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Behavioral development in animals undergoing domestication

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Abstract

The process of domestication involves adaptation, usually to a captive environment. Domestication is attained by some combination of genetic changes occurring over generations and developmental mechanisms (e.g., physical maturation, learning) triggered by recurring environmental events or management practices in captivity that influence specific biological traits. The transition from free-living to captive status is often accompanied by changes in availability and/or accessibility of shelter, space, food and water, and by changes in predation and the social environment. These changes set the stage for the development of the domestic phenotype. Behavioral development in animals undergoing domestication is characterized by changes in the quantitative rather than qualitative nature of responses. The hypothesized loss of certain behavior patterns under domestication can usually be explained by the heightening of response thresholds. Increases in response frequency accompanying domestication can often be explained by atypical rates of exposure to certain forms of perceptual and locomotor stimulation. Genetic changes influencing the development of the domestic phenotype result from inbreeding, genetic drift, artificial selection, natural selection in captivity, and relaxed selection. Experiential contributions to the domestic phenotype include the presence or absence of key stimuli, changes in intraspecific aggressive interactions and interactions with humans. Man's role as a buffer between the animal and its environment is also believed to have an important effect on the development of the domestic phenotype. The domestication process has frequently reduced the sensitivity of animals to changes in their environment, perhaps the single-most important change accompanying domestication. It has also resulted in modified rates of behavioral and physical development. Interest in breeding animals in captivity for release in nature has flourished in recent decades. The capacity of domestic animals to survive and reproduce in nature may depend on the extent to which the gene pool of the population has been altered during the domestication process and flexibility in behavioral development. "Natural" gene pools should be protected when breeding wild animals in captivity for the purpose of reestablishing free-living natural populations. In some

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cases, captive-reared animals must be conditioned to live in nature prior to their release. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Animal domestication is best viewed as a process, more specifically, the process by which captive animals adapt to man and the environment he provides. Since domestication implies change, it is expected that the phenotype of the domesticated animal will differ from the phenotype of its wild counterparts. Adaptation to the captive environment is achieved through genetic changes occurring over generations, and environmental stimulation and experiences during an animal's lifetime (Price, 1984). In this sense, domestication can be viewed as both an evolutionary process and a developmental phenomenon.

This review constitutes a summary of the literature dealing with the effects of domestication on the behavior of captive animals. The emphasis in this article is placed on environmentally induced changes in the development of behavior accompanying the domestication of farm, laboratory and companion animals. (See Price, 1998, for a companion review paper focusing on genetic contributions to the domestic phenotype). After defining domestication, the reader is introduced to some of the changes in the animal's environment associated with the transition from nature to captivity. Changes in the quantity and quality of space and shelter available to captive animals, changes in behaviors associated with feeding and drinking, the reduction of predation and changes in the social environment are discussed with respect to their role in behavioral modification and adaptation to the captive environment. While artificial selection and natural selection in captivity facilitate adaptation to the captive environment over generations, the unique experiences of individuals foster adaptation within their lifetime. Environmentally induced changes in the behavior of domestic animals are reflected in the role of key stimuli, changes in intraspecific aggression, interactions with humans, and responsiveness to environmental change as well as in rates of development including neoteny. The review concludes with a short treatment of feralization and concerns associated with rearing animals in captivity for release in nature.

2. Domestication defined

Darwin (1859; 1868) suggested that domestication is more than taming, that it includes breeding animals in captivity, is goal-oriented, may occur without conscious effort on the part of man, increases fecundity, may bring about the atrophy of certain body organs, enables animals to achieve greater plasticity, and is facilitated by subjugation to man, the domesticator. Some contemporary definitions postulate that domestication is a condition in which the breeding, care and feeding of animals are more or less controlled by humans (Bokonyi, 1969; Hale, 1969; Clutton-Brock, 1977). This definition

implies that a population of animals is rendered domestic by exposure to the captive environment and by the institution of certain management practices. Ochieng'-Odero (1994) proposes that domestication consists of habituation and conditioning to environmental stimuli associated with the captive environment. Whereas many important aspects of the domestic phenotype are environmentally induced or can be linked to certain experiences, there are many adaptations to the captive environment that can be best explained by genetic changes accompanying the domestication process.

In response to claims that animal domestication was solely an experiential phenomenon, Price and King (1968) proposed that "domestication is an evolutionary process involving the genotypic adaptation of animals to the captive environment". Ratner and Boice (1975) took a more ontogenetic approach by acknowledging the contributions of both genetic change and experience in the development of the domestic phenotype. More recently, Lickliter and Ness (1990) proposed a "developmental systems" approach to domestication. In their view, domestic phenotypes are not transmitted in the genes nor contained in features of captive environments but are constructed by the "coaction of organic, organismic, and environmental factors during ontogeny".

It is difficult to formulate a definition of domestication that is general enough to account for the many factors contributing to the domestication process yet specific enough to be meaningful in terms of the evolutionary and biological processes involved. For the purpose of this report, domestication is defined as "that process by which a population of animals becomes adapted to man and to the captive environment by genetic changes occurring over generations and environmentally induced developmental events reoccurring during each generation" (Price, 1984). This rather simplified definition of domestication does not assume that genes and environment operate as independent factors that additively combine to determine phenotypic outcomes. Neither does it assume that one can be understood in isolation from the other. As Lickliter and Ness (1990) point out, development of the domestic phenotype can only be understood in terms of the complex interplay of organic, organismic and environmental factors during ontogeny.

The domestic phenotype refers to that cadre of phenotypic traits that facilitates the adaptation of captive animals to their environment. The range of environmental conditions typically provided for some species (e.g., livestock) on a global basis will be greater than for other species (e.g., laboratory rodents). Hence, for any given captive population, attainment of the domestic phenotype must be evaluated on a relative scale, based on the degree of adaptation to the range of environmental circumstances in which the animals are most likely to be found. Since degree of adaptation forms a continuum and is difficult to measure, it is difficult to determine the extent to which a population has become domesticated. Such decisions will necessarily be somewhat subjective and arbitrary. Assuming a stable environment, the domestication process is complete only when the fitness of the population has reached some maximal steady state.

The degree to which a wild population of animals is preadapted for domestication largely depends on the degree of developmental plasticity of the species and the extent to which the captive environment allows for the development and expression of species-typical behavioral patterns compatible with husbandry techniques. The degree of

preadaptation is relative to the specific conditions under which a group of animals is maintained. Just as there is geographical variation in the environments of free-living animal populations, variation exists among the environments provided different populations of a given species in captivity (Hediger, 1964; Box, 1973). Hence, the degree of preadaptation of a species for domestication is dependent on the capacity of species members to adapt through developmental and evolutionary processes to a variety of environmental and husbandry conditions (Balon, 1995).

3. The transition from nature to captivity

Although there are many reported differences between wild and domestic stocks, there is little evidence that domestication has resulted in the loss of behaviors from the species repertoire or that the basic structure of the motor patterns for such behaviors has been changed (Scott and Fuller, 1965; Hale, 1969; Miller, 1977). In nearly all cases, behavioral differences between wild and domestic stocks are quantitative in character and best explained by differences in response thresholds. Likewise, the characteristic perceptual capabilities of most species remain highly stable under domestication (Kretchmer and Fox, 1975; Heaton, 1976).

The process of domestication implies a transition from nature to captivity. However, as Carlstead (1996) points out, “nature” and “captivity” are only extremes on a continuum. Free-living wild populations are found from wilderness areas to semi-wild preserves where provisioning takes place. Captive populations are found from small laboratory cages to complex zoo enclosures to large breeding parks or corrals. The degree of husbandry applied in different captive environments can be highly variable (Smits, 1990).

Domestic animals are sometimes provided with an environment that is physically similar to the habitat of their wild ancestors. Behavioral and physiological adaptations to such an environment will be readily achieved. Very often, however, the captive environment does not match the ancestral environment and adaptation is challenged.

3.1. Shelter

In nature, natural cover or shelter provides protection from rigorous climatic conditions, privacy for mating and rearing of offspring, and a means of escape from predators and aggressive social partners. An increase in the quantity or quality of cover permits higher population densities by reducing the incidence of interspecific and intraspecific contacts (Jenkins, 1961). Some of these same needs may exist in captivity. Species that use nest cavities for reproduction in nature may require nest boxes for successful breeding in captivity (Millam et al., 1988). Hansen and Damgaard (1991) reported that the physiological stress level of farmed mink increased when they were deprived of nest boxes in their cages. They hypothesized that nest boxes shielded the animals from stress-provoking external stimulation from neighboring cages. Clark and Galef (1977) have demonstrated that the tameness and docility of captive gerbils can be influenced by the physical design of their cages. Laboratory-reared gerbils given access to an enclosed

hiding place (e.g., burrow system or shelter) during ontogeny exhibited greater avoidance of a human-like stimulus than gerbils reared in open laboratory cages. Elicitation of escape responses (flight) into a concealed chamber was found to be the “critical” experience in the development of this avoidance response. Once flight and concealment responses were established, experience in an open-cage environment had little influence on avoidance behavior. More recently, Clark and Galef (1980; 1981) have reported that, in comparison with gerbils reared in cages with shelters, gerbils reared in standard open cages exhibited earlier eye-opening, faster growth, earlier sexual maturity, and a marked decrease in adrenal size, all of which are traits normally associated with domestication (King and Donaldson, 1929; Richter, 1949; Clark and Price, 1981). Nikolettseas and Lore (1981) found that domesticated Norway rats reared in cages with burrows were more aggressive toward strange intruders than rats reared in standard laboratory cages without shelter.

3.2. *Space*

The spatial requirements of free-living wild animals are determined by a variety of factors such as the distribution and availability of food and water, the frequency and intensity of social interactions, and the quantity and quality of cover or shelter. Home-range size often varies on a seasonal and annual basis. By comparison, the quantity and quality of space available to captive animals are almost always reduced (Hediger, 1964). Since food, water and shelter for confined animals are normally provided, spatial requirements are dictated primarily to avoid crowding and the need for perceptual and locomotor experience or exercise.

The spatial requirements of wild and domestic animals in captivity are often determined by some combination of intuition and knowledge of the species. Animals with large home ranges in nature are often assumed to require a great deal of space in captivity. This may not be the case inasmuch as home-range size in nature may be dictated more by feeding behavior (i.e., search strategies) and the distribution and abundance of food items than by a need for locomotor stimulation or activity. On the other hand, animals may be motivated to explore for its own sake (Stevenson, 1983). Failure to provide captive animals with the opportunity to explore may result in an apathy toward environmental stimuli and the development of atypical behaviors (Wood-Gush and Vestergaard, 1989). Limiting the movement and physical activity of captive animals can have other non-adaptive consequences. For example, handling stress (capture and confinement) was less severe (i.e., shorter duration) in captive striped bass that had been exercised-conditioned than in unexercised fish (Young and Cech, 1993). The point is that the space provided in captive environments should be behaviorally relevant, that is, it should allow for the development and expression of a normal complement of basic behavior patterns. It is not surprising that many animals isolated in relatively small enclosures develop a variety of stereotyped behavior patterns (Fraser, 1968; Mason, 1991; Lawrence and Rushen, 1993), since their social interactions with conspecifics and perceptual and locomotor experiences are limited (O’Neill et al., 1991). Lagadic and Faure (1987) used operant conditioning techniques to determine preferences for cage size, feeder space and floor types in intensively housed domestic hens.

The social structure of animal populations may change when space becomes limited (Calhoun, 1962; Lott, 1991). Butler (1980) reported that the social organization of wild house mice (*Mus musculus*) changes from territoriality to what resembles a dominance hierarchy if space is significantly reduced. The inability of subordinate animals to escape from more dominant conspecifics may result in the formation of more highly polarized social hierarchies than would otherwise occur in nature.

Animals born and reared in confinement may react more favorably to such conditions than animals born and reared in relatively unrestricted environments and then confined later in life. This hypothesis should be investigated, since it has particular relevance to the animal welfare issue.

Similarly, domesticated species may adapt more readily to a relatively small, physically uniform environment than do genetically wild stocks. Huck and Price (1975) obtained evidence that the development of behavior in a stock of domestic laboratory rats (*Rattus norvegicus*) may be more highly buffered against perceptual and locomotor deficits than the behavior of a stock of first generation laboratory-born wild Norway rats. Early experience in an enriched environment had a greater effect on the growth and open field behavior of the wild stock than their domestic counterparts, for eight of nine variables.

3.3. Feeding and drinking

In nature, animals spend a large share of their time and energy searching for and consuming food and water. Choices are made by animals with regard to feeding sites and diet selection. Most captive animals, on the other hand, are dependent on humans to provide appropriate diets which are often relatively uniform on a daily and seasonal basis. Since diet selection is largely learned in many species (Lynch and Bell, 1987; Forbes, 1995; Galef and Allen, 1995; Provenza, 1995) animals may be reluctant to sample unfamiliar food items and familiar foods presented in novel ways (Galef and Clark, 1971; Heinrich, 1988). Schoonhoven (1967) found that laboratory-reared tobacco hornworms (*Manduca sexta*) accepted host food plants that their wild counterparts rejected based on a change in the sensitivity of contact chemoreceptors.

In captivity, food and water is often provided at a single location and in sufficient quantities so that the time and energy spent in feeding are greatly reduced relative to what is experienced by their wild counterparts (Newberry, 1995). One could argue that the provision of food and water for captive animals has resulted in a relaxation of natural selection on traits associated with food selection (and avoidance), ability to locate and capture prey, and even the motivation to explore and investigate their environment. In reality, it appears that the greatest effect of food provisioning is in providing captive animals with more idle time to do other things, some of which can have important welfare implications. Consequently, food-delivery techniques have been developed for captive animals that are contingent on input from the animal and are more time consuming (Moore et al., 1975; Markowitz and Woodworth, 1978; Stevens, 1978; Young et al., 1994). A number of researchers have demonstrated that captive animals will work to obtain food that is otherwise freely available (Carder and Berkowitz, 1970; Duncan and Hughes, 1972; Inglis and Ferguson, 1986; Shepherdson et al., 1993; Reinhardt, 1994).

In captivity, adherence to feeding schedules may be of considerable importance. Carlstead (1986) demonstrated that domestic pigs fed on an unreliable intermittent schedule were more aggressive toward one another than pigs fed on a predictable schedule. Barnett and Taylor (1997) demonstrated that random feeding of pigs resulted in a chronic stress response.

3.4. Predation

Predation on free-living populations of wild animals can be intense (Wilson et al., 1992). Unconfined populations of domestic animals (e.g., sheep, goats) in range environments may still experience severe predation (Shelton and Wade, 1979). On the other hand, cages, pens and certain types of fencing used to confine animals and the close proximity of captive animals to human activity normally eliminate or greatly reduce contact with predators.

When predation on wild-caught animals (born and reared in nature) is compared with predation on their captive-reared counterparts, the latter almost always experience the heavier losses (Schroth, 1991). Hill and Robertson (1988) reported that free-living captive-reared ring-necked pheasants were three times more susceptible to predation than their wild counterparts. Waltz (1976) found wild-caught Norway rats more effective in avoiding predation by ferrets than first-generation laboratory-reared wild rats. Kardong (1993) found wild-caught deermice less susceptible than laboratory mice to predation by blindfolded rattlesnakes. Olla and Davis (1989) demonstrated that captive-reared salmon better avoided predation by lingcod after conditioning to live predators and predation-associated stimuli. It appears that the failure of captive-reared animals to exhibit appropriate predator avoidance behaviors is largely mediated by a rearing environment that consistently fails to provide certain key experiences during development.

3.5. Social environment

One of the greatest differences between the social environments of wild and captive animals is the reduction in number of options available to captive animals. In captivity, management decisions affecting the density and composition of populations are often made for the sake of human convenience or to expedite economic considerations. Humans often force captive animals to live under population densities they would normally not tolerate in nature (Hediger, 1964; Dawkins, 1980). Although increased population density may result in varying degrees of social stress, management practices and facility designs that minimize competition for food, water, shelter, mates and personal space permit captive animal populations to exist at relatively high densities with relatively little social strife. The fact that humans are in control of the social environment of captive populations places much of the responsibility for management on the animal caretaker. A thorough understanding of the behavioral biology of the species will help to minimize management errors (Baker, 1994).

Alternatively, captive animals may be socially isolated for economic reasons, to prevent the spread of infectious diseases or to preclude breeding. Social isolation can

cause stress, impaired health and the development of atypical behaviors. Veissier et al. (1994) has shown that individually penned veal calves are initially dominated by group-reared counterparts when allowed to freely interact. Artificial (hand) rearing of young animals is effective in socializing captive animals to humans but when combined with physical isolation from conspecifics can result in heightened aggressiveness toward people (Price and Wallach, 1990), inappropriate social interactions with conspecifics and impaired reproductive success (Beck and Power, 1988). Female rhesus monkeys separated from their mothers after infancy are more likely to reject or neglect their own offspring (Berman, 1990; Champoux et al., 1992). Hand-rearing can also limit opportunities for social learning by preventing critical early experiences with parents such as in the development of food preferences (Altbacker et al., 1995).

In general, the age and sex structure of captive animal populations are more uniform than is the case in natural populations. This generalization is particularly true of farm species, in which the young may have little or no contact with parents and are often reared and maintained in same-sex peer groups. While such management practices may be most practical from an economic standpoint, certain modifications in behavioral development may result. Price et al. (1994) reported that young rams denied heterosexual experience during their first year of life will exhibit reduced sexual performance as adults. Similarly, sexual behavior is adversely affected in male pigs reared in single-sex groups (Hemsworth et al., 1978).

Thresholds for agonistic behavior may be influenced by different opportunities for social conditioning in nature and in captivity. Swain and Riddell (1990) found that hatchery stocks of juvenile coho salmon were more aggressive than hatchery-reared wild stocks of juvenile salmon. Moyle (1969) reported this same result in brook trout. Other studies with fish (Robinson and Doyle, 1990; Ruzzante and Doyle, 1993) reported a reduction in agonistic behavior with domestication. Ruzzante (1994) proposes that changes in agonistic behavior of hatchery stocks of fish are correlated with selection for growth rate in captivity. If food is limited, larger and more aggressive fish will be better able to compete for existing resources.

Reproductively active animals often show preferences for certain individuals of the opposite sex (Bateson, 1983). Cheng et al. (1979) have demonstrated that wild and game-farm (semidomestic) stocks of mallard ducks prefer to mate with members of their own stocks when given a choice. Mate selection of animals in captivity is frequently determined by humans as part of the artificial selection process. The period of association between male and female may be nonexistent, as when artificial insemination is employed, or very brief, as in "hand-breeding", in which a receptive female is placed with a male only long enough for copulation to occur. Male and female foxes on commercial fur ranches are allowed limited access to each other in order to prevent pair-bonding that would preclude breeding the male to other females (Enders, 1945). Male–female incompatibility is considered a significant deterrent to successful reproduction among many animal populations in captivity (Spurway, 1955). Blohowiak (1987) found that when black ducks were randomly paired, fewer than a third of the pairs mated. When kept in large groups and allowed to select their own mates, a majority of them bred. To get fertile eggs in captivity, female canvasback ducks must choose their own mates and be housed with them in visual isolation from other ducks (Bluhm and

Phillips, 1981). In addition, a water depth of at least 35 cm is necessary for successful copulation. Special diets and large flight pens are unnecessary; a small, bare-walled pen with a nest box is sufficiently “natural” if an adequate social environment is provided. Hartt et al. (1994) have pointed out that age at pairing (in California condors) may affect reproductive success. Forced cohabitation of potential mating pairs starting early in life may result in a kind of “assumed kinship” and mating failure even when male and female are unrelated genetically.

4. Development of the domestic phenotype

4.1. Genetic mechanisms

The genetic phenomena with the greatest potential impact on the domestication process are inbreeding, genetic drift, and selection (Price, 1998). Whereas inbreeding and genetic drift produce random changes in gene frequencies, the changes resulting from selection are directional. Price and King (1968) proposed three primary selective phenomena that influence populations of animals undergoing domestication: (1) artificial selection, (2) natural selection in captivity, and (3) relaxation of natural selection. One could argue that relaxed selection only describes the absence of previous selective pressures and is not a distinct selective phenomenon. As a result of artificial and natural selection acting individually or in combination, selection with respect to specific traits may change in intensity or direction, or both.

4.2. Artificial selection

Artificial selection is perhaps the best understood aspect of the domestication process (Price and King, 1968) and it is the only selective mechanism unique to domestication. Artificial selection may be applied either intentionally (consciously) or inadvertently (unconsciously). Personal biases and preferences often influence the selection of breeding stock (Muntzing, 1959) and these biases may be very subtle.

Artificial selection for large breast size in domestic turkeys has nearly eliminated the ability of males to copulate naturally and females must be artificially inseminated. Artificial selection of laying hens for non-broody behavior has resulted in strains of chickens that normally do not incubate eggs or brood chicks. Selection of silver foxes for non-aggressive behavior towards man (i.e., tameness) was begun 40 years ago at the Institute of Cytology and Genetics in Novosibirsk, Siberia (Belyaev, 1979; Trut, 1999). As a result of this selection, foxes can now be bred that show little fear of people and resemble domestic dogs in their behavior. The unselected control population continues to exhibit wild-type behavior, including strong defensive responses toward humans.

Guttinger (1985) reported that the most striking difference between the songs of wild and domesticated canaries is in the degree of variability of song architecture (greater for wild birds) and the size of the individual repertoire (twice as many syllable types in wild breeds). Artificial selection among domestic stocks for long rhythmical repetitions of identical notes, especially low frequencies, can explain the reduction in song variability and repertoire size.

Marliave et al. (1993) reported that 10 generations of laboratory rearing of the coonstripe shrimp (*Pandalus danae*) resulted in inadvertent selection for reduced escape responses. Regular handling of the shrimp in a study of protandric hermaphroditism would often injure individuals with intense tail-flip escape responses. By the tenth generation, the intensity of escape responses had become greatly reduced and dopamine levels (frequently associated with emotional reactivity) were reduced to only 5.5% of the level in wild stock. Hybrids between wild and “domestic” shrimp were intermediate for both variables.

4.3. *Natural selection in captivity*

All of the selection imposed on captive populations that cannot be ascribed to artificial selection must be “natural” (Price and King, 1968; Hale, 1969; Wright, 1977). Animals selected to be parents of the next generation do not always reproduce (Mellen, 1991; Roest, 1991; Van Oorschot et al., 1992) and if they do, they do not always provide the theoretically expected number of offspring. Reproductive failure may result from physiological or psychological stress caused by such factors as sensory and locomotor deprivation (Hediger, 1964), social incompatibility (Bluhm and Phillips, 1981), dietary deficiencies (Johnson and Boyce, 1991), and parasitism (Hughes and Sokolowski, 1996). Searle (1984) reported that 12 of 14 litters (86%) of the common shrew, *Sorex ananeus*, conceived and born in captivity from wild-caught females were successfully reared to weaning age. By comparison, only 8 of 15 litters (53%) conceived in nature but born in the laboratory were successfully weaned. Females pregnant at the time of capture not only did not have as long to adapt to their new environment but some of them might not have been otherwise predisposed to reproduce in captivity. Six of 23 females (26%) paired with males in the laboratory did not conceive.

In the absence of artificial selection, natural selection provides the basic selective mechanism for genetic change in captive populations. The intensity of natural selection on captive populations undergoing domestication depends on: (1) the extent to which the captive environment allows for the development and expression of species-typical biological characteristics (Spurway, 1955), and (2) the number of generations in captivity. In theory, species that possess relatively few preadaptations for their respective captive environments will experience rather intense natural selection, and thus show relatively poor survival or reproductive success. In general, natural selection in captivity is most intense during the first few generations following the transition from field to captive environments. The degree of adaptation to the captive environment will increase as the frequencies of “favorable” genes increase in response to selective pressure. King and Donaldson (1929) reported a marked increase in the reproductive success of wild genotype female Norway rats during the first eight generations in captivity. During this period, the animals were maintained under the same conditions and were fed the same diet. Although conscious (and, perhaps unconscious) selection for “vigor” was practiced, it seems plausible that much of the improvement in reproductive success seen during the first five generations of breeding in captivity was due to natural rather than artificial selection. Kawahara (1972) reported on the breeding success of an unselected population of Japanese quail following the transition from nature to captivity (cages).

Starting with 268 wild-caught individuals, the percentage of birds that had laid eggs by 20 weeks of age was 50%, 61% and 67% in the first three generations, respectively. In a domestic control strain, all females were in lay by 20 weeks of age.

Sloan (1973) tested the hypothesis that the reproductive success of wild-caught Norway rats in captivity could be predicted based on their behavior in a battery of behavioral tests. Some 280 wild Norway rats (140 females and 140 males), trapped as juveniles and raised to adulthood in the laboratory, were subjected to a battery of nine behavioral tests that clearly differentiated wild and domestic Norway rats. They were then randomly paired (mated). An equal number of wild rats caught as adults were treated in the same fashion, except that they were not exposed to the battery of behavioral tests (control for testing effects). Domestic rats, both tested and untested and approximately of the same age, provided base-line data for both behavioral and reproductive performance. On the basis of individual scores in the behavioral tests, Sloan was unable to predict reproductive success. As a group, however, those wild females that eventually reproduced behaved more like domestic rats than did the wild females that did not reproduce, with respect to 10 of 11 variables in which reproducing and non-reproducing wild rats were significantly different. The hypothesis that reproductive success in captivity is greatest for those individuals that are most domestic-like in their behavior was therefore partially supported.

4.4. *Relaxed selection*

In many cases, relaxed selection can be expected to accompany the transition from field to captive environments (Price, 1976; Waples, 1991). Certain behaviors important for survival in nature (e.g., food finding, predator avoidance) lose much of their adaptive significance in captivity. As a result, both genetic and phenotypic variability for such traits are likely to increase. Kronenberger and Medioni (1985) demonstrated that domestic house mice, *M. musculus*, were more accepting of novel saccharin-flavored water (0.1% solution) than their wild counterparts. Since wild rodents are often subjected to poison baits, it is not surprising that they are more hesitant to ingest food or water possessing novel odors or tastes. Relaxed selection for food neophobia provides a likely explanation for the more ready acceptance of the tainted water by the domestic strain. Frank (1980) reviews evidence that domestic dogs are inferior to wolves in observational learning. In nature, fitness is determined partly by the ability of individuals to learn quickly the consequences of their own behavior or the behavior of other animals. In captivity, humans serve as ever-present providers and buffers between the domestic animal and the consequences of its mistakes, and thus reduce the selective advantages of observational learning. Relaxed selection can also be inferred when captive populations experience greater survival rates than their wild counterparts.

4.5. *Correlated effects of selection*

Selection for one trait may, by pleiotropy, affect the frequencies of genes that influence correlated characters (Lerner, 1954). Eysenck and Broadhurst (1964) found that following artificial selection for high and low rates of defecation in a novel

environment, the Maudsley “reactive” and “nonreactive” strains of domestic Norway rats differed significantly in 24 of 32 different behavioral tests and in 19 of 24 physiological measures.

5. Experiential contributions to the domestic phenotype

5.1. Presence or absence of key stimuli

The absence of certain “key” stimuli in the physical environment of captive animals can result in a failure to express certain behavioral patterns. Whereas burrows constructed by wild and domestic Norway rats are similar in every respect, Boice (1977) noted that domestic Norway rats seldom initiate burrowing without an object (e.g., stone) to dig under. Wild rats were less dependent upon such stimulation. Similarly, Huck and Price (1976) reported that a wild stock of Norway rats would exhibit climbing behavior even when denied early climbing experience; male domestic Norway rats would not climb unless they had early climbing experience.

Both genetic and experiential contributions to behavioral development are illustrated by the account of Wecker (1963) of the development of habitat preferences in wild and semidomestic deer mice. Wild-genotype prairie deer mice (*Peromyscus maniculatus bairdii*) preferred a field over a woodland environment, even when born and reared in the laboratory. A semi-domesticated stock of the same subspecies originally obtained from the same area and approximately 12 to 20 generations removed from the wild preferred the field habitat only if given early experience in a small field enclosure. After fifteen years of laboratory breeding, the semidomestic stock had “lost” the innate tendency to prefer field over woodland stimuli (presumably through relaxed selection or a correlated response to selection for some other trait) but it had not lost the psychological bias toward a grassland habitat once this preference was reinforced by early field experience. Perhaps the capacity to acquire the field bias would have been lost following further domestication of this population.

Behaviors are not always attenuated by domestication; in some cases thresholds are lowered and frequencies of expression increased. Numerous claims have been made (e.g., Hale, 1969) that the sexual behavior of domestic animals is exaggerated relative to that of their wild counterparts. Villavaso and McGovern (1986) reported that males of a laboratory strain of boll weevils (*Anthonomus grandis grandis*) were over twice as competitive as wild males for wild females and that laboratory males were nearly 3.5 times as attractive to wild females as wild males. Raina et al. (1989) found that males of a population of the corn earworm (*Heliothis zea*) maintained in the laboratory for over 120 generations were less discriminating than wild males in their response to female sex pheromone that had been experimentally modified. Domesticated males had also lost the requirement of low light intensity to respond to the pheromone. It is true that the breeding season of many species has been extended and many psychosocial inhibitions to breeding have been attenuated during the domestication process, possibly due to conditions in captivity more favorable to survival and reproduction. Females of most breeds of domestic dogs have multiple (usually two) estrous cycles approximately 6–7

months apart without regard to season (Christie and Bell, 1971) whereas wolves breed only once a year, in the winter months (Scott and Fuller, 1965). In addition, the monogamy or specific mate preferences of wild canids has been largely eliminated in domestic dogs (representing a shift toward more promiscuous sexual relations), along with the psychological inhibition to mating exhibited by subordinate individuals in many wild canid species (Scott and Fuller, 1965). However, in studies that have been controlled for stimulus novelty, there is no evidence that domestic animals have higher libido or sexual motivation than their wild counterparts (Estep et al., 1975; Price, 1980). As stated previously, the hypersexuality (i.e., frequent sexual responses) sometimes attributed to captive animals may be mediated through constant exposure to a sexually stimulating environment. Similarly, barking by domestic dogs is much more frequent than by wild canids and is elicited in a greater variety of contexts (Cohen and Fox, 1976). Wolves, the presumed wild ancestors of domestic dogs (Isaac, 1970), seldom bark in nature or in captivity (Scott and Fuller, 1965; Harrington and Mech, 1978). The barks of domestic dogs appear to be attention-getting and their lack of context-specificity and the frequency of elicitation may be due to: (1) selection by humans for guarding ability (Manwell and Baker, 1984), (2) selection for retention of juvenile (i.e., care-soliciting) characteristics, or (3) relaxed selection for ‘silence’ necessary for a wild predator (Cohen and Fox, 1976). Rood (1972) also noted lower thresholds for most vocalizations in the domestic guinea pig, *Cavia porcellus*, than in its wild relative, *C. aperea*. Wood-Gush (1959) has discussed selection for more frequent crowing in chickens.

5.2. *Intraspecific aggression*

Although the defensive aggressiveness of most domestic animals toward humans has been sharply reduced during domestication, there has not necessarily been a corresponding decline in their aggressiveness toward each other. For many years it was thought that the aggressive behavior of the Norway rat had been so attenuated by domestication that what fighting behavior remained was relatively immature and seldom resulted in physical harm to opponents (Barnett, 1975). We now know that under certain rearing and stimulus conditions the attack and other offensive aggressive behaviors of domestic Norway rats can be just as savage as those of their wild counterparts (Blanchard et al., 1975; Adams, 1976; Takahashi and Blanchard, 1982). It is the defensive behaviors of Norway rats that have become attenuated by the domestication process (Blanchard et al., 1986), perhaps as a correlated effect of selection for ease of handling.

If the domestic Norway rat has not lost its aggressive potential toward members of its own species, why is there not more fighting among domestic rats in the laboratory environment? One hypothesis is that the threshold for aggressive behavior in laboratory rats is raised by being reared and maintained with peers in small, open laboratory cages (Price, 1978; Barnett et al., 1979; Lore and Flannelly, 1981; Nikolettseas and Lore, 1981; Boice and Adams, 1983). Under these conditions, laboratory rats do not often encounter unfamiliar animals which are likely to incite aggressive interactions (Adams and Boice, 1989). Consequently, a stronger stimulus is required to incite attack behavior (i.e., the threshold for attack behavior is raised). However, once an animal is attacked, the

ensuing aggressive interactions can be as intense as seen in their wild counterparts. Interestingly, domestic laboratory rats reared in outdoor enclosures are more aggressive in their social interactions and readily develop dominant–subordinate relationships (Nikoletseas and Lore, 1981; Boice and Adams, 1983; Adams and Boice, 1989). Perhaps the instability of the social environment under these circumstances and/or the experience of defending nest sites from intruders results in a lowering of the threshold for aggressive behavior. Social experience and physical aspects of the rearing environment play an important role in the expression of aggression in this species (Lore and Flannelly, 1981; Adams and Boice, 1989).

Associated with these changes in the frequency and intensity of aggressive behaviors in domestic animal populations, there appears to be a corresponding decrease in the frequency and intensity of submissive behaviors. The “loss of social inhibitions” ascribed to domestic animals by Lorenz (1965, p. 94) may reflect higher thresholds for aggressive behavior. The uninhibited manner in which domestic Norway rats engage in social interactions stands in sharp contrast to the naturally more cautious and ambivalent demeanor of their wild counterparts in social situations (Boreman and Price, 1972; Price, 1978). In a study comparing the social interactions of wild and domestic house mice (*M. musculus*), Smith et al. (1994) found that social encounters were more frequent among domestic mice than their wild counterparts; subordinate domestic mice were more likely to interact with dominant conspecifics.

Some domestic strains have been selected for their aggressive behavior (e.g., fighting bulls and cocks). It has been postulated that in the breeding of fighting cocks selection against submissiveness may be more intense than selection for increased aggressiveness (Siegel, 1975).

5.3. *Interactions with humans*

Unless wild animals have been habituated to the presence of humans (Geist, 1971; Van Lawick-Goodall, 1968), they tend to avoid close contact with man. In captivity, the capacity to adapt to the presence of people and frequent handling is an important fitness-determining factor. The ease with which wild golden hamsters (*Mesocricetus auratus*) can be handled was a key feature for their domestication and adoption as a laboratory animal and pet species (Murphy, 1985). Tameability (capacity to be tamed) is obviously desirable in animals undergoing domestication (Hediger, 1938; Hale, 1969). The process of taming is an experiential (learning) phenomenon occurring during the lifetime of an individual. Acquired or learned tameness is not transmitted from dam to offspring. Avoidance of humans by the offspring of hand-reared (tame) and mother-reared (relatively untamed) ungulates is very similar when exposed to humans in the absence of their mother or herd-mates (Blaxter, 1974; Lyons et al., 1988a). However, Lyons et al. (1988b) reported that mother-reared dairy goats (relatively timid) exhibited less avoidance of humans when accompanied by tame herd-mates.

Hemsworth et al. (1990) reported that fear of humans in domestic pigs is a moderately heritable characteristic. Tameness is an important behavioral trait of captive animals, since it facilitates animal handling (Grandin, 1993) and improves animal

welfare (Hemsworth and Barnett, 1987). Tameness can minimize the negative effects of handling in animal agricultural enterprises (Barnett et al., 1994; Hemsworth et al., 1994) and when conducting scientific investigations (Gross and Siegel, 1979). Acquired tameness can be achieved by habituation or positive associative conditioning and it may be attained without any deliberate effort on the part of the animal caretaker. In habituation, the animal's fear of humans is gradually reduced by repeated exposures in a neutral context; that is, man's presence has neither positive nor negative reinforcing properties. Taming may also be achieved by positive associative conditioning in which the animal's fear of humans is reduced by the latter's role as a secondary reinforcer. As providers of such necessities as food, water, shelter and grooming, humans become secondarily associated with such positive stimuli and the threshold for avoidance behaviors is raised. For some species such as the domestic dog, humans can also take on the role of a social object (i.e., "companion") whose presence, itself, is rewarding. Contact with humans during a "sensitive period" for socialization very early in life can greatly facilitate (i.e., accelerate) the process of taming (Hediger, 1938; Pedersen and Jeppesen, 1990; Mateo et al., 1991). Artificial (hand) rearing of captive animals during the sensitive period of socialization is particularly effective in taming animals (Lyons, 1989) but is labor intensive.

Tameness toward humans and associated ease of handling are among the more important aspects of the domestic phenotype. Popova et al. (1991a) have demonstrated that the tameness of silver foxes in the presence of humans can be directly related to brain chemistry. Tame foxes have higher levels of serotonin and its metabolite 5-hydroxyindole acetic acid and greater tryptophan hydroxylase activity in the midbrain and hypothalamus than their unselected counterparts. Interestingly, these same changes in brain chemistry have also been found in Norway rats selected for reduced aggressiveness toward humans (Naumenko et al., 1989; Popova et al., 1991b) and when comparing domestic and wild Norway rats (Hammer et al., 1992). Selection for tameness in foxes and rats have also influenced the catecholamine system of the brain (Cuomo-Benzo et al., 1977; Nikulina, 1990; Nikulina et al., 1985). In both species, selected (tame) animals possessed higher levels of noradrenaline in the hypothalamus than was found in the unselected (non-tame) control lines. Dopamine levels did not differ.

Support for a genetic influence on tameability comes from twin studies. Lyons et al. (1988a) demonstrated with twin dairy goats that a group of hand-reared animals ranked nearly the same as their mother-reared co-twins in tameness toward humans (i.e., the tamest hand-reared animals were co-twins to the tamest mother-reared animals).

While the genes can set limits to the degree of tameness achieved under a given set of circumstances, experience can determine the extent to which taming actually occurs. The taming process appears to be relatively situation-specific. Galef (1970) tested the effects of several rearing experiences on the ease with which wild Norway rats could be handled by humans. Second and third generation laboratory-reared wild rats were reared by either wild or domestic mothers, reared with either wild or domestic litter mates, given either minimal or maximal exposure to humans in a laboratory environment, and either not handled at all or handled for 2 min/day from age 10 to 23 days. At weaning (about 23 days of age), each rat was subjected to a handling test which scored such behaviors as difficulty of capture, escape behaviors, vocalizations, and bites directed

toward the hand that restrained the animal. Only direct handling experience increased the ease of capture and handling.

5.4. Responsiveness to environmental change

We have seen how the presence or absence of key stimuli, intraspecific aggressiveness and interactions with humans can have profound effects on the development of specific traits associated with the domestic phenotype. It appears that these factors together with genetic changes accompanying domestication can also contribute to more general traits associated with the domestication process. For example, one can argue that the single most important effect of domestication on behavior is reduced responsiveness (i.e., sensitivity) to environmental change. This characteristic is observed in virtually all populations of domestic animals and pervades a wide variety of behavioral traits (e.g., response to novel stimuli, intraspecific interactions, reaction to the presence of people). Reduced responsiveness to environmental change is seen as an adaptation to living in a biologically “safe” environment with (1) limited opportunities for perceptual and locomotor stimulation, (2) frequent invasions of personal space, with little opportunity to escape from dominant conspecifics, and (3) frequent association with humans, who are prone to cull untamed and intractable individuals.

5.5. Rates of development and the concept of neoteny

Heterochrony refers to alterations or shifts in rate of development (Gould, 1977). Developmental rates can be either accelerated or reduced by selective mechanisms (Cairns, 1976). There is considerable support for the hypothesis that domestication has accelerated attainment of sexual maturity. Clark and Price (1981) have demonstrated that domestic Norway rats reach sexual maturity and breed at an earlier age than wild Norway rats reared under identical conditions. Shishkina et al. (1993) reported this same result in wild Norway rats selected for reduced aggressiveness toward humans. Kawahara (1972) indicated that the age at first egg for wild Japanese quail bred in laboratory cages for the first three generations averaged 110 ± 2.7 , 82 ± 2.3 and 81 ± 1.5 days, respectively. Domesticated quail (controls) averaged 50 ± 0.3 days. There is evidence that most domestic dogs become sexually mature at 6 to 9 months of age, which is considerably earlier than for wolves and other wild canid species (Scott and Fuller, 1965; Fox, 1978). Hale (1969) and Setchell (1992) postulate that in a number of species, domestication has resulted in an improvement in reproductive efficiency. Improved nutrition, reduced energy expenditure and, in some cases, reduced stress in captivity could also contribute to the improved reproductive performance of domesticated animals.

Whereas the development of reproductive capabilities has been accelerated by domestication, other developmental processes have been prolonged. Miller and Gottlieb (1981) reported that domestication has decelerated the rate of development of behavioral arousal in the newly hatched mallard (Peking) duck. Belyaev et al. (1984/1985) found that the sensitive period of primary socialization has been extended in a population of silver fox by 25 years of selection for tameness toward humans. The retention of

juvenile behaviors into adulthood has also been cited as an effect of domestication (Fox, 1968). This process has been referred to as neoteny or paedomorphosis. In many domesticated species certain anatomical characteristics of the juvenile (e.g., shortening of the jaws and facial region) are retained into adulthood, perhaps as a result of selection to preserve the greater esthetic appeal of the young animal (Dechambre, 1949; Clutton-Brock, 1981; Morey, 1994). Coppinger and Smith (1983) suggest that behavioral neoteny has been selected for in certain wild species (e.g., the ancestors of our common domestic animals) and is a prerequisite to successful domestication. However, their argument is based on the assumption that tameability is necessarily linked to neoteny (i.e., that neoteny is a prerequisite for the development of a placid temperament). The idea that neoteny may accompany domestication is further supported by the fact that traditional animal management practices allow for the retention of juvenile social behaviors by reducing the selective advantages of aggressive potential in securing needed resources. In captivity, where food and water are normally provided and mating is largely controlled by humans, survival and reproductive success are not necessarily contingent on the attainment of high social status. Selection for early sexual maturation, before the animal's aggressive potential is fully developed, is also made possible by mating and management systems which largely eliminate competition for the opportunity to breed. Multi-sire mating programs are the exception rather than the rule for most of our common domestic animals.

Comparative studies of domestic dogs and wolves (Fox, 1978; Frank and Frank, 1982; Ginsburg and Hiestand, 1992; Morey, 1994) have suggested that the behaviors of the adult dog are relatively juvenile compared to wolves. Neoteny may characterize the behavioral development of the dog because of selection for tractability or the capacity to be closely controlled by humans, a trait frequently associated with juvenile animals. The ease with which most dogs can be trained to perform various tasks may reflect a high degree of plasticity relative to the more structured (i.e., less variable) adult-like behavior of their wild relatives. Coppinger et al. (1987) has pointed out that different dog breeds may express different degrees of behavioral neoteny. Dog breeds selected for herding livestock exhibit the eye/stalk/chase/and (sometimes) bite sequence of predatory behaviors but refrain from attack. Dog breeds selected for protecting livestock (from predators) lack these predatory behaviors and will sometimes engage them (livestock) in play. The behavior of the dog provides the most compelling case of behavioral neoteny accompanying the domestication process. In spite of claims by Coppinger and Smith (1983), Budiansky (1992; 1994) and others, it is not clear that behavioral neoteny has had a significant role in the domestication of other species.

An alternative to the selection hypothesis is that behavioral neoteny in domesticated animals may be environmentally induced. First, captive young animals may be conditioned to retain their juvenile behaviors. Offering positive rewards for juvenile behaviors (e.g., care-soliciting, playfulness, submissiveness to humans) may, in effect, retard the development of more independent adult activities, or alternatively, may mask their expression. This latter effect could be achieved by raising the threshold for elicitation of adult behaviors or by sufficiently lowering the threshold for juvenile behaviors to allow for the continued expression of many juvenile characteristics throughout adulthood. Rearing animals in physical isolation from older, socially dominating conspecifics may

further discourage the development of normal adult-like patterns of agonistic behaviors (Price, 1978) and facilitate the retention of many juvenile social behaviors. The proclivity of dogs to socialize to humans, who normally assume the role of dominant “pack” member, and the sensitivity of dogs to their social environment (Ginsburg and Hiestand, 1992) may facilitate the development and expression of juvenile social behaviors in this species.

Lastly, behavioral neoteny may be induced by early experiences related to the biological and physical characteristics of the rearing environment. Clark and Galef (1982) demonstrated that the development of adult-like patterns of exploration in the Mongolian gerbil was retarded by the presence of shelter in the rearing environment. It should also be noted that for many species (e.g., livestock) neoteny may be more apparent than real. Species raised for meat are normally slaughtered before reaching maturity; adult behavior patterns are seldom observed (Beilharz and Zeeb, 1982).

6. Feralization as a developmental phenomenon

As in the case of domestication, the process of feralization has meant different things to different people. Some definitions assert that feral animals are merely free-living populations of animals that originated from domestic stock (Pullar, 1950; Shank, 1972). Others suggest that in addition to their free-ranging status, feral animals must be unowned, not intentionally cared for by humans, and not dependent on humans for breeding (McKnight, 1976; Baker and Manwell, 1981). Those with a more evolutionary viewpoint describe feral animals as undergoing the domestication process in reverse (Letts, 1964; Hale, 1969; Brisbin, 1974; Price, 1984). This latter definition implies that feral animals are no longer exposed to artificial selection by man or natural selection imposed by the captive environment. If one accepts the thesis that domestication involves genetic change, it is only logical to postulate that feralization will involve evolutionary processes as well. Consequently, the process of feralization, like domestication, is seldom achieved in a single generation. Daniels and Bekoff (1989) propose a more ontogenetic approach to feralization. In their view, domestic animals undergo feralization when they fail to become socialized (or become desocialized) to humans and behave as untamed, wild animals. Under these conditions, de-domestication is an unnecessary criterion; a single domestic individual can become feral during the course of its lifetime.

Wolfe and Bekoff (unpublished) maintain that the term “feral” should be restricted to animals that have reached an endpoint in the feralization process in much the same manner that we use the term “domestic” to refer to animals that have reached an endpoint of the process of domestication. Although the gene pools of feral populations will not necessarily be identical to that of their wild progenitors, it does not seem inappropriate from a biological perspective to use either “feral” or “wild” to refer to populations which have completed the feralization process. Even wild populations do not have static gene pools; change is continually occurring in nature.

Daniels and Bekoff (1989) maintain that feralization of the dog is attained through emancipation from the social environment and food provisioning of humans. The

implication is that the domestic behaviors of the dog are largely induced by its social attachment and dependence on humans. This is a reasonable hypothesis considering the social biology of wolves (ancestors of the dog) and humans and the relatively strong social attachments that typically develop between dogs and their human caretakers.

A problem associated with restocking programs is that animals reared in captivity for release in nature may lack some of the natural physiological and behavioral responses to environmental stimuli that are normally acquired (often early in life) by their free-living counterparts (Shrimpton et al., 1994; Kleiman, 1996). Behavioral deficits may result in relatively high mortality for captive-reared animals released in nature (Hessler et al., 1970; Schladweiler and Tester, 1972; Kraus et al., 1987; Roseberry et al., 1987; McCall et al., 1988). In many cases, reproductive success is negligible following release (Cresswell and Williams, 1984; Haensly et al., 1985). It has been found that the survival of released animals can often be improved by preconditioning (i.e., training) individuals to respond appropriately to important environmental stimuli prior to their release (Mydans, 1973; Spivey, 1973; Suboski and Templeton, 1989; Box, 1991; Kleiman, 1996; Brown and Smith, 1998). Hessler et al. (1970) and Haensly et al. (1985) reported increased survival of semi-domestic captive-reared ring-necked pheasants if reared with wild-genotype birds prior to release.

One could gain a better understanding of the process of feralization by monitoring domesticated populations over generations following release into a suitable natural environment. The rate of feralization will, of course, depend on the ontogenetic processes involved and how completely the population is divorced from human influence. Populations of domestic animals (e.g., dogs or cats) living on the fringe of captivity that may rely on humans for food or shelter but are otherwise independent of man (Coman and Brunner, 1972; Beck, 1973; Iverson, 1978) will revert to the wild (feral) phenotype at a slower rate than animals living on their own.

7. Conclusions

Development of the domestic phenotype is nurtured by the interplay of genetic changes occurring over generations and the experiences of captive animals during their ontogeny. The process of domestication is realized when the gene pool is sufficiently altered and when specific captive environments and management techniques are consistently applied over generations to produce a phenotype that fosters adaptation to the captive environment and human intervention.

Behavioral changes accompanying the process of domestication are quantitative in nature. Perhaps the most well-documented behavioral modification in domestic animals is their reduced sensitivity to changes in their environment. This is reflected in their response to unfamiliar living environments, novel objects, strange conspecifics and humans, and in improved reproductive success over generations in captivity. Reduced emotional reactivity facilitates handling by humans and adaptation to a variety of physical and social environments commonly imposed on captive animals. While artificial selection (both conscious and inadvertent) and natural selection (in captivity) may contribute to a reduction in emotional reactivity over generations in captivity, the

consistently applied management practice of housing captive animals in cages or enclosures where they have continual exposure to humans and conspecifics has an important effect of reducing emotional reactivity within an animal's lifetime.

The rate of maturation of sexual behaviors may be accelerated in domestic animals since reproductive success under many mating systems employed in captivity may not be contingent on attainment of high social status. Except in domestic dogs, there is little evidence that neoteny (retention of juvenile characteristics) has had a significant role in the behavioral development of animals undergoing domestication.

Feralization has been viewed as the domestication process in reverse or as merely denoting the lack of socialization to humans. The successful introduction of captive-reared animals in nature is often dependent on preconditioning them to locate and harvest suitable food items and to avoid predators.

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