenotypic traits (i.e., egg production, growth rates, plumage coloration, fearfulness, and aggression) (Jensen 2006). Specifically, several of the QTLs responsible for various productive traits were closely linked with QTLs for behavior. Extrapolating from these results, the author of this study suggests that the pleiotropic cascade of traits observed in domestic animals may be caused by mutations in regulatory genes responsible for the orchestration of gene expression during development. Under such a scenario only a handful of mutations in regulatory genes are needed to account for major and rapid evolutionary changes that separate wild from domestic animals. If so, the intense selection for certain behavioral attributes of animals embarking on a domestic partnership with humans could be responsible for a suite of other behavioral, physiological, and morphological changes in domestic animals.

2.4   The imprint of domestication

The lasting impact of the changes associated with domestication in animals can be clearly seen in feral animals that have left the domestic relationship and have reverted to living in a wild state. Sometimes referred to as a process of domestication in reverse, feralization is often looked to as a model for understanding the nature and permanence of the changes associated with domestication (Letts 1964, Hale 1969, Brisbin 1974, Price 1984, 1999, 2002).

Domestication-induced changes in brain size and function may well be irreversible. Feral dogs, cats, goats, donkeys, and ferrets that have lived outside of a direct association with humans for many generations show no sign of regaining the brain mass (Herre and Röhrs 1990, Birks and Kitchener 1999). Wild mouflon (*Ovis orientalis musimon*) on Mediterranean islands that a combination of morphological, cytological and genetic studies confirm are the feralized descendents of the domestic stock of Neolithic colonizers (Nadler *et al*. 1973, Poplin *et al*. 1986, Bruford and Townsend 2006) retain the smaller brain size of their domestic ancestors even though they look in every other regard like wild sheep (Groves

1989). Dingos (*Canis familiaris dingo*) in Australia and New Guinea, which have been living outside of a domestic relationship for thousands of years, have the same brain size as domestic dogs (Schultz 1969).

A study of feral pigs in the Galapagos found that although there was some evidence of a reversal of the effects of domestication in certain attributes, other attributes remained unchanged (Kruska and Röhrs 1974). Over the approximately 150 years since these animals were introduced onto the islands they have regained some of the body structure of European wild boar (i.e., longer legs and snouts), but still retain the coloration of domestic pigs. An examination of the brains of four of these feral animals found some increase in size of structures related to olfaction, and the size of the hippocampus may have increased slightly, although it still remained at least 30% smaller than in wild boar. The brains of feral Galapagos pigs also exhibited a greater degree of variability in the size of the limbic center. A similar degree of variability in the size of this region of the brain is also seen in wild pigs, but not in domestic swine. Kruska and Röhrs suggest that the greater degree of variability in the size of limbic structures in the Galapagos pigs might be linked to an increase in aggression and reactivity among these animals, which, though they lack natural predators on the Galapogos, have been intensively hunted by humans. However, these feral pigs showed no signs of overall brain size increase, nor was there any detectable increase in the size of the telencephalon, the region of the brain generally most significantly affected by domestication-induced brain size decrease.

The domestic imprint is also quite evident in the behaviors of feral animals. Feeding habits of feral domestic cats (*Felis catus*) in Hungary are quite generalized and include a relatively wide range of small animals, especially terrestrial mammals (Bíró *et al.* 2005). Hungarian European wild cats (*Felis silvestris*), on the other hand, specialize to a greater degree on particular small mammal species. They also consume a much higher proportion of arboreal prey that includes both small perching birds and some larger birds like pheasant and woodcock, suggesting that wild cats had more hunting prowess than feral cats. Studies of feral and wild cats in Scotland (Corbett 1979) and Iberia (Gil-Sánchez *et al.* 1999) lend support to this conclusion. Where rabbit (*Oryctolagus cuniculus*) populations are large, wild cats predate them heavily. Feral cats, in contrast, only occasionally consume rabbits in quantity and when they do they focus mainly on juvenile or sick individuals. Moreover, although the Hungarian feral cats are much less likely to consume household foods than scavenging domestic cats, they nevertheless derive one-fifth of their prey from human settlements (Bíró *et al.* 2005). Wild cats in this study took no prey from human settlements. Free-ranging cats and dogs in southeastern Brazil are found in significantly higher density in suburban areas than in rural ones, suggesting that these animals retain a strong connection to the human environment and are not exploiting more open niches in rural areas to the same extent (Campos *et al.* 2007).

In a broad-ranging synthesis of the literature on the social ecology of feral dogs (*Canis familiaris*), Boitani and Cuicci (1995) conclude that even fully feralized

animals, which receive no food or shelter from humans and show a strong avoidance of human contact, are still dependent on the human niche for survival and have not regained the self-sustaining behaviors found in wolves (*Canis lupus*). Whereas wolves live in single family packs with established hierarchical social structure, feral dogs live in fluid groups made up of breeding pairs. The size of these groups is limited by the lack of social structure and other social bonds that keep wolf packs operating as functional units. Although feral dogs generally have larger litters and breed more frequently than wolves, they lack the parenting skills of wolves, often leaving very young pups unattended, resulting in high juvenile mortality. Older feral pups also suffer higher mortality rates than wolf pups of comparable age when they leave the den to explore and forage on their own or when their mother enters a new oestrous cycle and loses interest in her most recent litter. As a result, groups of feral dogs are not self-sustaining and can only be maintained through recruitment of new members from populations of stray dogs. Feral dogs do not hunt in packs like wolves and, again unlike wolves, feral pups are not taught to hunt by adult animals. As a result these dogs have a highly diversified diet comprising primarily smaller, easier to catch prey. Although they may not receive food directly from humans, they still concentrate on human-mitigated landscapes when foraging for food.

Thus the imprint of domestication on animals is profound. Domestication-induced changes in brain size and function are deep-rooted and perhaps irreversible. Behavioral attributes selected for during domestication make it difficult, if not impossible, to recapture the behaviors and social ecology that sustained their progenitors in the wild. Feral animals attempting to divorce themselves from the domestic partnership with humans seem only partly successful in doing so and in many ways remain strongly tied to humans, even if indirectly.

3 Pathways to domestication

There seem, then, to be universal attributes found in almost all domestic animals in the behaviors selected for under domestication and the impact of this selection on brain form and function. But did all domestic animals acquire these attributes in the same way? Did all animal domesticates travel the same general pathway that took them from free-living wild animals to animals forever tethered to a partnership with humans, even when they attempt to revert to the wild state? I think that there is ample evidence that this is not the case and that even though there are universal attributes found in all animal domesticates, the pathways to animal domestication were highly variable and contingent on broadly defined biological and cultural parameters, as well as a range of highly localized factors that shaped the trajectories of individual cases of animal domestication (Zeder 2009). These varied pathways can, however, be grouped into three general domestication scenarios that seem to account for the full spectrum of animal domesticates – a commensal pathway, a prey pathway, and a directed pathway (Figure 9.6).
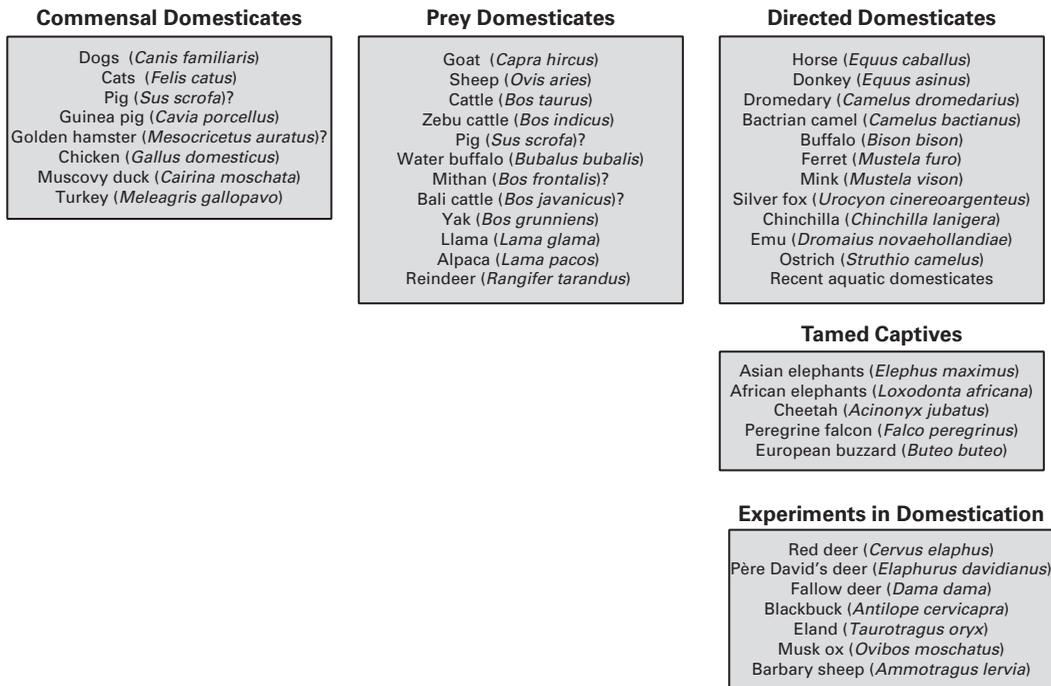
Commensal Domesticates

Dogs (*Canis familiaris*)
Cats (*Felis catus*)
Pig (*Sus scrofa*)?
Guinea pig (*Cavia porcellus*)
Golden hamster (*Mesocricetus auratus*)?
Chicken (*Gallus domesticus*)
Muscovy duck (*Cairina moschata*)
Turkey (*Meleagris gallopavo*)

Prey Domesticates

Goat (*Capra hircus*)
Sheep (*Ovis aries*)
Cattle (*Bos taurus*)
Zebu cattle (*Bos indicus*)
Pig (*Sus scrofa*)?
Water buffalo (*Bubalus bubalis*)
Mithan (*Bos frontalis*)?
Bali cattle (*Bos javanicus*)?
Yak (*Bos grunniens*)
Llama (*Lama glama*)
Alpaca (*Lama pacos*)
Reindeer (*Rangifer tarandus*)

Directed Domesticates

Horse (*Equus caballus*)
Donkey (*Equus asinus*)
Dromedary (*Camelus dromedarius*)
Bactrian camel (*Camelus bactianus*)
Buffalo (*Bison bison*)
Ferret (*Mustela furo*)
Mink (*Mustela vison*)
Silver fox (*Urocyon cinereoargenteus*)
Chinchilla (*Chinchilla lanigera*)
Emu (*Dromaius novaehollandiae*)
Ostrich (*Struthio camelus*)
Recent aquatic domesticates

Tamed Captives

Asian elephants (*Elephus maximus*)
African elephants (*Loxodonta africana*)
Cheetah (*Acinonyx jubatus*)
Peregrine falcon (*Falco peregrinus*)
European buzzard (*Buteo buteo*)

Experiments in Domestication

Red deer (*Cervus elaphus*)
Père David's deer (*Elaphurus davidianus*)
Fallow deer (*Dama dama*)
Blackbuck (*Antilope cervicapra*)
Eland (*Taurotragus oryx*)
Musk ox (*Ovibos moschatus*)
Barbary sheep (*Ammotragus lervia*)

Figure 9.6. Possible pathways to domestication of animal species mentioned in the text.

3.1   Commensal pathway

The first of these pathways, the commensal pathway, is most frequently traveled by animals that come into initial contact with humans to feed on refuse or to prey on other animals attracted to human settlements. At some point in their association with humans and human habitats, these animals developed closer social or economic bonds with their human hosts than did other commensals inhabiting this niche. These bonds brought them, eventually, into a domestic partnership with humans. The classic example of an animal that likely traveled this pathway to domestication is the dog, whose domestication is thought to have begun when less wary wolves were drawn to human encampments to scavenge on human refuse (Coppinger and Coppinger 2001, Morey 1994). In a comparative study of the skeletal morphology of wolves and dogs, Morey (1992) concludes that the principal difference between the dog and its wild progenitor lies in the juvenilization of the adult dog's cranial morphology, which resembles that of a juvenile wolf in its shorter face, steeped forehead, and wider cranial dimensions. Morey suggests that these differences in cranial morphology are artifacts of neotenization arising out of a general process of paedomorphism in develop-mental rates (see also Trut 1999, but see Wayne 1986, who contends that dog and wolf skulls differ primarily in cranial width, which is not a paedomorphic trait). The mandibles of dogs are shorter than those of wolves and there is

considerable reduction in the length of their molars (Wayne 1986). These features are found in even the earliest examples of domestic dogs like the 13,000-year-old mandible recovered from Palegawra Cave in northeastern Iraq, which shows clear evidence of tooth size reduction and crowding in a shortened jaw (Turnbull and Reed 1974). The dogs buried with humans at the roughly contemporary site of Ain Mallaha in the southern Levant also display these traits, and their occurrence in burial contexts speaks to the strong social bonds that had been forged between dogs and humans at this early date (Davis and Valla 1978, Tchernov and Valla 1997, Morey 2005). This same site also contains some of the earliest remains of commensal animals like the house mouse (*Mus musculus*), the spiny rat (*Echimys chrysurus*), and the house sparrow (*Passer domesticus*) (Tchernov 1991), species that traveled a commensal pathway into close association with humans but that, unlike dogs, did not complete the journey to domestication. Recent genetic data support archaeological evidence that suggests initial dog domestication took place in the Near East (vonHoldt *et al*. 2009).

A surprising number of common domestic animals may have traveled this same pathway to domestication. Archaeological evidence pushes back the date of cat domestication to at least 8,500 years ago (Vigne *et al*. 2004), and new genetic evidence points to a Near Eastern origin for initial cat domestication (Driscoll *et al*. 2007). It is likely, then, that cats, like dogs, were drawn into initial contact with humans when humans began to live in more permanent settlements and these obligate carnivores were attracted to human habitats to prey on other small commensal species occupying this niche. Interestingly, however, cats did not experience similar changes in cranial morphology, nor does the social ecology of these more solitary animals seem as profoundly altered by domestication.

Chickens, which genetic evidence suggests were domesticated multiple times in southeast Asia, China, and perhaps India (Liu *et al*. 2006, Kanginakudru *et al*. 2008), may also have entered the domestic relationship with humans through a commensal pathway as wild jungle fowl sought out human dump heaps for easy sources of grain. A similar pathway might be suggested for the domestication of the turkey in the southwestern US (Munro 2011). Muscovy ducks (*Cairina moschata*) in Amazonia have been argued to played an important role in reducing insect populations in human settlements (Angulo 1998), an outgrowth, perhaps of a similar initial commensal introduction into the human sphere. Another likely commensal domesticate is the guinea pig (*Cavia porcellus*), first domesticated in the highland Andes around 7,000 years ago (Spotorno *et al*. 2006). Golden hamsters (*Mesocricetus auratus*), which are indigenous to Syria, Israel, and eastern Turkey and known for the ease with which they can be handled in the wild, are another candidate for a commensal domesticate – although the hamsters kept so widely today as pets and laboratory animals are thought to be descendants of a quite recent and deliberate domestication of hamsters from dwindling wild populations (Murphy 1985).

It is also possible that pigs, a major livestock species, entered into domestication through a commensal pathway. Archaeological evidence from the site of Hallan Çemi in southeastern Anatolia suggests that, as with dogs and cats, a special

relationship between pigs and humans began as early as about 12,000 calendar years ago, soon after humans began living in more established year-round settlements (Redding 2005). There are multiple lines of evidence for the intensification of this relationship over the course of nearly 3,000 years of occupation (from 10,500 to 8,300 cal BP) at the near by site of Çayönü (Ervynck *et al*. 2001, Hongo *et al*. 2002). As with dogs, the leading edge indicator of pig domestication is a gradual reduction in molar length, a marker of domestication in pigs thought to result from the neotenization of skull morphology (Flannery 1983). These gradual changes in tooth morphology are first detected several hundred to a thousand years prior to the appearance of other markers of pig domestication at this site. Ervynck *et al*. (2001) see this long lead-up period as evidence of an evolving mutualism between pigs and humans initiated by wild pigs originally drawn to human settlements to scavenge off refuse dumps.

3.2   Prey pathway

Most major livestock species, however, entered into domestication through what might be called a prey pathway. Rather than initiating the relationship, these animals were primary prey species that humans had hunted for their meat and hides for thousands of years. The prey pathway likely began when, perhaps as a response to depletion of local stocks of these prey animals, humans developed hunting strategies designed to increase prey availability. Over time and under certain circumstances, these game management strategies developed into actual herd management and, eventually, the controlled breeding of managed animals.

Archaeological evidence from the Near East suggests that sheep (*Ovis aries*), goats *(Capra hircus)*, and cattle (*Bos taurus*) all followed this pathway to domestication, with the transition from generalized hunting to specialized hunting and then herd management taking place within the natural habitats of wild progenitor species (Zeder 2008a, 2009, 2011). This process seems to have unfolded over many hundreds, if not thousands, of years without any clear-cut, archaeologically detectable morphological changes in the animals traveling down this pathway to domestication. These early stages of the transition from hunting to initial management may only be detectable in the demographic profiles of the animals harvested by humans, especially in the separate harvest patterns of male and female animals. Constructed using the fusion patterns of post-cranial skeletal elements, these sex-specific harvest profiles are capable of distinguishing between the prey strategies of hunters that seek to maximize immediate meat return (often reflected by an emphasis on large adult males) from those of herders directed at promoting herd growth (most commonly met by the early harvest of all but a few males and the delayed cull of older females past peak reproductive years) (Zeder 2006b, 2008b). This distinctive herd management harvest profile is first detected in goat assemblages from the archaeological site of Ganj Dareh in the Central Zagros Mountains of modern-day Iran at about 10,000 calendar years ago (Zeder and Hesse 2000, Zeder 2006b, 2008b). Lower-resolution harvest data collected by

using other methods, however, suggest that the management of both sheep and goats began perhaps 500 to 1,000 years earlier in the highland regions of the eastern Taurus and northwestern Zagros Mountains (Peters *et al*. 2005, Zeder 2008a, 2009, 2011). The initial phases of the transition from hunting to herding in this region may also reach back to about 12,000 to 13,000 calendar years ago. New demographic data from southeastern Turkey and northwestern Iraq point to the development of hunting strategies, which may have helped restock local herds of wild sheep depleted by people living in increasingly sedentary settlements (Redding 2005, Zeder 2008b, 2009). Demographic data for cattle suggest that a similar process was underway in the upper Euphrates Valley by about 10,500 to 10,000 years ago (Helmer *et al*. 2005).

A recent genetic analysis by Naderi *et al*. (2008) has identified all six domestic goat lineages among modern wild bezoar goats from eastern Turkey and western Iran. The authors of the study argue that the presence of these domestic haplogroups among wild goats is not an artifact of recent introgression between domestic and wild goats. They maintain instead that genetic signatures of population growth and geographic translocation represent residual evidence of initial human domestication of these different lineages and the human-mitigated movement of managed animals within and out of this heartland region of initial domestication. This exciting new study suggests that although the prolonged periods of human management of goats within their natural habitat had no detectable morphological impact on these animals, it nevertheless left a genetic imprint observable even today among the descendant populations of wild goats from which domestic lineages were originally drawn.

Domestication-induced morphological change in animals traveling along this prey pathway may only be detectable once humans took managed herds out of the natural habitat of their wild progenitors where factors like genetic drift and adaptation to new environments came into play. The movement of managed herds outside of the range of wild populations also eliminated the chance of introgression between wild and managed animals or the possibility of restocking managed herds with wild animals – both probably quite common occurrences in the initial phases of herd management. Once this link was cut in managed sheep and goats, we begin to see distinctive changes in horn size and shape like those evidenced at about 9,500 to 9,000 cal. BP among the remains of goats recovered from the archaeological site of Ali Kosh in lowland Iran (Zeder 2006b). Changes in the size and shape of horns of domesticated ungulates like sheep, goat, and cattle likely arose from a combination of factors including: (1) the relaxation of selective pressures for large horns previously used to both attract and compete for females, (2) the expression of random mutations previously selected against when horns were used in mate competition, (3) the impact of new selective pressures against energetically expensive and no-longer-needed horn architecture, and (4) directed human selection for more tractable males.

These same factors likely also played a role in changes in body size in these early domestic livestock species. However, rather than an overall reduction in the body

size of initial domesticates as was once thought to be the case (Uerpmann 1979, Meadow 1989), it now seems more likely that domestication-induced body size changes in early livestock species took the form of a reduction in the degree of sexual dimorphism, especially a shortening in the length of the legs of males (Zohary *et al.* 1998, Zeder 2001, 2006b, Helmer *et al.* 2005). Smaller body size in archaeological populations of managed sheep and goats is not seen until sometime after 9,000 cal BP, and it is not clear whether the smaller size of these animals is an artifact of domestication, of climate change, of the introduction of smaller-bodied domestic stock from different regions, or of a general process of body size reduction that began with the end of the last Ice Age and has affected domestic and wild ungulates alike (Zeder 2006b, 2008b).

In addition to these core Near Eastern livestock species, it is likely that other common animal domesticates followed this prey pathway to domestication. This includes East Asian sheep, which genetic data suggest were independently brought under domestication (Guo *et al.* 2005) and perhaps the pigs independently domesticated in East Asia and in Europe (Larson *et al.* 2005, 2007). It is hard to say in the case of pigs, however, whether these separate domestication events followed a commensal path, a prey path, or in the case of the European wild boar the final directed pathway discussed below. Other likely prey pathway domesticates are the humped zebu cattle (*Bos indicus*) and the water buffalo (*Bubalus bubalis*) domesticated in South Asia (Fuller 2006, Kumar *et al.* 2007). The yak (*Bos grunniens*) is another early domesticate that may have been brought under domestication in this way in the Himalayas (Olsen 1990, Guo *et al.* 2006). The mithan (*Bos frontalis*) of South Asia and the Bali cattle (*Bos javanicus*) of island Indonesia, whose origins are poorly understood (Clutton-Brock 1981:137–8), may represent additional examples of prey pathway domesticates. The increasingly well-resolved record of the domestication of South American camelids clearly points to a prey pathway along which the heavy predation of the guanaco (*Lama guanaco*) and the vicuña (*Vicugna vicugna*) developed into initial management and then full domestication of the llama (*Lama glama*) and the alpaca (*Lama pacos*) (see Mengoni-Goñalons and Yacobaccio 2006, Wheeler *et al.* 2006).

Reindeer (*Rangifer tarandus*) may be the most recent, and perhaps last, species to follow a prey pathway to domestication. In many ways, reindeer herding serves as a good model for the initial stages of domestication of other prey pathway domesticates like sheep and goats. The only successfully domesticated cervid species, these cold-adapted gregarious herd animals have been heavily predated by humans since the last Ice Age (Speiss 1989). The close association between hunters and reindeer in the northern Eurasian Holarctic stretches back thousands of years with the loose domestic partnership between humans and reindeer thought to have developed sometime in the past 2,000 to 3,000 years (Mirov 1945, Gordon 2003). Baskin (1974) sees reindeer herding as the product of sophisticated hunting methods in which reindeer hunters, familiar with the migratory routes of wild reindeer herds, drove reindeer into stone traps or human settlements where they could be harvested at will. Over time northern peoples

developed a number of different reindeer herding strategies including a "close" herding system that involves following large demographically diverse herds of migrating animals, a "free-camp" system in which smaller herds are kept within the vicinity of human settlements, and a "loose system" in which free-ranging animals are periodically gathered and moved to different pastures (Baskin 2000). Managed reindeer are exploited for their meat, hides, and antlers, for their use as draft animals and for riding and traction, and, to a lesser extent, for milk. Reindeer herding takes place alongside active hunting of wild reindeer, with domestic females sometimes used in the past as "bait" to attract wild males (Manker 1963:16). As appears to have been the case with other prey domesticates like sheep and goats during initial stages of their management, there are no major morphological differences between wild and domesticated reindeer that would be detectable archaeologically (Clutton-Brock 1981:134).

Recent genetic analysis of modern wild and domestic reindeer from localities across Eurasia (Røed et al. 2008) extends the homology between reindeer herding and the initial stages of caprine domestication even further. As with sheep and goat, there is evidence for multiple independent reindeer domestication events within the natural habitat of the wild reindeer. One such "event" was apparently localized in the western part of their range in Fennoscandia, with perhaps two additional events occurring in western and eastern Russia. The high level of genetic diversity in domestic reindeer herds is seen as an artifact of the frequent augmentation of domestic herds with local wild reindeer. The authors of this study also found evidence for the frequent introgression of domestic haplotypes into wild herds. Some wild populations in Finland and Norway and a population in southeastern Russia, however, seem to have contributed no genetic material to domestic stock. Røed et al. interpret the different contribution of various wild populations to domestic populations as evidence of the differential domestication potential of wild reindeer. The more gregarious populations residing in open tundra habitats, they argue, were more attractive candidates for domestication. Forest-dwelling populations that may have been less well pre-adapted to domestication, however, seem not to have played a role in this process. This system has many parallels with that documented in the Naderi et al. (2008) study of goats in the Zagros, providing a living model of a management system which, though it leaves no mark in the morphology of the managed animals, has a lasting genetic imprint on both managed animals and the wild populations from which they were drawn.

3.3   Directed pathway

The prey pathway was likely driven by the goal of securing a predictable source of protein in the form of animal flesh. But it did not take long before people started to exploit other, largely regenerative secondary animal resources. Recent analysis of lipid residues found in pottery from sites in Turkey and the Levant indicates that dairying may have been well established, especially in northwestern Anatolia,

by about 8,500 calendar years ago (Evershed *et al*. 2008). A figurine of a wooly sheep from the site of Sarab in the highlands of western Iran has been interpreted as evidence that changes in coat composition needed for wool production were in place by about 7,500 calendar years ago (Bökönyi 1977). Finding direct evidence for the use of animals like cattle for traction is difficult, but the discovery of a ceramic bull with a churn on its back in the southern Levant suggests that the use of cattle for both dairy products and labor had been established by 6,000 years ago (Ussishkin 1980). The precedent set by the domestication of former prey species and the broadening of the range of resources extracted from them paved the way for the final category of animal domestication – the directed pathway. This fast-track to domestication begins when humans use knowledge gained from the management of already domesticated animals to domesticate a wild species that possesses a resource or a set of resources that humans see as desirable.

This is likely the pathway followed in the domestication of the horse (*Equus caballus*), which both archaeological and genetic evidence suggests was domesticated, perhaps multiple times, across the steppe regions of central Eurasia (Levine 1999, Olsen 2006, Vilà *et al*. 2006). Possibly originally domesticated to help in the hunting of wild horses (Olsen 2006), domestic horses also provided people with a wide array of primary and secondary resources, including meat, hides, milk, draft, traction, and transport. It is interesting to note that none of the traditional markers used to track domestication in animals that followed the commensal or prey pathways is useful in documenting horse domestication. There are no apparent morphological markers that can be used to discriminate domestic horses from wild horses (*E. ferus*), nor are demographic profiles much use in distinguishing management strategies from prey strategies. Instead, archaeologists employ multiple lines of circumstantial evidence to monitor this process, including butchery practices, evidence of corrals, the presence of quantities of manure signaling corral cleaning, or the use of manure as building materials, and changes in long-distance transport of lithic resources (Olsen 2006). The most recent, and perhaps most compelling, evidence of horse domestication is provided by the successful retrieval of equine milk lipids in 5,500-year-old pottery from northern Kazakhstan (Outram *et al*. 2009).

Donkeys (*Equus asinus*) are another animal that likely entered into the domestic partnership with humans through this route. Genetic evidence puts the initial domestication of two populations of wild Nubian ass (*E. a. africanus*) in northern and northeastern Africa (Kimura *et al*. 2010), with recent thinking crediting their domestication to pastoral people who about 6,000 years ago began to use these desert-adapted animals to carry heavy loads across arid lands (Rossel *et al*. 2008). As with the horse, however, traditional archaeological markers of animal domestication have been of little utility in tracing the process of donkey domestication. Rossel *et al*. (2008) provide compelling evidence for the use of donkeys as beasts of burden in their analysis of ten complete ass skeletons recovered from an early pharaonic mortuary context at Abydos in Middle Egypt. All of these ritually

slaughtered animals show unambiguous signs of, often quite advanced, spondylo-arthopathies, vertebral pathologies consistent with the exertion of considerable pressure on the spine. Appendicular skeletal elements of these animals also display considerable compression-induced pathologies, leading to the unmistakable conclusion that these were fully domesticated animals used to carry heavy loads. Morphometric analysis, however, found that the metapodials of these domestic donkeys (the bone thought most likely to respond to any changes in body size or life habits in these animals), closely resemble the metapodials of wild asses (especially the Nubian wild ass) and, in most respects, are quite distinct from the metapodials of modern domestic donkeys. Even though the ass was likely brought under domestication at least 1,000 years before the burial of these ten sacrificial animals, the only hint of domestication-induced morphological change in the Abydos donkeys is a slight modification in metapodial mid-shaft depth and distal breadth dimensions.

Other likely instances of directed domestication are provided by Old World camels, both the one-humped dromedary (*Camelus dromedarius*) of the Arabian Peninsula and the two-humped Bactrian camel (*C. bactrianus*) of Central Asia. Once again there is little direct evidence for camel domestication. There are no archaeologically detectable morphological differences between the domestic and wild two-humped camels (Peters and von den Driesch 1997). Moreover, although there are no longer any wild one-humped camels to compare with the domestic dromedary, there is little evidence of morphological differences in the skeletons of camels from likely pre- and post-domestication contexts in the Arabian Peninsula (Clutton-Brock 1981:124–6). In the absence of distinctive morphological change, the presence of camel dung and hair at the site of Shahri-Sokhta in far eastern Iran and the recovery of figurines of camels attached to clay carts from archaeological sites in Turkmenistan dated to between 3,000 and 2,500 BC have been interpreted as circumstantial evidence that two-humped camels had been domesticated by the third millennium BC (Masson and Sarianidi 1972, Compagnoni and Tosi 1978, but see Peters and von den Driesch 1997). A case of the domestication of the one-humped camel in the Arabian Peninsula is based on the abundance of camel remains from third millennium sites in Oman and associated mortality patterns indicating a shift from a prime adult harvest strategy to an emphasis on the slaughter of juvenile animals (Hoch 1979, but see Uerpmann and Uerpmann 2002). If indeed both these species were brought under domestication during the third millennium BC, the primary target of these two instances of directed domestication may well have been their utility in carrying people and goods across vast arid regions in both Central Asia and in the Arabian Peninsula and the important role these animals might have played in the active global trade networks that developed during this time (Zeder 2006c, Zeder *et al*. 2006).

Elephants, both Asian and African (*Elephas maximus* and *Loxodonta africana*), also represent animals brought under human control for a directed purpose – either for carrying large loads or for heavy labor (a purpose for which Asian elephants are still used today), or for use in hunting, warfare, or in public

spectacles (as was the case for both African and Asian elephants in antiquity and today with circus performers) (Clutton-Brock 1981). Given the long life span of elephants, their slow maturation rate, the difficulty in getting captive elephants to breed, and the relative ease with which captive young adults can be tamed and trained to perform desired tasks, elephants used for these purposes are generally not bred in captivity (Baker and Manwell 1982). Instead, domestication begins anew with each young animal that is captured and tamed. Another captive animal that has been tamed and used for a directed purpose is the cheetah (*Acinonyx jubatus*) that Ancient Egyptians, Assyrians, Mogul emperors, and Medieval European elites kept as pets and hunting companions (Clutton-Brock 1981). Falcons and other trained birds of prey (e.g., *Falco peregrinus* and *Buteo buteo*) used in hunting are also generally not bred in captivity, another example of a captive animal brought under human control for a specific purpose that did not follow the subsequent pathway to full-fledged domestication.

Recent examples of directed domestication include the various carnivore and rodent species, like mink (*Mustela vison*) and chinchilla (*Chinchilla lanigera*) that have been selectively bred for coat quality over the past 100 – 200 years. Other examples of animals following this pathway to domestication also include even more recent domesticates, like buffalo (*Bison bison*), emu (*Dromaius novaehollandiae*), and ostrich (*Struthio camelus*) bred for their meat and hides. Experiments in domestication are currently underway, with mixed success, with a number of terrestrial mammals including red deer (*Cervus elaphus*), Père David's deer (*Elaphurus davidianus*), fallow deer (*Dama dama*), blackbuck (*Antilope cervicapra*), eland (*Taurotragus oryx*), musk ox (*Ovibos moschatus*), and Barbary sheep (*Ammotragus lervia*) (Clutton-Brock 1981:177–87, Hemmer 1990:161–77). The number of freshwater and marine species (both vertebrates and invertebrates) brought under human management has increased markedly over the past 100 years. Ninety-seven percent of the 430 currently managed aquatic species were brought under human control during the twentieth century, 100 of these species in just the past 10 years (Duarte *et al*. 2007). The staggering explosion of aquaculture as a major world-wide industry has momentous implications for the human food supply, for biodiversity, and for the environment.

3.4   A domestication road atlas

There are, then, multiple pathways to animal domestication, which vary in length, direction, and travel time (Figure 9.7). The progress of individual animal domesticates and their human partners down these different paths is highly variable and shaped by the combination of constraints and opportunities, biological and cultural, that these fellow travelers face while they make the domestication journey.

It probably took a long time for animals traveling the commensal pathway to move from being simply habituated to humans and human habitats to developing an active partnership with humans (Figure 9.7a). The timing and the nature of the
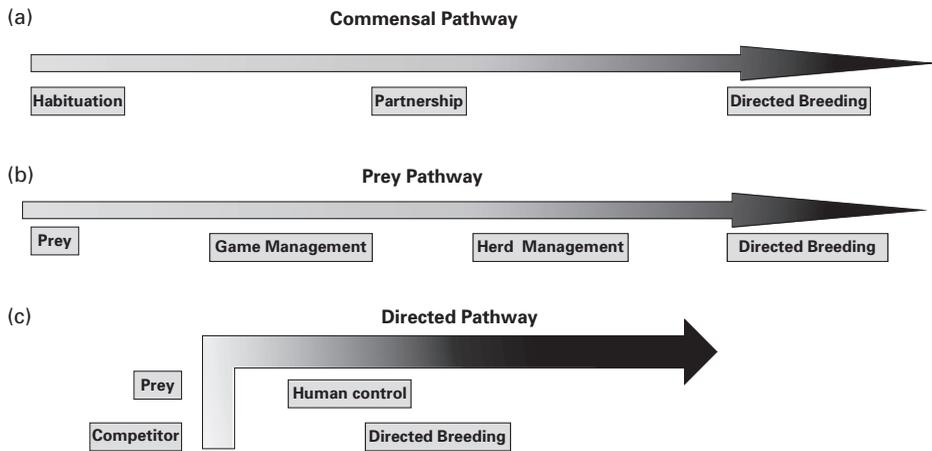
Figure 9.7. Pathways to domestication. (a) Commensal pathway, (b) prey pathway, (c) directed pathway.

forces that propelled the next and final stage of the journey – human-directed breeding and more or less complete subjugation to human control – likely varied in different commensal domesticates. And some animals entering into domestic partnership through this route – like the cat – have arguably never reached this final destination.

While animals traveling the commensal pathway began the journey on their own initiative, animals entering into a domestic partnership with humans though the prey pathway were likely less willing fellow travelers. As with the commensal route, however, progress down the prey pathway was also likely quite slow and possibly circuitous, as generalized hunting strategies evolved into game management strategies aimed at promoting availability of prey species, which, in turn, morphed into the selective harvest of managed animals, followed, at some perhaps quite distant part of the road, by directed breeding (Figure 9.7b). But not all animals traveled this route in the same way, nor did all animals embarking on this pathway reach its conclusion. A strong case can now be made that sheep, goats, and cattle all traveled a quite direct, if lengthy and slow, prey pathway to domestication in central and eastern portions of the Fertile Crescent arc that stretches from southern Iran, across northwestern eastern Iraq and southeastern Turkey, into Lebanon, Israel, and eastern Jordan. Pigs in the central Fertile Crescent, in contrast, may have wandered between prey and commensal pathways at different points of the journey. Moreover while humans and these four future livestock species were beginning down pathways to domestication, in the western arm of this Fertile Crescent region people and gazelle (*Gazella subgutturosa* and *G. gazella*), the primary prey species in the northern and southern Levant, may also have been taking the first tentative steps down a prey pathway to domestication. Gazelle hunting strategies seem to intensify in the Levant at about 12,000 calendar years ago (Munro 2004) and there is some

indication that humans were altering prey strategies to promote availability of this key resource in ways that were having some impact on the demographic structure of gazelle populations (Davis 1983, Henry 1989, Cope 1991, but see Sapir-Hen *et al.* 2009). Parallels can be found between the corrals and traps used much later by Eurasian Arctic peoples early on in the process of reindeer domestication (Baskin 1974) and the stone kites and possible corrals found throughout the Levant that are thought to have been used to capture migrating gazelle (Legge and Rowley-Conwy 1987, Betts and Yagodin 2000, Bar-Oz *et al.* 2011). Redding (2005) has recently suggested these structures may also have served as holding areas for animals that could be consumed as needed, clearly a step toward animal management. Gazelle, however, are behaviorally less well suited than sheep and goat to domestication. They have very strongly developed flight reflexes and an aversion to penning, and are highly territorial and unlikely to breed well in captivity (Clutton-Brock 1981:172). These behaviors are thought to have made it impossible for gazelle to travel much further down the prey pathway than the early stages of game management.

The final directed pathway is a much shorter and speedier route to animal domestication. Animals traveling down this path may have begun as human prey or competitors for prey, or may have had little or nothing to do with humans. However, once embarked on this pathway they took an immediate and abrupt departure from a free-living state to one in which they were under tight human control that often involved intensive and deliberate breeding to enhance targeted resources. Animals selected for the directed pathway may have possessed few of the pre-adaptive behaviors that qualified other animal domesticates for a trip down either the commensal or prey pathways, and their domestication likely required intensive efforts to overcome behavioral and biological barriers to domestication. Today this route has become a kind of domestication super-highway as animals that previously would never have been considered candidates for domestication are brought under human control through the application of increasingly sophisticated technology for animal breeding and care, and the enhanced understanding of animal behavior, reproduction, and biological requirements coming out of the animal sciences (Price 2002:22).

4   Questions for future research

Categorization of the various pathways to animal domestication in this way raises a number of questions that point to productive areas for future research. First, it would be interesting to know whether there are differences in the timing and the nature of the behavioral, physiological, and morphological responses animals make to the selective pressures they experience along these different pathways to domestication. A related question asks whether these selective pressures leave distinctive genetic, morphological, or other archaeological markers that can be used to detect the various paths taken to domestication. Are animals that enter

domestication through a commensal route, with its long "getting-to-know-you" phase of habituation to humans and human environments, tamer and more integrated into human society than animals that traveled the prey pathway? Are the changes in cranial form seen as an early marker of domestication in dogs and pigs, but not as apparent in animals such as sheep, goats, or horses, an artifact of a more prolonged and perhaps more intense selection for human habitation? If so, why is it that other animals that may have taken this same commensal route, such as the cat, do not display similar cranial morphology? Why is there often little evidence of morphological change in animals brought into the domestic relationship by way of the directed route? Are there different genetic signatures that can be used to trace the behavioral adaptations that grew out of the commensal relationship and differentiate them from those that arose through the prey pathway? Does the intensive, focused selection for specific traits under directed domestication leave a distinctive genetic signature distinguishable from the genetic signatures left by the broader play of selective factors and random events that shaped both the commensal and prey routes?

The different capacities for feralization of different domesticates and the residual imprint of domestication seen on these animals raises another set of questions. Among them, are commensal domesticates more successful feral animals because they can revert to the commensal behaviors that brought them into the relationship in the first place? How do feral commensal domesticates vary in behavior, physiology, and morphology from commensal species that never traveled any further down this path?

Looking forward, this discussion raises a series of questions about ongoing processes of domestication and breed improvement. Are there lessons that might be drawn from the different pathways humans and animals followed to domestication in ancient times that might be applied to current-day breed improvement programs? Do ancient efforts at game management and initial herd management have bearing on current-day ranching practices directed at animals like the eland and the fallow deer? Can this perspective help animal scientists better balance the dual goals of enhancing both animal productivity and animal welfare (Grandin and Dessing 1998, Price 2002:204–29, Keeling and Jensen 2002)? What are the environmental and biodiversity impacts of the massive wave of recent directed domestications, especially those involving aquatic species, and how can a broader understanding of the multiple pathways to domestication help mitigate these impacts?

Finally, recognition of the multiple pathways to domestication and their impact on domestic animals has a bearing on a range of issues involving the care and welfare of captive animals, as well as conservation efforts directed at endangered species (O'Regan and Kitchener 2005). Can these different models of domestication contribute to a better understanding of the impact of captivity on wild animals kept in zoos or in captive breeding programs? Are there parallels to be drawn between feralized domesticates and the reintroduction of captive animals into the wild?

Answering these questions requires drawing broadly from genetics, animal sciences, and archaeology. As this review has shown, researchers based in each of these general disciplinary areas are actively contributing to a large and growing body of knowledge on animal domestication and the potential for cross-illumination between these different perspectives is only just beginning to be realized. Clearly the interdisciplinary model set by Jack Harlan in his career-long study of crop evolution holds much promise for the study of animal domestication. And it is rewarding to see researchers from all of these different disciplinary backgrounds included in the second Harlan International Symposium and the publication of the proceedings of that stimulating meeting. Hopefully, contributors to the third Harlan International Symposium will be able to report considerable progress in addressing the questions raised here and other questions about pathways to animal domestication.

References

Andersson M, E Nordin, and P Jensen. 2001. Domestication effects on foraging strategies in fowl. *Applied Animal Behavior* **72**: 51–62.

Angulo E. 1998. Interpretación biológica acera de la domesticatión del pato criollo (*Cairinia moschata*). *Bulletin de la Instituto Frances de Estudios Andines*. **27**: 17–40.

Baker CMA and C Manwell. 1982. Man and elephant, The 'dare theory' of domestication and the origin of breeds. *Zeitschrift für Tierzüchtung und Züchtungsbiologie* **100**: 55–75.

Bar-Oz G, MA Zeder, and F Hole. 2011. Role of mass-kill hunting strategies in the extirpation of Persian gazelle (*Gazella subgutturosa*) in the northern Levant. *Proceedings of the National Academy of Sciences, USA* **108**: 7345–50.

Baskin LM. 1974. Management of ungulate herds in relation to domestication. Pp. 530–41 *in* V Geist and F Walther (eds.) *The Behavior of Ungulates and its Relation to Management*. Vol. 2. IUCN Publication, New Series 24. Morges, Switzerland: International Union for the Conservation of Nature.

Baskin LM. 2000. Reindeer husbandry/hunting in Russia in the past, present, and future. *Polar Research* **19**: 23–9.

Betts A and V Yagodin. 2000. A new look at 'Desert Kites'. Pp. 31–44 *in* L Stager, J Greenen and M Coogan (eds.) *The Archaeology of Jordan and Beyond. Essays in Honour of James Sauer*. Winona Lake, IN: Eisenbrauns.

Birks JDS and AC Kitchener. 1999. *The Distribution and Status of the Polecat* Mustela putorius *in Britain in the 1990s*. London: The Vincent Wildlife Trust.

Bíró Zs. J Lanszki, L Szemethy, M Heltai, and E Randi. 2005. Feeding habits of feral domestic cats (*Felis catus*), wild cats (*Felis silvestris*) and their hybrids: Trophic niche overlap among cat groups in Hungary. *Journal of Zoology, London* **266**: 187–96.

Boitiani L and P Cuicci. 1995. Comparative social ecology of feral dogs and wolves. *Ethology, Ecology, and Evolution* **7**: 49–72.

Bökönyi S. 1977. *Animal Remains from the Kermanshah Valley, Iran*. British Archaeological Reports Supplementary Series, No. 34. Oxford: Archaeopress.

Bökönyi S. 1989. Definitions of domestication. Pp. 1–4 *in* J Clutton-Brock (ed.) *The Walking Larder: Patterns of Domestication, Pastoralism, and Predation*. Cambridge: Unwin.

Brisbin LL. 1974. The ecology of animal domestication: Its relevance to man's environmental crises – past, present, and future. *Association of Southeastern Biological Bulletin* **21**: 3–8.

Bruford M and SJ Townsend. 2006. Mitochondrial DNA diversity in modern sheep: Implications for domestication. Pp. 306–16 *in* MA Zeder, DG Bradley, E Emshwiller, and BD Smith (eds.) *Documenting Domestication: New Genetic and Archaeological Paradigms*. Berkeley, CA: University of California Press.

Budiansky S. 1992. *The Covenant of the Wild: Why Animals Chose Domestication*. New York, NY: William Marrow.

Campos CB, CF Esteves, KMPMB Ferraz, PG Crawshaw Jr, and LM Verdade. 2007. Diet of free-roaming cats and dogs in a suburban and rural environment, south-eastern Brazil. *Journal of Zoology, London* **273**: 14–20.

Clutton-Brock J. 1981. *Domesticated Animals from Early Times*, 1st edition. London: British Museum of Natural History.

Clutton-Brock J. 1994. The unnatural world: Behavioural aspects of humans and animals in the process of domestication. Pp. 23–35 *in* A Manning and JA Serpell (eds.) *Animals and Human Society: Changing Perspectives*. London: Routledge.

Compagnoni B and M Tosi. 1978. The camel. Pp. 92–106 *in* RH Meadow and MA Zeder (eds.) *Approaches to Faunal Analysis in the Middle East*. Cambridge, MA: Peabody Museum.

Cope C. 1991. Gazelle-hunting strategies in the southern Levant. Pp. 341–58 *in* O Bar-Yosef and FR Valla (eds.) *The Natufian Culture in the Levant*. Ann Arbor, MI: International Monographs in Prehistory.

Coppinger R and L Coppinger 2001. *Dogs*. New York, NY: Schribner.

Coppinger R and R Schneider 1995. Evolution of working dogs. Pp. 21–47 *in* J Serpell (ed.) *The Domestic Dog. Its Evolution, Behavior, and Interactions with People*. Cambridge: Cambridge University Press.

Coppinger R, J Glendinning, R Torop *et al*. 1987. Degree of behavioral neoteny differentiates canid polymorphs. *Ethology* **75**: 89–108.

Corbett LK. 1979. Feeding ecology and social organization of wild cats (Felis silvestris) and domestic cats (Felis catus) in Scotland. PhD Thesis, University of Aberdeen.

Davis SJM. 1983. The age profiles of gazelles predated by ancient man in Israel: Possible evidence for a shift from seasonality to sedentism in the Natufian. *Paléorient* **9**(1): 55–62.

Davis SJM and FR Valla. 1978. Evidence for domestication of the dog 12,000 years ago in the Natufian of Israel. *Nature* **276**: 608–10.

Driscoll C, M Menotti-Raymond, AL Roca *et al*. 2007. The Near Eastern origin of cat domestication. *Science* **317**: 519–23.

Duarte CM, N Marbá, and M Holmer. 2007. Rapid domestication of marine species. *Science* **316**: 382–3.

Ducos P. 1978. "Domestication" defined and methodological approaches to its recognition in faunal assemblages. Pp. 49–52 *in* RH Meadow and MA Zeder (eds.) *Approaches to Faunal Analysis in the Middle East*. Peabody Museum Bulletin 2. Cambridge, MA: Harvard University Press.

Ebinger P. 1995. Domestication and plasticity in brain organization in mallards (*Anas platyrhynchos*). *Brain, Behavior, and Evolution* **45**: 286–300.

Ebinger P and M Röhrs. 1995. Volumetric analysis of brain structures, especially the visual system in wild and domestic turkeys (*Meleagris gallopavo*). *Journal of Brain Research* **36**: 219–28.

Ervynck A, K Dobney, H Hongo, and RH Meadow. 2001. Born free!: New evidence for the status of pigs from Çayönü Tepesi, Eastern Anatolia. *Paléorient* **27**(2): 47–73.

Evershed RP, S Payne, AG Sherratt *et al.* 2008. Earliest date for milk use in the Near East and southeastern Europe linked to cattle herding. *Nature* **455**: 528–31.

Flannery KV. 1983. Early pig domestication in the Fertile Crescent: A retrospective look. Pp. 163–88 *in* TC Young, PEL Smith, and P Mortensen (eds.) *The Hilly Flanks. Essays on the Prehistory of Southwest Asia*, Studies in Ancient Oriental Civilization, No. 36. Chicago, IL: Oriental Institute, University of Chicago.

Fox MW. 1978. *The Dog: Its Domestication and Behavior*. New York, NY: Garland Press.

Fuller DQ. 2006. Agriculture origins and frontiers in South Asia: A working synthesis. *Journal of World Prehistory* **20**: 1–86.

Gil-Sánchez JM, G Valenzuela, and JF Sánchez. 1999. Iberian wild cat *Felis silvestris* predation on rabbit *Oryctolagus cuniculus*: Functional response and age selection. *Acta Theriologica* **44**: 421–8.

Goodwin D, JWS Bradshaw, and SM Wickens. 1997. Paedomorphosis affects agonistic visual signals of domestic dogs. *Animal Behavior* **53**: 297–304.

Gordon B. 2003. *Rangifer* and man: An ancient relationship. *Rangifer* (Special Issue) **14**: 15–27.

Grandin T and MJ Dessing 1998. Genetics and animal welfare. Pp. 319–46 *in* T Grandin (ed.) *Genetics and the Behavior of Domestic Animals*. San Diego, CA: Academic Press.

Groves C. 1989. Feral mammals of the Mediterranean islands: Documents of early domestication. Pp. 46–58 *in* J Clutton-Brock (ed.) *The Walking Larder: Patterns of Domestication, Pastoralism, and Predation*. London: Unwin Hyman.

Guo J, L-X Du, Y-H Ma, *et al.* 2005. A novel maternal lineage revealed in sheep (*Ovis aries*). *Animal Genetics* **36**: 331–6.

Guo S, P Savolainen, J Su *et al.* 2006. Origin of mitochondrial DNA diversity of domestic yaks. *BMC Evolutionary Biology* **6**: 73.

Hale EB. 1969. Domestication and the evolution of behavior. Pp. 22–42 *in* ESE Hafez (ed.) *The Behaviour of Domestic Animals*, 2nd edition. London: Bailliere, Tindall, and Cassell.

Harlan JR. 1994. Domesticated animals. Pp. 538–40 *in* RA Eblen and WR Eblen (eds.) *Encyclopedia of the Environment*. Boston, MA: Houghton Mifflin Co.

Harlan JR. 1995. *The Living Fields: Our Agricultural Heritage*. Cambridge: Cambridge University Press.

Harris D. 1996. Introduction: Themes and concepts in the study of early agriculture. Pp. 1–9 *in* D Harris (ed.) *The Origins and Spread of Agriculture and Pastoralism in Eurasia*. London: University College Press.

Helmer D, L Gourichon, H Monchot, J Peters, and M Saña Segui. 2005. Identifying early domestic cattle from pre-pottery Neolithic sites on the middle Euphrates using sexual dimorphism. Pp. 86–95 *in* J-D Vigne, J Peters, and D Helmer (eds.) *The First Steps of Animal Domestication*. Oxford: Oxbow Books.

Hemmer H. 1990. *Domestication: The Decline of Environmental Appreciation*. Cambridge: Cambridge University Press.

Henry DO. 1989. *From Foraging to Agriculture*. Philadelphia, PA: University of Pennsylvania Press.

Herre W and M Röhrs. 1990. *Haustiere – Zoologisch Gesehen*, 2nd edition. Stuttgart: G Fischer.

Hoch E. 1979. Reflections on prehistoric life at Umm an-Nar (Trucial Oman) based on faunal remains from the third millennium BC. Pp. 589–638 in M Taddei (ed.) *South Asian Archaeology* 1977. Naples, Italy: Istituto universitario orientale.

Hongo H, RH Meadow, B Öksuz, and G Ilgesdi, 2002. The process of ungulate domestication in Prepottery Neolithic Çayönü, southeastern Turkey. Pp. 153–6 in H Buitenhuis, AM Choyke, M Mashkour, and AH Al-Shiyab (eds.) *Archaeozoology in the Near East* 4A. Groningen, The Netherlands: ARC-Publicaties 62.

Jensen P. 2006. Domestication – From behaviour to genes and back again. *Applied Animal Behaviour Science* **97**: 3–15.

Kanginakudru, M Metta , RD Jakati , and J Nagaraju. 2008. Genetic evidence from Indian red jungle fowl corroborates multiple domestication of modern day chicken. *BMC Evolutionary Biology* **8**: 174 doi:10.1186/1471–2148–8–174.

Keeler LF, S Ridgway , L Lipscomb, and E Fromm.1968. The genetics of adrenal size and tameness in colorphase foxes. *Journal of Heredity* **59**: 82–4.

Keeling L and P Jensen. 2002. Behavioural disturbances, stress, and welfare. Pp. 79–98 in P Jensen (ed.) *The Ethology of Domestic Animals*. Wallingford: CABI Publishing.

Kimura B, FB Marshall, S Chen *et al*. 2010. Ancient DNA from Nubian and Somali wild ass provides insights into donkey ancestry and domestication. *Proceedings of the Royal Society* B DOI: 10.1098/rspb.2010.0708.

Kruska D. 1988. Mammalian domestication and its effect on brain structure and behavior. Pp. 211–50 in HJ Jerison and I Jerison (eds.) *Intelligence and Evolutionary Biology*. New York, NY: Springer-Verlag.

Kruska D. 1996. The effect of domestication on brain size and composition in the mink (*Mustela vison*). *Journal of Zoology, London* **239**: 645–61.

Kruska D and M Röhrs. 1974. Comparative-quantitative investigations on brains of feral pigs from the Galapogos Islands and the European domestic pigs. *Zeitschrift für Anatomie und Entwicklungsgeschichte* **144**: 61–73.

Kumar S, M Nagarajan, JS Sandhu *et al*. 2007. Mitochondrial DNA analyses of Indian water buffalo support a distinct genetic origin of river and swamp buffalo. *Animal Genetics* **38**: 227–32.

Künzl C and N Sachser. 1999. The behavioral endocrinology of domestication: A comparison between the domestic guinea pig (*Cavia aperea* f. *porcellus*) and its wild ancestor, the Cavy (*Cavia aperea*). *Hormones and Behavior* **35**: 28–37.

Künzl C and N Sachser. 2000. Behavioural and endocrinological changes during the process of domestication in guinea pigs. *Archives of Animal Breeding (Archiv für Tierzucht, Dummerstorf)* **43**: 153–8.

Künzl C, S Kaiser, E Meir, and N Sachser. 2003. Is a wild mammal kept and reared in captivity still a wild animal? *Hormones and Behavior* **43**: 187–96.

Larson, G, U Albarella, K Dobney *et al*. 2007. Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. *Proceedings of the National Academy of Sciences, USA* **104**: 15,276–81.

Larson G, K Dobney, U Albarella *et al*. 2005. Worldwide phylogeny of wild boar reveals multiple centers of pig domestication. *Science* **307**: 1618–21.

Legge AJ and PA Rowley-Conwy. 1987. Gazelle killing in Stone Age Syria. *Scientific American* **255**: 88–95.

Letts GA. 1964. Feral animals in the Northern Territory. *Australian Veterinary Journal* **40**: 84–8.

Levine M. 1999. Botai and the origins of horse domestication. *Journal of Anthropological Archaeology* **18**: 29–78.

Liu Y-P, W Gui-Sheng, Y-G Yao *et al.* 2006. Multiple maternal origins of chickens: Out of the Asian jungles. *Molecular Phylogenetics and Evolution* **38**: 12–19.

Manker E. 1963. *People of the Eight Seasons*. Gothenburg, Sweden: Tre Tryckare Cagner & Co.

Marchetti MP and GA Nevitt. 2003. Effects of hatchery rearing on the brain structure of rainbow trout, O*ncorhynchus mykiss*. *Environmental Biology of Fishes* **66**: 9–14.

Marliave JB, WF Gergits, and S Aota. 1993. F_{10} pandalid shrimp: Sex determination; DNA and dopamine as indicators of domestication and outcrossing for wild pigment pattern *Zoo Biology* **12**: 435–51.

Masson VM and VI Sarianidi 1972. *Central Asia: Turkmenia Before the Achaemenids*. London, UK: Thames & Hudson.

Meadow RH, 1989. Osteological evidence for the process of animal domestication. Pp. 80–90 in J Clutton-Brock (ed.) *The Walking Larder: Patterns of Domestication, Pastoralism, and Predation*. London: Unwin Hyman.

Mengoni-Goñalons G and H Yacobaccio. 2006. The domestication of South American camelids: A view from the South-Central Andes. Pp. 228–244 in MA Zeder, DG Bradley, E Emshwiller, and BD Smith (eds.) *Documenting Domestication: New Genetic and Archaeological Paradigms*. Berkeley, CA: University of California Press.

Mirov NT. 1945. Notes on the domestication of the reindeer. *American Anthropologist* **47**: 393–408.

Morey DF. 1992. Size, shape, and development in the evolution of the domestic dog. *Journal of Archaeological Science* **19**: 181–204.

Morey DF. 1994. The early evolution of the domestic dog. *American Scientist* **82**: 336–47.

Morey DF. 2005. Burying the evidence: The social bond between dogs and people. *Journal of Archaeological Science* **33**: 158–75.

Munro N. 2004. Zooarchaeological measures of hunting pressure and occupation intensity in the Natufian implications for agricultural origins. *Current Anthropology* **45**: S6–S33.

Munro N. 2011. Domestication of the turkey in the American Southwest. Pp. 543–56. in BD Smith (ed.) *The Subsistence Economies of Indigenous North American Societies – A Handbook*. Washington, D.C.: Smithsonian Institution Scholarly Press.

Murphy MR. 1985. History of the capture and domestication of the Syrian golden hamster (*Mesocricetus auratus* Waterhouse). Pp. 3–20 in H Siegel (ed.) *The Hamster: Reproduction and Behavior*. New York, NY: Plenum.

Naderi S, H-R Rezaei, F Pompanon *et al.* 2008. The goat domestication process inferred from large-scale mitochondrial DNA analysis of wild and domestic individuals. *Proceedings of the National Academy of Sciences, USA* **105**: 17,659–64.

Nadler, CF, KV Korobitsina, RS Hoffman, and NN Vorontsov. 1973. Cytogenic differentiation, geographic distribution and domestication in Palaearctic sheep (*Ovis*). *Zeitschrift für Saugetierkunde* **38**: 109–25.

Naumenko EV, NK Popova, EM Nikulina *et al.* 1989. Behavior, adrenocortical activity, and brain monoamines in Norway rats selected for reduced aggressiveness towards man. *Pharmacology, Biochemistry, and Behavior* **33**: 85–91.

O'Connor TP. 1997. Working at relationships: Another look at animal domestication. *Antiquity* **71**: 149–56.

Olsen SJ. 1990. Fossil ancestry of the yak, its cultural significance and domestication in Tibet. *Proceedings of the Philadelphia Academy of Natural Sciences* **142**: 73–100.

Olsen S. 2006. Early horse domestication on the Eurasian Steppe. Pp. 245–69 *in* MA Zeder, DG Bradley, E Emshwiller, and BD Smith (eds.) *Documenting Domestication: New Genetic and Archaeological Paradigms*. Berkeley, CA: University of California Press.

O'Regan HJ and AC Kitchener 2005. The effects of captivity on the morphology of captive, domesticated, and feral mammals. *Mammal Review* **35**: 215–30.

Outram AK, NA Stear, R Bendrey *et al.* 2009. The earliest horse harnessing and milking. *Science* **323**: 1332–5.

Peters J and A von den Driesch. 1997. The two-humped camel (*Camelus bactrianus*): New light on its distribution, management, and medical treatment in the past. *Journal of Zoology, London* **242**: 651–79.

Peters J, A von den Driesch, and D Helmer. 2005. The upper Euphrates-Tigris Basin, cradle of agro-pastoralism? Pp. 96–124 *in* J-D Vigne, J Peters, and D Helmer (eds.) *The First Steps of Animal Domestication*. Oxford: Oxbow Books.

Plogmann D and D Kruska. 1990. Volumetric comparison of auditory structures in the brains of European wild boars (*Sus scrofa* f. dom.). *Brain, Behavior, and Evolution* **35**: 146–55.

Poplin F, T Poulain, P Méniel *et al.* 1986. Les débuts de l'élevage en France. Pp. 37–51 *in* J-P Demoule and J Guilaine (eds.) *Le Néolithique de la France (Hommage à G Bailloud)*. Paris: Picard.

Popova NK, NN Voitenko, AV Kulikov, and DF Agustinovich. 1991a. Evidence for the involvement of central serotonin in mechanism of domestication of silver foxes. *Pharmacology, Biochemistry, and Behavior* **40**: 751–6.

Popova NK, AV Kulikov, EM Nikulina, EY Kozlachkova, and GB Maslova. 1991b. Serotonin metabolism and serotonergiv receptors in Norway rats selected for low aggressiveness to man. *Aggressive Behavior* **17**: 207–13.

Price EO. 1984. Behavioral aspects of animal domestication. *Quarterly Review of Biology* **59**: 1–32.

Price EO. 1998. Behavioral genetics and the process of animal domestication. Pp. 31–66 *in* T Grandin (ed.) *Genetics and the Behavior of Domestic Animals*. San Diego, CA: Academic Press.

Price EO. 1999. Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science* **65**: 245–71.

Price EO. 2002. *Animal Domestication and Behavior*. Wallingford: CABI Publishing.

Redding RW. 2005. Breaking the mold, a consideration of variation in the evolution of animal domestication. Pp. 41–8 *in* J-D Vigne, J Peters, and D Helmer (eds.) *The First Steps of Animal Domestication*. Oxford: Oxbow Books.

Rehkämper G, HD Frahm, and J Cnotka. 2008. Mosaic evolution and adaptive brain component alteration under domestication seen on the background of evolutionary theory. *Brain, Behavior, and Evolution* **71**: 115–26.

Rindos D. 1984. *The Origins of Agriculture: An Evolutionary Perspective*. Orlando, FL: Academic Press.

Røed KH, Ø Flagstad, M Nieminen *et al.* 2008. Genetic analyses reveal independent domestication origins of Eurasian reindeer. *Proceedings of the Royal Society* B **275**: 1849–55.

Röhrs VM. 1985. Cephalization, neocorticalization and the effects of domestication on brains in mammals. Pp. 544–7 *in* H-R Duncker and G Fleischer (eds.) *Functional Morphology in Vertebrates*. Stuttgart: G Fischer.

Rossel S, F Marshall, J Peters *et al.* 2008. Domestication of the donkey: Timing, processes, and indicators. *Proceedings of the National Academy of Sciences, USA* **105**: 3715–20.

Sapir-Hen L, G Bar-Oz, H Khalaily, and T Dayan. 2009. Gazelle exploitation in the early Neolithic site of Motza, Israel: The last of the gazelle hunters in the southern Levant. *Journal of Archaeological Science* **36**: 1538–46.

Schultz T, UG Mueller, CR Currie, and S Rehner. 2005. Reciprocal illumination: A comparison of agriculture in humans and in fungus-growing ants. Pp. 149–90 *in* F Vega and M Balckwell (eds.) *Ecological and Evolutionary Advances in Insect-Fungal Associations*. New York, NY: Oxford University Press.

Schultz W. 1969. Zur Kenntnis des Hallstromhundes (*Canis hallstromi*, Troughton 1957). *Zoologischer Anzeiger* **183**: 42–72.

Smith BD. 2001. Low level food production. *Journal of Archaeological Research* **9**: 1–43.

Smith BD. 2006. Documenting plant domestication in the archaeological record. Pp. 15–24 *in* MA Zeder, DG Bradley, E Emshwiller, and BD Smith (eds.) *Documenting Domestication: New Genetic and Archaeological Paradigms*. Berkeley, CA: University of California Press.

Smith BD. 2007a. The ultimate ecosystem engineers. *Science* **315**: 1797–8.

Smith BD. 2007b. Niche construction and the behavioral context of plant and animal domestication, *Evolutionary Anthropology* **16**: 189–99.

Speiss AE. 1989. *Reindeer and Caribou Hunters. An Archaeological Study*. New York, NY: Academic Press.

Spotorno, AE, JC Marín, G Manríquez *et al.* 2006. Ancient and modern steps during the domestication of guinea pigs (*Cavia porcellus* L.). *Journal of Zoology* **270**: 57–62.

Tchernov E. 1991. Biological evidence for human sedentism in Southwest Asia during the Natufian. Pp. 315–40 *in* O Bar-Yosef and FR Valla (eds.) *The Natufian Culture in the Levant*. Ann Arbor, MI: International Monographs in Prehistory.

Tchernov E and FR Valla. 1997. Two new dogs, and other Natufian dogs, from the southern Levant. *Journal of Archaeological Science* **24**: 65–95.

Tennessen T and RJ Hudson 1981. Traits relevant to the domestication of herbivores. *Applied Animal Ethology* **7**: 87–102.

Trut LN. 1999. Early canid domestication: The farm-fox experiment. *American Scientist* **87**: 160–9.

Turnbull PF and CA Reed. 1974. The fauna from the terminal Pleistocene of Palegawra Cave. *Fieldiana: Anthropology* **63**: 81–146.

Uerpmann H-P. 1979. *Probleme der Neolithisierung des Mittelmeeraumes*. Beihefte zum Tübinger Atlas des Vordern Orients, Reihe B, Nr. 28. Wiesbaden: Dr Ludwig Reichert.

Uerpmann H-P and M Uerpmann. 2002. The appearance of domestic camel in south-east Arabia. *Journal of Oman Studies* **12**: 235–60.

Ussishkin E. 1980. The Ghassulian Shrine at Ein Gedi. *Tel Aviv* **7**: 1–44.

Vigne J-D, J Guilaine, K Debue, L Haye, and P Gérrard. 2004. Early taming of the cat in Cyprus. *Science* **304**: 259.

Vilà C, J Leonard, and A Beja-Pereira. 2006. Genetic domestication of horse and donkey. Pp. 342–53 *in* MA Zeder, DG Bradley, E Emshwiller, and BD Smith (eds.) *Documenting Domestication: New Genetic and Archaeological Paradigms*. Berkeley, CA: University of California Press.

vonHoldt B, JP Pollinger, KE Lohmueller *et al.* 2009. Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature* **464**: 898–902.

Waples RS. 1991. Dispelling some myths about hatcheries. *Fisheries* **24**: 12–21.

Wayne RK. 1986. Cranial morphology of domestic and wild canids: The influence of development on morphological change. *Evolution* **40**: 243–61.

Wheeler JC, L Chickhi, and MW Bruford. 2006. Genetic analysis of the origins of South American camelids. Pp. 329–41 *in* MA Zeder, DG Bradley, E Emshwiller, and BD Smith (eds.) *Documenting Domestication: New Genetic and Archaeological Paradigms*. Berkeley, CA: University of California Press.

Zeder MA. 2001. A metrical analysis of a collection of modern goats (*Capra hircus aegargus* and *Capra hircus hircus*) from Iran and Iraq: Implications for the study of caprine domestication. *Journal of Archaeological Science* **28**: 61–79.

Zeder MA. 2006a. Central questions in the domestication of plants and animals. *Evolutionary Anthropology* **15**: 105–17.

Zeder MA. 2006b. Archaeological approaches to documenting animal domestication. Pp. 171–80 *in* MA Zeder, DG Bradley, E Emshwiller, and BD Smith (eds.) *Documenting Domestication: New Genetic and Archaeological Paradigms*. Berkeley, CA: University of California Press.

Zeder MA. 2006c. Archaeozoology in Southwest Asia: A status report based on the eighth meeting of the Archaeozoology of Southwest Asia and Adjacent Areas Working Group. *Paléorient* **32**: 137–47.

Zeder MA 2008a. Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. *Proceedings of the National Academy of Sciences, USA* **105**: 11,597–604.

Zeder MA. 2008b. Animal domestication in the Zagros: An update and directions for future research. Pp. 243–78 *in* E Vilà, L Goucherin, A Choyke, and H Buitenhuis (eds.) *Archaeozoology of the Near East VIII, Proceedings of the Eighth International Symposium On the Archaeozoology of Southwestern Asia and Adjacent areas*. Lyon: Travaux de la Maison de l'Orient et de la Méditerranée (TMO).

Zeder MA. 2009. The Neolithic macro-(r)evolution: Macroevolutionary theory and the study of culture change. *Journal of Archaeological Research* **171**: 1–63.

Zeder MA. 2011. The origins of agriculture in the Near East. *Current Anthropology* **52**(S4): S221–S225.

Zeder MA and B Hesse. 2000. The initial domestication of goats (*Capra hircus*) in the Zagros Mountains 10,000 years ago. *Science* **287**: 2254–7.

Zeder, MA, E Emshwiller, BD Smith, and DG Bradley. 2006. Documenting domestication, The intersection of genetics and archaeology. *Trends in Genetics* **22**: 139–55.

Zohary D, E Tchernov, and LK Horwitz. 1998. The role of unconscious selection in the domestication of sheep and goats. *Journal of Zoology* **245**: 129–35.