<Barresi12e, Further Development_c26_01>

Evolution and Domestication: Selection on Developmental Genes?

Price (1984) defined domestication as "a process by which a population of animals becomes adapted to man and the captive environment, by some combination of genetic changes occurring over generations and environmentally induced developmental events recurring during each generation." Domesticated animals differ significantly from animals in the wild. There appears to be a suite of characteristics that accompany domestication, and these characteristics have be linked to pedomorphosisothe retention of juvenile characteristics in the adult body (Coppinger and Smith 1983; Price 1984; Morey 1994).

When one thinks about domestication, the case of dogs becomes paramount. The dog was probably the first animal to be domesticated (although some anthropologists have said that humans, themselves, actually deserve this title). Indeed, we shouldn't even call these animals dogs, since *Canis familiaris* (the scientific name for dog) is more a name of convenience than that denoting a real species (see Isaac 1970). The actual name might be *Canis lupus*, the wolf. Wolves and dogs can interbreed, and the morphological differences between wolves and dogs are certainly as close as that between the different dog types (such as Great Dane, French poodle, and Chihuahua). Perhaps the dogs we are dealing with are *Canis lupus familiaris,* a subspecies of the wolf.

Many arguments about domestication (see Morey 1994) focus on the notion of intentionality. That is to say, did humans select the traits they wanted (human intention), or did humans merely provide a new ecological niche that the wolves exploited ("self domestication")? In the latter scenario, (Zeuner 1963; Coppinger and Smith 1983) the wolves that became dogs may have started out as scavengers around human camp sites and became accustomed to human handouts. Such debates focus more on what it is to be human (as a manipulator of nature) than on what it is to be a dog. There probably was a reciprocal relationship (something that any dog "owner" can tell us about) between wolves finding a new niche and humans finding a furry friend and helper. Both natural selection and artificial selection may have contributed to wolf domestication.

So whether by human intention or niche exploitation, some wolves have become dogs. How did this occur? In becoming domesticated, wolves have undergone numerous morphological, physiological, and behavioral changes. Morey (1994) finds a common factor in pedomorphosis. The adult dog has retained many of the phenotypic traits of the juvenile wolf. The skulls are broad for their length, and juvenile behavioral traits such as whining, barking, and submissiveness, are retained in the adult dog. Morey considers pedomorphosis as a byproduct of natural selection for early sexual maturity and small body size that would increase the fitness of wolves in exploiting a new ecological niche.

Interestingly, the constellation of pedomorphic behaviors and morphologies is also seen in the domestication of other animals. These morphological changes include: the appearance of dwarf or giant varieties, piebald coat colors, curly tails, shortened tails with fewer vertebrae, and floppy ears. Physiological changes also occur as both herbivores and carnivores are domesticated. The most notable of these involves changes in the reproductive cycles that end the yearly estrus. Behavioral changes mostly involve tameness, a suite of characteristics that make the animal docile and malleable to human intentions. Moreover, these changes appear to be inherited.

In the 1950s, Dmitry Belyaev of the Soviet Union's Institute of Cytology and Genetics in Novosibirsk, Siberia, began testing a hypothesis to look at whether selection for a behavioral traitotamabilityocould bring with it the morphological and physiological traits associated with

domestication and pedomorphosis. He postulated that if human intention was involved, humans would have selected their wolves for tameness, whatever that was. Since tameness and aggression were probably regulated by hormones, then selecting for tameness and against aggression would mean selecting for physiological variants as well. The physiological variants, in turn, might be those associated with the retention of juvenile traits (see Belyaev 1979; Trut 1999).

Belyaev and his colleagues decided to initiate a breeding program that would strongly select tamability and see what happened to the biological phenotype after several generations. He chose as his test animal a species close to the wolf, namely the silver fox, *Vulpes vulpes*, an animal never before domesticated. The experiment began with 30 male foxes and 100 vixen from a commercial fur farm. (Such animals had been bred without conscious selection for over 50 years, so these were already foxes that survived in caged conditions). The criteria for tamability were very strict. Only about 5 percent of the males and 20 percent of the females are selected to breed. The foxes were not trained, so the major component of their tameness should be genetic. Tameness was measured by the ability of young, sexually mature foxes to behave in a friendly manner to their handlers, wagging their tales and whining. Eventually, a "domesticated elite" classification arose—these were the foxes that actually sought to establish human contact, licking the scientists like dogs would. By the tenth generation, 18 percent of the young foxes were in this elite category. By the twentieth generation, 35 percent were in this category. Today, over forty years after the breeding had begun, these domesticated foxes comprise from 70-80 percent of the test population.

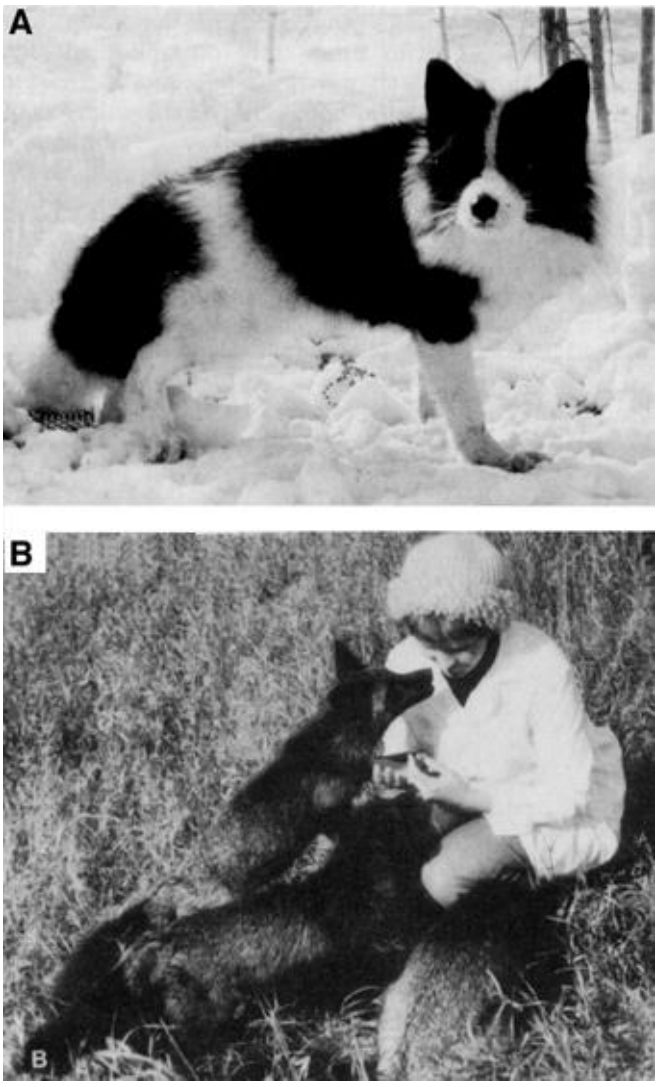

Figure 1 Changes taking place during domestication. (A) Changes in the foxes coat color were the first novel traits noted, appearing in the eighth to tenth selected generations. In a fox homozygous for the *Star* gene, large areas of depigmentation similar to those in some dog breeds are seen. (B) Tame foxes enjoy and seek out human contact. (From Belyaev 1979.)

After 40 years and over 30 generations of selection, has the physical nature of the population changed? The most obvious physiological changes involved corticosteroids. In wild foxes, the levels of corticosteroids, hormones involved in adaptation to stress, rise sharply between the age of 2–4 months, reaching adult levels by 8 months of age. The domesticated wolves had their corticosteroid surge significantly later. The domesticated foxes have a much lower adrenal response to stress, and they have more serotonin in their blood. Other physical changes produced by selection for tamability were the constellation of characters associated with domestication: regional depigmentation, floppy ears, and rolled tails. Belyaev claimed that the finding of the same suite of morphological changes in different types of domesticated animals selected for different traits (milk production, wool quality, strength, etc.), by different groups of people, was not just an artifact of the gene pool of these particular 130 foxes but was the common outcome of selecting for this behavioral trait (Trut 1988, 1999).

By selecting for a behavioral trait associated with juveniles, Belyaev's group may have selected for those animals whose growth rates were such that pedomorphism would result. Floppy ears, for instance, are characteristics found in newborn wolves, and even the coat pigmentation patterns may be due to the selection of certain genes. The gene *Star* is involved in the timing of melanoblast migration in foxes (Belyaev et al. 1981; Trut 1996). Certain alleles of this gene appear to have been selected and cause the piebald pigmentation patterns in the adults. Skull size has also changed to a more juvenile condition, though not by selecting directly for size but for behavior.

The domestic fox is not yet a domestic wolf. It has not gotten to the point of domestication that we associate with dogs. However, in just a few decades, the fox has been domesticated by this group to such a degree that they can be sold as pets. Indeed, this might become their fate, as funds for these and other experiments in the former Soviet Union are in jeopardy, and there were no funds allocated last year for the feeding of these animals.

Literature Cited

Belyaev, D. K. 1979. Destabilizing selection as a factor in domestication. *J. Hered.* 70: 301-308.

Belyaev, D. K. , Ruvinsky, A. O., and Trut, L. N. 1981. Inherited activation/inactivation of the star gene in foxes. *J. Hered.* 72: 264-274.

Coppinger, R. P, and Smith, C. K. 1983. The domestication of evolution. *Environ. Conserv*. 10, 283-292.

Isaac, E. 1970. *Geography of Domestication*. Prentice-Hall, Englewood Cliffs, N.J.

Morey, D. F. 1994. The early evolution of the domestic dog. *Amer. Sci*. 82: 336-347.

Price, E. 0. 1984. Behavioral aspects of animal domestication. *Q. Rev. Biol.* 59: 1-32.

Trut, L. N. 1988. The variable rates of evolution transformations and their parallelism in terms of destabilizing selection. *J. Animal Breeding and Genet.* 105: 81-90.

Trut, L. N. 1996. Sex ratio in silver foxes: effects of domestication and the star gene. *Theoret. Appl. Genet*. 92: 109-115.

Trut, L. M. 1999. Early canid domestication: the farm-fox experiment. *Amer. Sci. 87*: 160-168.

Zeuner, F. E. 1963. *A History of Domesticated Animals*. Harper & Row, New York.