

FERALIZATION: THE MAKING OF WILD DOMESTIC ANIMALS

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ABSTRACT

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The widely accepted viewpoint that feralization is the reverse of domestication requires that the feralization process be restricted to populations of animals and, therefore, cannot occur in individuals. An alternative, ontogenetic approach is presented in which feralization is defined as the process by which individual domestic animals either become desocialized from humans, or never become socialized, and thus behave as untamed, non-domestic animals. Feralization will vary among species and, intraspecifically, will depend upon an individual's age and history of socialization to humans. Because feralization is not equated with morphological change resulting from evolutionary processes, species formation is not an accurate indicator of feral condition.

Key Words: feralization, domestication, feral dogs, Canis familiaris

INTRODUCTION

Given the vast numbers of domestic animals on every populated continent, the potential for feralization is greater today than at any time previously. Feral animals can have severe impacts on the environment and endemic species of an area (Kruuk and Snell, 1981; Barnett and Rudd, 1983), and

knowledge of the process by which domestic animals become feral may contribute to an understanding of the effects of domestication and habitat on learning, as well as the flexibility and reorganization of behavior.

In this paper, we suggest that feralization is an ontogenetic (developmental) process, not an evolutionary one and, therefore, should not be considered the opposite of domestication. The two processes occur at different levels (individual and population) on different temporal scales and thus require different theoretical and research approaches (Caro and Bateson, 1986). Throughout this paper, particular attention will be paid to dogs Canis familiaris, the archetypical domestic animal. Dogs are excellent subjects in which to examine the argument that feralization is an ontogenetic process; their behavior and development has been documented thoroughly (Scott and Fuller, 1965; Fox, 1971; Bekoff, 1972a, b; Fox and Bekoff, 1975; Daniels, 1987; Daniels and Bekoff, 1989a, b), and they are known to become feral.

DISCUSSION

Definitions of the Term Feral

Definitions of the word feral can be categorized into two major classes. First, feral animals have been defined as individuals living in the wild (Pullar, 1950; Shank, 1972; Gipson, 1983) or those that have reverted to a wild state (Fiennes and Fiennes, 1970; Fox, 1978). McKnight (1976) noted that feral animals were (1) no longer under human breeding control, (2) not being intentionally cared for, and (3) unowned. In these cases, researchers have defined the endpoint in the feralization process with little attention given to the mechanism by which the process occurs.

A second class of definitions takes a clear evolutionary perspective. Feral animals are said to have undergone the domestication process in reverse (Letts, 1964; Hale, 1969; Price, 1984) such that they are now "de-domesticated" (Baker and Manwell, 1981). Consequently, de-domestication has been widely accepted as synonymous with

feralization. This is not a new idea. Darwin (1868) noted that the idea of a gradual reversion of domestic animals to a wild form had often been expressed prior to publication of The Origin of Species in 1859. Before discussing the implications of defining feralization as the opposite or reverse of domestication, it is necessary to review briefly the topic of domestication.

What is Domestication?

Animal domestication has been reviewed extensively by Downs (1960), Zeuner (1963), Price and King (1968), Hale (1969), Ucko and Dimbleby (1969), Hyams (1972), Boice (1973), Clutton-Brock (1977), Cole and Garrett (1980), and Price (1984), and the reader is referred to those works for details not discussed here.

Darwin (1859, 1868) was among the first to deal seriously with the topic of domestication by comparing human-mediated selection and the subsequent production of various animal breeds to natural selection and speciation. Darwin (1868) recognized three forms of selection, each varying in the degree of human control involved in the process. Aside from natural selection, which is free of human interference, methodical selection and unconscious selection together compose what is generally referred to as artificial selection, the driving force of domestication. Price (1984) listed five unique aspects of the domestication process: (1) it involves artificial selection, either deliberate (methodical) or unconscious, (2) humans exercise control over animal breeding, (3) losses in the animal's fitness are frequently negated by management practices, (4) food is provisioned, and (5) the animals' cognitive mechanisms may have been altered because humans act to buffer them from their environment.

The last three points amount to a lessening of the intensity of natural selection whereas the first two points indicate that artificial selection largely supplants natural selection as the dominant selective force. Basically,

domestication is an evolutionary process in which the relative importance of artificial selection becomes much greater than that of natural selection, although the role of the latter process is never completely subverted.

Price (1984) further defined domestication as "that process by which a population of animals becomes adapted to man and to the captive environment by some combination of genetic changes occurring over generations and environmentally induced developmental events reoccurring during each generation" (p.3). However, "environmentally induced developmental events" must be part of any process involving live subjects and do not imply that domestication is anything but an evolutionary process. This is an important point, considering the reliance of science on accurate terminology. For instance, perusal of virtually any dictionary will indicate that the word "domestic" is invariably defined as "tame". While tameness is a general characteristic of domestic animals, it can be induced in many non-domestic species and need not ever be part of a domestic animal's behavioral repertoire. Such definitions confuse the issue of phylogenetic and ontogenetic phenomena. However, even if it is agreed that domestication is an evolutionary process, it can take place relatively quickly, with genetic changes that are evident in only a few generations (Anderson, 1952; Donaldson and Menasveta, 1961; Baker and Maxwell, 1981).

The Effects of Domestication

Perhaps the most widely recognized result of domestication is the ease with which the animals involved can be tamed. Manageability, or ease in manipulating the behavior of domesticants, has always been a primary goal of domesticators. In addition, most domestic animals are derived from social-living ancestors and readily form bonds with conspecifics early in life (see Scott and Fuller, 1965 and Fox and Bekoff, 1975 for discussions of socialization in dogs).

Vertebrate domestication apparently has enhanced the

generalization of bond formation to non-species members, specifically to humans, and also has probably led to a lengthening of the socialization period. In essence, domestication involves a loss of social inhibitions (Lorenz, 1965) through the raising of thresholds for avoidance or for submissive responses (Price 1984), whereby bond formation is facilitated. Likewise, the trend toward greater neoteny, or the retention of juvenile characteristics into adulthood (Fox, 1968), in domestic animals is the result of selection for heterochrony, or shifts in rates of development (Gould, 1977). This, in turn, may result in greater behavioral plasticity (Boice, 1973; Frank, 1980), although further comparisons between domestic and non-domestic animals under various environmental and experimental conditions are needed (Ratner and Boice, 1975; Price, 1984). Therefore, tameness, or the lack of avoidance responses by the animal when humans approach (Hediger, 1964), which is a learned trait (Price, 1984), can be viewed as an ontogenetic phenomenon facilitated through artificial selection.

Thus, an important result of domestication is the modifiability of behavior, though not necessarily its modification. In fact, data suggest that the qualitative nature of domestic dogs' behavioral patterns (the form of the behavior) is relatively resistant to change while the quantitative aspects of the behavior (frequencies or rates of performance) have been modified (Scott and Fuller, 1965; Bekoff, 1972; Scott and Causey, 1973).

Domestication has also resulted in morphological and physiological changes in animal species (Zeuner, 1963). However, the directions of change that animals take during domestication are not uniform, particularly with regard to physical appearance. Price (1984) noted that body size has increased in some species (e.g. horse *Equus caballus* and rabbit *Oryctolagus cuniculus*) but has decreased in others (e.g. sheep *Ovis aries* and cattle *Bos taurus*), leading to the conclusion that generalizations are of limited value.

Variability among species is likewise evident when

domestic and non-domestic animals within the same genus are compared. Domestication may lead ultimately to speciation, as in dogs and chickens, or to a domestic form that is taxonomically indistinct from its non-domestic counterpart, as in the case of the reindeer (domestic) and caribou (non-domestic), both classified as Rangifer tarandus.

It may be incorrect to conclude that domestication is any farther along in cases where domesticants are dissimilar to non-domestic forms than in cases where the two populations are physically similar. Species classifications have historically been questioned by researchers, given that a large number of recognized species readily interbreed (Gray, 1971) and produce fertile offspring (Mengel, 1971; Gipson, 1972; Mahan et al., 1978). Also, depending on the domesticators' goals and the particular gene pool with which they have to work, retention of the physical similarities between domestic and non-domestic forms might be selectively favored while behavior patterns between the two might be more dissimilar than in animals where the domestic and non-domestic forms are physically distinct. Not all characteristics should be expected to change equally, leaving the possibility that a population will be classified as domestic, based on the goals of the domesticator, although the animals resemble a non-domestic form.

Implications of Defining Feralization as De-Domestication

The first implication of the evolutionary viewpoint is that feralization, in which the results of generations of artificial selection would be undone, cannot occur over a span of time less than one generation. Given that premise, several questions remain that have yet to be addressed by proponents of an evolutionary viewpoint. For instance, are there characteristics that remain in the domestic form or must all traits altered during domestication also change during feralization? Likewise, must reversal take as long as the original domestication process? An evolutionary feralization process may, in fact, take longer than

domestication. Haldane (1949) noted that the average rate of phenotypic change in artificially selected populations is markedly faster than the relatively slow rate of evolutionary change in populations of free-living wild animals.

An additional difficulty is that even among researchers espousing the evolutionary viewpoint, there is disagreement as to what constitutes a feral animal. For instance, Brisbin (1974, 1977) used the term feral to denote a non-domestic population, whereas Price (1984) noted that animals "in transition" are feral and that once the "wild phenotype is attained the term feral is no longer appropriate" (p.24).

A second implication, resulting from the widespread concept of feralization as a "reversion" to a wild form, is that the feral animal will approach the ancestral phenotype in appearance. This expectation is not as rigid as it seems; few researchers would suggest that feral animals can actually reattain the ancestral phenotype (Price, 1984), primarily because changes in the gene pool of domestic animals over time preclude identical reversion (Brisbin, 1974). Considering that the ancestral phenotype of many domesticated species is unknown (Zeuner, 1963; Hyams, 1972), we "cannot possibly know whether or not there has been any close degree of reversion" (Darwin, 1868 vol. 2, p.5).

However, the term "reversion" implies a going backward that is not entirely unjustified. The pre-feral animal, in becoming wild, will necessarily draw on behavioral resources that have been derived from its ancestors. It is therefore not unusual that certain similarities to non-domesticated ancestors will arise. At the same time, though, the present environment will select for certain characteristics that may diverge markedly from the ancestral form. Thus, assumptions that feralization leads to marked similarities between neo-feral animals and the ancestor (or at least an approximation of the ancestor) may only be justified with regard to some characteristics (e.g., behavior) but not for others (e.g., coat color, body size, and reproductive habits).

A third implication of defining feralization as de-

domestication, and a significant point of divergence between the evolutionary and ontogenetic perspectives, is that behavior cannot be the main criterion for defining feral animals. Feralization as de-domestication requires a complement of genetic changes that not only influences behavior, but a number of other phenotypic characters as well. Behavioral adaptation to a new environment is not considered an adequate sign of feralization under the evolutionary view unless a genetic basis for the differences between animals reared in the wild and those reared in captivity underlies that behavior (Price, 1984).

One difficulty with this view is that determination of the feral endpoint is subjective. Assume, for instance, that a number of dogs is living on the outskirts of a town and behave like "wild" dogs. Further assume that continued recruitment into the wild population results from breeding between owned and wild dogs. It is likely that even after numerous generations the physical appearance of wild dogs will have changed little, although overt differences in behavior, such as sociality and predation, persist. Adherents to the view of feralization as de-domestication would necessarily conclude that the wild-behaving population is not yet feral.

At the other extreme, assumptions of pleiotropy, in which a number of genes controlling the physical characteristics of an animal also have an effect on behavior, are not justified either. Animals may reattain physical similarity to the ancestral form but not behave as wild animals. In an attempt to uncover pleiotropic effects on dog behavior, Scott and Fuller (1965) unsuccessfully sought correlations between hair length, hair color, and body size, and behavior.

A fourth implication of the evolutionary perspective is that populations maintaining some contact with humans will become feral at a slower rate than populations completely isolated from human influence (Price, 1984). Such a prediction is difficult to substantiate over the span of time

involved in de-domestication. Furthermore, the assumption that feralization will occur to a semi-isolated population, albeit over a longer time than one in isolation, may not be valid.

The types of control humans have over animal populations maintaining peripheral contact with humans are likely to be as important as the degree of control. For instance, whether or not (1) dogs have access to human-provided (intentionally or not) food and shelter, (2) potential mates are derived from captive, owned dog populations, and (3) some form of population control is exercised by the human populace on unowned dog populations are conditions that may be important. Thus, a hierarchy of effects may be involved whereby different types of selection pressures affect feralization to varying degrees. Subsequent to that, the amount or degree of pressure exerted becomes important. There currently are no data to support the assumptions that (1) dog populations having less to do with man, yet not completely divorced from human contact, will ultimately become feral or, (2) that the amount of contact alone is the key factor in determining the rate of feralization.

Ontogeny and Feralization: An Alternative View

As with domestication, feralization derives its meaning from the context of human-animal relationships. The underlying basis of feralization is a change in those relationships reflecting changes in habitat use and behavior. We suggest that the mechanism for feralization is an ontogenetic one involving the development of individuals from a tame to a wild condition, and not the evolution of populations. Specifically, the single most important criterion for determining whether or not an animal is feral should be a behavioral one.

The term feral has always been understood implicitly by researchers and laymen alike to mean behaving like a non-domestic animal, regardless of its formal definitions. Feralization is therefore defined as the process by which

individual domestic animals become desocialized from humans, or never become socialized, and consequently behave as untamed or wild, non-domestic animals.

While one may consider that genetic change has occurred in animal populations that have been feral for some time, acceptance of a behavioral-ontogenetic approach omits the need to demonstrate such changes. Morphological changes over time are neither necessary nor predicted; feralization is equated here with learning, in reasonably short periods. The ontogenetic approach requires that individual animals be capable of becoming feral in their lifetime, which is precluded in the evolutionary approach. Although these kinds of data have not been routinely collected, König (1979) noted that individual domestic cats (Felis catus) can become wild and behave like untamed, non-domesticated relatives. In addition, Gipson (1983) suggested a similar pattern for feral dogs in Alaska.

One way to gauge feralization is through observation of the loss of tameness or approachability (Hediger, 1964). Inasmuch as tameness and socialization to humans are positively correlated, the loss of tameness may serve as an accurate indicator of desocialization. Likewise, in cases where socialization of domestic animals to humans has never taken place, the lack of tameness and development of fear responses to unfamiliar stimuli (Scott and Fuller (1965) provide data on the development of fear responses in dogs) will denote feralization.

For animals born in the wild, feralization will not involve a loss of socialization to humans, but the development of a fear response that essentially precludes subsequent positive social interactions with humans. Although the fear response is a general one to unfamiliar stimuli, its display toward humans is an important characteristic of feral animals and, in the dog for example, develops between 7 and 14 weeks of age (Scott and Fuller, 1965). Freedman et al. (1961) examined the phenomenon in pups by exposing different-aged, naive individuals to a

passive observer for ten minute periods. At 3 weeks of age the pups quickly came to the observer; by 7 weeks of age it took 2 days before the pups approached, and by 14 weeks of age they would not approach the observer, even after a week of testing. Freedman et al. (1961) noted that these pups were like wild animals, that is, they behaved like feral animals.

Two other points must be made. First, the feral condition in one habitat may be different from the feral condition in another habitat, even within a species. All feral animals may exhibit avoidance of humans, for instance, but some may scavenge while others prey on live animals. The habitat will ultimately determine the feral condition. Second, the habitat will determine if feralization is a likely result of the conditions under which the animal is attempting to survive. For example, there are dogs that have a long history of being unowned (Daniels, 1983) but these effectively can be excluded from the population of dogs that successfully go feral. A dog that has survived for a long time as an unowned, though non-feral, animal is likely to remain that way unless changing environmental pressures push it closer to the feral state.

Successful feralization should vary among individuals, among breeds, and among species. Furthermore, given that different-aged animals are subject to different selective pressures and will exhibit different behavioral responses to those pressures, one might expect various cohorts, as well as animals with different prior experiences, to undergo feralization via distinct pathways. These differences will be expressed as variations in the time required to become feral and in changes in behavioral repertoire (Daniels, 1987).

For domestic animals born in the wild, we need not postulate survival to reproductive age, simply survival to a feral state. Thus, the issue of whether or not a population meets Baker and Manwell's (1981) requirement that it be self-perpetuating to be feral is not germane. Although habitat

and methodological differences among different studies make comparisons difficult, Scott and Causey (1973), Oppenheimer and Oppenheimer (1975), and Daniels (1987) report a low survival rate among free-ranging dogs. Wild-born pups are susceptible to a number of pathogens, and predation on pups may significantly influence overall survival rates, as will the ability of one or both parents to provide ample care.

Feralization and Speciation

Because feralization defines behavioral adaptations to an existence disassociated from man, breeding, which is a requirement for reversion in the evolutionary view, is unimportant in the ontogenetic scheme. An individual may become feral, never associate with another feral animal (but this is highly unlikely), never breed, and die. Theoretically, it could take any number of generations before a feral population becomes established, despite the development of numerous feral animals.

However, the ontogenetic approach is compatible with the prediction that given time and a significant measure of reproductive isolation, genetic changes in a population of feral animals will occur. It does not make this a necessity; the animals are feral regardless of the genetic make-up of the population. Furthermore, no predictions as to the direction of phenotypic change are necessary aside from the requirement that the feral animal behave in a way similar to an untamed, non-domestic relative. For instance, Barnett and Rudd (1983) reported a trend toward homogeneity in the physical appearance of feral dogs on the Galapagos Islands: they tended to be large, have short hair, were generally white with brown or black spots, and had unusually large ears. Barnett and Rudd suggested that the evolutionary development of these traits may be a response to high temperatures and the need to facilitate cooling. It is clear that these dogs, which have changed over time, are not approaching the ancestral phenotype.

Although the Galapagos dogs do not warrant distinction

from Canis familiaris, the dingo, often considered a feral domestic dog (Buehler, 1973) and classified as C. f. dingo (Corbett and Newsome, 1975), is also often referred to as a separate species, C. dingo (Buehler, 1973). However, the (possible) difference in classification between the Galapagos dogs and the dingo should not imply that one group is any more feral than the other. Animals may become feral and never become de-domesticated, or de-domestication may occur at different rates for different populations, although each population is already feral.

CONCLUSION

The longstanding view that feralization and domestication represent opposing evolutionary processes has been reevaluated. Although feralization as de-domestication may be superficially an intuitively attractive concept, further examination of the implications of such a theory point to several shortcomings that have yet to be addressed by its proponents. An ontogenetic perspective, however, based on the behavior of animals rather than genetic and morphological changes over time, more reasonably defines the process by which domestic animals become "wild." Feral animals generally will still be domestic animals which live free of human interference and characteristically behave negatively to humans. The ontogenetic perspective does not preclude evolutionary effects of continued isolation on a population of feral animals. Such effects are secondary, however, and do not define the process of feralization.

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