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Domestication and the Behavior-Genetic Analysis of Captive Populations

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ABSTRACT

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Captive environments are believed to produce behavioral changes in animal populations that may limit our ability to generalize back to natural populations. These behavioral changes are thought to be associated with one or both of the following: (a) changes in frequencies of genes or gene complexes due to the effects of inbreeding or to changes in selection pressure; (b) changes in development of the phenotype due to the effects of changes in environmental variables. Inbreeding leads to increase in homozygosity, that may result in developmental anomalies because of a breakdown in developmental homeostasis. Changes in selection pressure may disrupt coadapted gene complexes that have evolved in the wild. Often, domestication is believed to result in individuals that are “degenerate”; i.e. inferior to individuals in the wild. However, this notion has received no empirical support. In fact, if phenotype changes do occur under domestication, these are usually quantitative, not qualitative, in nature. We suggest that the study of the domestication process may reveal evolutionary principles that would be difficult to discover in other ways, and the zoological parks may be ideal situations for such research.

INTRODUCTION

In their discussion of the advantages of the zoological park for behavioral research, Moran and Sorensen (1984) drew a distinction between two approaches to the study of behavior:

“One of the many ways to conceptualize the study of behavior is according to two sources of influence — organismic and environmental. Traditionally, “ethological” study of animal behavior has focused on the organism and “psychological” research has concerned itself primarily with influences in the animal’s environment.” (p. 143).

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That is, ethology has concerned itself with the study of "species-typical" adaptive (i.e. evolved) behavioral patterns, whereas psychology, even though research has usually been interpreted in terms of averages, has studied behavioral patterns that vary in expression among individuals. This variability has been assumed to be the result of differences in environments among individuals (and with little or no consideration of the possible adaptiveness of behavior). Therefore, psychology has studied the importance of environmental differences for phenotypic differences within species, and ethology has studied the importance of genotypic differences for phenotypic differences between species. This is because the former has usually been concerned with the development of behavior (usually learned behavior), whereas the latter has been concerned with its evolution (in the form of instinctive behavior).

With a re-emphasis on evolutionary thinking in psychology (e.g. Hinde and Stevenson-Hinde, 1973), a more useful distinction between the ethological and psychological approaches may now be between the study of non-variable versus variable behavior. However, even this distinction may no longer be valid. Alcock (1979) discussed the importance of the study of behavioral variability in modern ethology, and contrasted this newer approach with that of the past:

"Historically, ethologists have devoted their attention to the description of species-specific behavior patterns as an essential first step in understanding the adaptive significance of behavior. They have had little enthusiasm for variation in behavior patterns, which only seemed to muddy the picture. As a result, animals that failed to exhibit the "typical" behavior of their species were either ignored or treated as deviants destined for early removal from the population by natural selection." (pp. 224–225).

Barlow (1977) emphasized the variability to be found in what have usually been considered stereotyped patterns of behavior. This had been shown previously for geotaxis in *Drosophila melanogaster* by Hirsch and Erlenmeyer-Kimling (1961; see also Hirsch, 1963; Hirsch and McGuire, 1982). The concept of *evolutionarily stable strategy* (Maynard Smith, 1976) requires that there be differences among individuals, as does the notion of dominance. Because ethologists have often selected the more invariable patterns of behavior to study, variability has often not been recognized. Therefore, the present rapprochement between ethology and psychology has been two-fold; involving a greater emphasis on the importance of behavioral variability in ethology and of evolution in psychology.

We suggest that the study of differences among individuals in "species-typical" patterns of behavior is a productive approach in the study of both function and development. Because most of the research into genetics and behavior in psychology has not dealt with the behavioral patterns so important for ethology, a behavior–genetic analysis within a species (Hirsch, 1967) using such patterns would be a unique contribution. The importance
of genetic analysis for ethology has been emphasized by Gould (1982). Although we disagree with the role in development that he gives to genes, we agree with the following sentiment:

"Ethologists rarely mention genetics or use genetic techniques — a strangely illogical phenomenon since the logical extension of Lorenz's "dissect the parts" argument must lead to that ultimate unmoved[?] mover, the gene itself." (p. 297).

Although ethology depends upon the concept of the gene for its approach to behavior study, the notion of "genetic" in ethology has usually been synonymous with "evolved". Yet these are two distinct notions and each must be studied with different techniques.

However, the genetic analysis of captive animals in zoos may be impractical in many (but not in all) instances, because such research involves techniques that may change the genetic structure of the population. The goals of a zoological park involve more than the scientific study of animal species and their behavior. Deliberate changes in the population gene pool might compromise these other goals. (One possible solution to this problem may be to take sub-lines from the original population, that one would then be able to manipulate. However, this may not be a practical solution in some cases.)

Genetic changes that are not deliberate (such as inbreeding and genetic drift) might result from the management and breeding practices in zoos, and may introduce some problems for behavioral research. Also, the captive environment may introduce changes in selection pressures that, over generations, may change the behavioral patterns expressed by individuals. In addition to such evolutionary changes, there is the possibility of changes in individuals of a given generation due to the interaction of the developing organism with the captive environment. We shall discuss the effects of captivity on behavior, using both theoretical arguments and actual examples. In doing this, some inaccurate beliefs about the effects of domestication will be exposed and we shall argue for the importance of research into the domestication process. The zoological park may be an ideal situation for such research. However, it should become clear that the effects of domestication on the behavioral phenotypes of individuals require one to outline clearly the goals of research in captive environments.

INBREEDING

Population size is important because, according to theory in population genetics, small population sizes should result in increases in homozygosity (Falconer, 1981). Because population sizes in captive environments are often small, we shall examine whether an increase in homozygosity may occur in actuality. We shall do this by considering electrophoretic studies and behavior-genetic analyses of both domesticated and natural populations.

Because genetics is a science of differences, a genetic analysis often requires phenotypic variability that is correlated with genetic variability.
However, techniques are now available that allow one to assay directly the products of structural (polypeptide-producing) genes, thereby making allelic differences unnecessary. An example of the latter analysis is gel electrophoresis, which can detect enzymes and non-enzymatic proteins through their mobility in a charged electrophoretic (gel) medium. Differences in mobility indicate the presence of at least one amino acid difference between proteins associated with the same locus. Lack of a difference in mobility, however, does not necessarily indicate an identity of amino acid sequence because the genetic code is redundant and only four of the 20 amino acids in organisms are charged electrically (Lewontin and Hubby, 1966; Powell, 1975; Selander, 1976). Electrophoretic studies are useful in estimating three different parameters (Powell, 1975): (a) the amount of genetic variability in a population; (b) the effects of geographic and temporal variation on genetic variation among populations; (c) the amount of genetic divergence between species. We shall be concerned only with the amount of genetic variability in a population, because we wish to examine the effects of small population size on this parameter.

Two statistics often used in electrophoretic studies are the mean heterozygosity for one locus \((h)\) and across all loci \((H)\) in a given individual in a population (Selander, 1976). The former statistic is calculated, at each locus, as 1 minus the frequency of homozygotes; and the latter as the mean of all \(h\)'s. It has been found that populations contain large amounts of genetic variability. On average, individuals are estimated to be heterozygous at 5–15% of their loci (Selander, 1976), although some estimates are larger (Powell, 1975).

The effects of the small population sizes often occurring in domesticated populations usually result in a decrease in the amounts of heterozygosity within populations. For example, in a study of mostly domesticated (laboratory-reared for 75–120 generations) populations of \(D.\ pseudosobscura\), Lewontin and Hubby (1966) found less genetic variability than in natural populations, although much still remained:

"Most remarkable of all, is the widespread occurrence of segregation in strains that have been in the laboratory for as many as seven years. . . . [The results give] the impression of an effect of inbreeding. . . . [The recently-caught] strains segregate far more frequently than any of the others, and, in general, more of the genetic variation in the other populations is between homozygous strains." (p. 599). "We can assume that most of the variation from nature has been preserved in the laboratory stocks but has been converted to variation between strains by the inbreeding attendant on laboratory culture." (p. 602).

Therefore, if the effective population sizes (Falconer, 1981) are small, inbreeding will occur and increases in homozygosity are expected. Because genetic analysis usually involves the effects of genetic differences on the phenotype, increases in homozygosity may make a behavior-genetic analysis more difficult (unless, of course, one wishes to compare inbred populations).
However, even very small populations that have undergone severe “bottlenecks” will not necessarily result in complete homozygosis, as is illustrated above and in studies by Ricker and Hirsch (1985a, b). These latter studies describe long-term divergent selection for geotaxis in domesticated populations of *D. melanogaster* and the resulting evolutionary changes. After more than 600 generations (28 years) of intermittent selection pressure and the occurrence of bottlenecks in population size, the lines nevertheless responded to changes in selection pressure (indicating the presence of genetic variation). In fact, in the mid-1960’s, even when a deliberate attempt was made to make these lines homozygous (through continued brother × sister mating), genetic variance remained.

**Individual development and genetic variability**

The amount of inbreeding is important for behavioral research in general because it may have drastic effects on individual development. For example, Wright (1980) discussed his early research on inbreeding in guinea pigs and stated that the “primary effect [of inbreeding] was a profound differentiation among the strains relative to their common foundation.” (p. 831). Decreases in the average fitness of inbred strains were inferred from developmental anomalies in behavior and morphology, as well as from increases in mortality rates. Ralls et al. (1979) discussed the effects of inbreeding in captive populations of ungulates and found that, in the majority of species studied, inbred animals suffered higher juvenile mortality than non-inbred animals. (Lewin (1985) restates the commonly held misconception that any population becomes homozygous with 20 generations of sibling mating. Hirsch (1967, pp. 423–425) explains that the calculation involved applies to only one locus, whereas inbreeding to homozygosity across all loci in the genotype would probably require over 60 generations.)

The enormous changes that may result from the effects of small population size in nature are well illustrated in the following two studies. Using electrophoresis, O’Brien et al. (1983) studied the variability at 47 loci in 55 cheetahs, 50 of which were recently caught or first generation captive-bred, and 5 of which were from zoos. No electrophoretic variants were found at any of the 47 loci even though 18 were “polymorphic cluster genes” (i.e. highly variant in several species). O’Brien et al. (1985) surveyed five additional enzymes in the cheetah and all 52 in four closely related species of felids. They found no variability in the cheetah and moderate to high variability in the other species. Cheetahs were found to be highly susceptible to a coronavirus; this disease being often fatal even though it had little effect on more genetically variable domestic cats and lions. Semen samples of 18 cheetahs were compared to those from domestic cats and it was found that spermatozoan concentrations were 10 times less in cheetahs. Morphological abnormalities were found in 71% of cheetah and 29% of cat spermatozoa. O’Brien et al. (1985) concluded that
From these examples, it becomes apparent that genetic variability may have a role in Darwinian fitness. The mechanisms of this relationship have not been subjected to detailed analysis, but some hypotheses have been formulated.

Lerner (1970) discussed the effects of inbreeding on the development of domesticated animals. From many sources of evidence, Lerner proposed the concept of genetic homeostasis — defined as “the property of the population to equilibrate its genetic composition and to resist sudden changes” (p. 2) — and hypothesized that its mechanism is the “superiority with respect to fitness of the heterozygous over the homozygous genotypes” (p. 6). This superiority is manifested in an increased developmental homeostasis expressed by the more heterozygous individuals. Developmental homeostasis is defined as the self-regulation of the developing individual “leading to a uniformity of phenotypic expression in individuals of a given population, in spite of the genetic variability between them” (p. 6); i.e. the development of the so-called “wild-type” phenotype.

Mayr (1975) infers from these ideas that genes increasing fitness are brought together during evolution into “complexes” on chromosomes. These co-adapted gene complexes (Dobzhansky, 1970) allow for greater fitness because genes that “work well together” during ontogeny will be more likely to be inherited as a unit:

“the interaction of macromolecules at the cellular level produces individual phenotypes of different fitness, and natural selection will therefore tend to hold together those alleles at different loci that produce individuals of the greatest selective value.” (p. 380).

Such complexes may exist along with large amounts of genetic variability (Mayr, 1970). Therefore, they may allow the development of phenotypes with little inter-individual variability in the presence of large amounts of genetic variation. These ideas are very similar to those developed by Sewall Wright in his “shifting balance” theory of evolutionary change (see Wright, 1980, for a summary). Although such ideas are potentially of great importance, little research has been done to substantiate them. Yet, it appears very likely that some minimum amount of heterozygosity is important for the “proper” development of an individual. To the extent that this is true, the effects of small population size in captivity will influence the results of research.

We have been discussing the effects of small population sizes on the amount of genetic variability, and the possible importance of heterozygosity for individual development. The genetic systems that are the result of millions of years of evolution may become changed in captivity, not only through inbreeding but also through two other types of change: (a) the
mating of organisms whose parents were from populations separated geographically (allopatric); (b) the possible changes in selective pressures that accompany the transfer of animals into captive environments. Furthermore, the behavior expressed may be altered not only because of changes in frequencies of genes and gene complexes, but also because of changes in environmental conditions important for the production of species-typical behavioral patterns. Both types of change will be discussed in the next section.

PHYLOGENY AND ONTOGENY

As discussed above, under natural selection, a behavioral pattern may evolve to such an extent that little inter-individual variability in development is observed. The evolution of the population with respect to the development of such a trait is associated with changes in a unique gene pool and set of environments. The environment has an effect of two types: (1) on evolution through its selective pressures for behavior; (2) on development through its interaction with the developing organism. A population evolves within particular environmental situations which have exerted selective pressures upon individuals and, at the same time, have affected the development of these same individuals through reciprocal (and extremely complex) interactions with the genotype. These two effects of the environment are not mutually exclusive because the developmental process evolves as well (for further discussion see Hogben, 1939; Schmalhausen, 1949; Lehrman, 1953; Spurway, 1955; Dobzhansky, 1970; Waddington, 1975; Oyama, 1982).

Domestication of a population is a process involving the removal of organisms from nature to a captive environment in which their breeding and care are controlled by man. Price (1984) has 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 recurring during each generation." (p. 3).

Changes in natural selection because of a move to captivity may result in changes in behavior. The changes incurred may be small if the animals are "pre-adapted" for domestication; i.e. if they have a constellation of behavioral characteristics that are not disrupted by human control of living space, breeding, feeding, social environment, etc. (Hale, 1969). Usually, this will require that there be many physical similarities between the captive and natural environments. Price (1984) states that, although this may be true in many cases, it is not true necessarily:

"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.” (p. 7).

If individuals in a population are not very sensitive to changes in their environment (i.e. if they show developmental homeostasis), the move to a captive environment may result in few changes in behavior. However, Price notes that if there are few pre-adaptations, there will be strong selective pressures on the individuals “in terms of (1) the number of traits affected, (2) the direction of selection, and (3) the intensity... of selection” (p. 7).

Phenotypic changes brought about by a move to a captive environment have been supposed by some to result in degeneration. For example, Spurway (1955) asserted:

“In all human cultures breeds are named after places from which they are supposed to have been brought. Such transplantation removes the ecotype from the habitat to which it has evolved an adapted developmental homoeostasis, 'degeneration' occurs, and artificial selection becomes necessary if breed characters are to be preserved.” (p. 340).

By breeding a group of animals in an environment different from the one in which their ancestors had evolved, one might expect changes in development because environmental factors important for development of the “normal” phenotype may have been altered or lost. Spurway states that such changes in captivity are ubiquitous and result in a large amount of quantitative variation among individuals:

"Zoo-keepers consider that high variation reveals 'bad' culture conditions and conversely... In a changed environment fewer genotypes are completely developmentally homoeostatic than in the environment for which this property was evolved, and this homoeostasis may break down completely... This implies that the phenotypic variation observed in captivity is... highly correlated with genotypic differences.” (pp. 334—335).

A species-typical behavioral pattern is one for which genotypic differences have little correlation with phenotypic differences (because there is little phenotypic variation). However, a move to a captive environment may disrupt developmental homeostasis. This might result in genotypic differences becoming expressed phenotypically. Obviously, this would limit the ability to generalize research back to nature.

In addition to a breakdown in developmental homeostasis due to inbreeding and changes in the environment, crosses between individuals from populations separated geographically (and, therefore, possibly subjected to differing selection pressures in their evolutionary histories) may result in a similar breakdown (see Dobzhansky (1970) for a summary of such work with D. pseudoobscura). Spurway (1955) used Lerner's term "phenodeviants" — "grossly deformed phenotypes [that] often segregate in cultures” (p. 336) — and extended its use to such hybrids:
"These products of inadequate developmental homoeostasis... are called examples of hybrid inviability and hybrid breakdown, and interpreted as evidence that the parent populations had diverged genetically." (p. 337).

However, one might expect that less severe anomalies in behavior and morphology might be common in the progeny of crosses between animals of different geographic origin. These less severe breakdowns in development may limit the generalizability of behavioral research in captivity. That is, breeding in captivity may require a balance between inbreeding and outbreeding if one wishes to generalize back to nature.

There is evidence that, in nature, animals tend to avoid close inbreeding. A feral population of Camargue horses showed less inbreeding than would have been expected under random mating (Duncan et al., 1984). Natural habitat studies also report inbreeding avoidance (Koenig and Pitelka, 1979; Packer, 1979). See Bateson (1978, 1979) for a discussion of behavioral mechanisms in nature that may have evolved to achieve a balance between inbreeding and outbreeding.

EXAMPLES

So far, we have discussed concepts and theory concerning the domestication process. In this last section, we shall briefly discuss some examples of behavioral changes in captivity and some hypotheses regarding these changes.

Lorenz asserted that the domestication process in man and other animals results in "domestication-induced degeneracy" (Lorenz, 1940, translated in Eisenberg, 1972, p. 124). This viewpoint is made explicit in Lorenz's title — "Domestication - caused Disturbances in Species-specific Behavior" (translated in Kalikow, 1978, p. 176) — and elaborated in the text of his article published in Germany under the Nazi regime. The notion that domestication results in degeneracy was once common among ethologists, yet it was unsubstantiated. Boice (1973) stated:

"This notion, contrasted with that of adaptiveness, does not lend itself to objectivity but its rationale is well founded in two beliefs: Wild creatures are hardier and wiliier, and man's selfish goals in domesticating an animal will necessarily produce its degrading and disfiguring... The belief that mental deterioration accompanies domestication seems so commonsensical that contemporary articles... assert the intellectual idiocy, vegetalization, and degeneracy of domestic rodents although no published data support their claims." (p. 218).

Assumptions about degeneracy are not usually subjected to thorough investigation. When subjected to more detailed analysis, it is often observed that the effects of domestication are not nearly as drastic or as ubiquitous as some have suggested.
The frequency of performance of behavioral patterns sometimes changes in captivity although the patterns themselves do not. Thus, certain aspects of sexual behavior may increase in frequency in captive individuals (Hale, 1969). For example, in domestic dogs, estrous cycles occur about every 6 months and in all seasons, whereas in wolves (the presumed ancestors of dogs), these occur only once a year and only during winter. In addition, dogs show greater promiscuity than wolves (Price, 1984, and references therein). Scott (1969) suggested that these behavioral changes are the result of evolution because hypersexuality may increase the reproductive success of captive individuals (and, therefore, be selected for naturally). However, Price postulated that hypersexuality in dogs may be the result of "constant exposure to a sexually stimulating environment" (p. 21) and, therefore, may be developmental in origin. Because they are not mutually exclusive, both hypotheses may be correct.

Lockard (1968) asserted that learning ability in domestic (laboratory) rats is inferior to that of wild rats. Boice (1973) opposed that conclusion:

"most writers on rat domestication have favored the notion that wild rats are more intelligent than domestics. Lockard (1968) promotes two misconceptions in this regard. First, he argues that learning, as a collection of processes, almost necessarily degenerates in domestication, and second, he implies that degeneration in learning has 'been found in a wide variety of learning situations'." (p. 225).

Boice argued that this belief, held by many psychologists, is without substance because experimental evidence usually indicates the opposite: domestic rats perform better than wild rats in most learning tasks. However, this difference may be due to the wild rat becoming relatively more "disturbed" in the experimental situation. Yet, even "when performance problems are minimized, the learning rate of wild and domestic rats may be more similar than... expected" under an hypothesis of degeneracy (p. 225). That is, there is little evidence that domestication results in a decrease in learning ability.

Boreman and Price (1972) studied dominance hierarchies in domestic and wild Norway rats and in their F1 progeny. They observed two types of social interaction in obtaining their measure of dominance: (1) spontaneous interaction was defined as social behavior not involving competition for a "tangible commodity" (water, food, nest-box, etc.); (2) competitive interaction was defined as social behavior involving competition for such commodities. It was found that

"Domestic rats were most dominant in both spontaneous and competitive cross-strain interactions. Assuming that a positive correlation exists between aggressive potential and dominance... this does not support the hypothesis. ... that the laboratory rat is more 'docile' and less aggressive than its wild ancestors." (p. 540).
However, it may not be correct to assume that there is a non-zero correlation between rank in the dominance hierarchy and the amount of aggressiveness:

"The fact that all subjects were placed in the experimental room at the same time could have inhibited any expression of the territorial behavior. This same stock of wild rats was found to be extremely aggressive toward domestic rats when the latter were introduced into an area familiar to the former. . . whereas 'established' domestic rats showed little or no aggression toward intruders." (p. 541).

This latter observation suggests that an evolutionary change may have occurred in the domestic rat. In the crowded conditions in which domestic rats are usually kept, a social organization based on a dominance hierarchy may have evolved, whereas in nature, an organization based on territoriality may result in greater reproductive success on average.

CONCLUSIONS

The discussion in the preceding section suggests that large changes in behavior are not to be expected in captivity a priori. Price (1984) concluded that most changes in captivity are the result of quantitative changes in thresholds for performing the patterns and not qualitative changes in the patterns themselves. However, this conclusion should not be accepted too readily. There is a paucity of detailed studies on the domestication process and little interest among behavioral scientists in performing such studies. This attitude is surprising, because captive animals are often used in behavioral research. This is one area where the study of animals in zoological parks may result in important contributions.

It should be kept in mind that the captive environment is not a degenerate version of the natural environment and that, depending upon the goals of the research, the study of behavior in captive environments is legitimate even if captivity has resulted in behavioral change. Similarly, the population that has evolved (become domesticated) in a captive environment is not a degenerate version of the ancestral population; but it is different. Boice (1973) argued:

"Domestic animals show morphological and behavioral adaptations to the particular demands of their unnatural environment. . . . It is illogical to judge the domestic animal as unfit or degenerate because he is not adapted to live in a wild environment." (p. 226).

Therefore, it is no more or no less legitimate to study behavior in either captive or wild animals. However, it is important to state the goals of research clearly beforehand. If one wishes to study behavioral patterns occurring in nature, the use of captive animals is not justified unless one determines whether captivity has resulted in changes. If it has, then these
must be taken into account. It may turn out that the study of changes associated with the domestication process may reveal principles that have much relevance for evolutionary processes in nature. Therefore, it may behoove researchers in zoological parks to study the effects of domestication in captivity in addition to the study of behavioral patterns as they occur in the wild.

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