

Influence of Genetic and Environmental Factors on Animal Behavior

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Abstract: Behavioral genetics has become an increasingly important field as modern technology has allowed researchers to locate specific genes and alleles responsible for some behaviors. The field has also stirred controversy: people are hesitant to attribute behavior to genetics in the age-old nature versus nurture debate. But nature versus nurture is a false dichotomy. The truth is that both can play a key role in determining a behavior. The genotype determines the potential for a behavior to exist, while nature determines what phenotypic behavior actually results. 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.

Keywords: Domestication; Domestic animals; Behavioral development; genetics.environmental.

INTRODUCTION

Behavioral genetics are more complicated than Mendelian genetics because while Mendel's pea plants showed clearly distinctive characteristics, animal behavior does not always fit into such hard and fast categories. Successful identification of behavioral genes is most likely when the gene shows a high *penetrance*, that is, the genotype is expressed in the phenotype. Further, more often than not, the environment will mediate the effects of those genes. Such a complex situation can be troublesome for researchers seeking to isolate the genetic mechanisms of behavior. In order to create some standard to measure specific behaviors in relation to genes and environment, scientists have devised a scale of heritability.

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. 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.

Domestication defined

Darwin 1859; 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.

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 Otero 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 neither 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, organism 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.

METHODOLOGICAL CONSIDERATIONS

In standard biometrical formulations, the phenotypic variance is decomposed into genetic and environmental components. The genetic component is further decomposed into additive and nonadditive components, the latter reflecting interactive effects within (dominance) and among (epistasis) loci. The environmental component is decomposed into a shared environmental component, representing the effects of characteristics such as family income, parental strategies on child-rearing, and level of intellectual stimulation within the home that are shared by reared together relatives and are thus a potential source of their behavioral similarity; and a nonshared environmental component, representing the effects of characteristics such as accidents, peer affiliations, and differential parental treatment that are not shared by reared together



relatives and are thus a source of their behavioral dissimilarity. Three general strategies have been used to resolve the separate influence of genetic and shared environmental factors on the familial resemblance that characterizes the vast majority of behavioral traits: twin studies, adoption studies, and gene identification methods.

The classical twin study involves the comparison of monozygotic and dizygotic twins reared together (MZTs and DZTs). If genetic factors influence the trait in question, MZTs, who share 100% of their genetic material, should be more similar than DZTs, who, like ordinary siblings, share on average only 50% of their genetic material. In a classical twin study, the proportion of phenotypic variance associated with additive genetic factors (i.e. the narrow heritability) is estimated by doubling the difference in correlation between the MZTs and DZTs, the contribution of shared environmental factors is estimated by subtracting the heritability estimate from the MZT correlation, and the contribution of nonshared environmental factors and measurement error is estimated by subtracting the MZT correlation from 1.0. These estimates, like any statistics, can change over time and vary across culture; nonetheless, they have proven to be useful indices for characterizing the sources of individual differences in psychological traits (e.g. Neisser et al 1996). Powerful methods for analyzing twin data and estimating environmental and genetic components of variance are now available (Neale & Cardon 1992). Owing to the availability of several large population-based twin registries in Western Europe, the United States, and Australia, the classical twin study is a popular behavioral genetic design. The assumptions that underlie the classical twin study have drawn substantial empirical attention that has generally supported the basic validity of this method (Plomin et al 1990b).

An adoption study involves determining the degree to which adopted individuals resemble their biological relatives, an indication of genetic influences, as well as their adoptive relatives, an indication of shared environmental influences. Although there are some notable US adoption studies, most adoption research has been undertaken in Scandinavian countries, where the availability of national registries has allowed researchers to ascertain relatively large and representative cohorts of adopted individuals as well as both their adoptive and biological relatives. As is the case with twin studies, the assumptions that underlie the adoption study have drawn much empirical investigation, most of which is generally supportive of the utility of this method (Cadoret 1986, Plomin et al 1990b). Nonetheless, one limitation bears noting. As adoptive homes are likely to under represent those who are living at the extremes of poverty and deprivation, the importance of environmental influences may be underestimated in adoption studies. Environmental inferences may apply only to the broadly constituted middle class.

GENETIC MECHANISMS DEVELOPMENT

Genetic mechanisms

The genetic phenomena with the greatest potential impact on the domestication process are in breeding, 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.

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 was towards man. 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 \bar{Z} 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.

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. 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 .

THE NATURE OF ENVIRONMENTAL INFLUENCE

Whereas the dominant theoretical and empirical traditions within developmental psychology have emphasized the influence of shared rather than nonshared environmental factors, behavioral genetic research is consistent in showing that environmental influences on most psychological traits are of the nonshared rather than the shared variety (Plomin & Daniels 1987). For personality characteristics, the MZT correlation has consistently exceeded the corresponding DZT correlation by more than a factor of two. This observation, first noted by Loehlin & Nichols (1976) but replicated in diverse cultures with thousands of twin pairs implies a shared environmental component of zero. Alternatively, the consistently high ratio of MZT to DZT correlation could reflect genetic non additivity, or greater environmental sharing among MZT as compared with DZT twins.



It is thus significant that findings from studies of reared together twins have been replicated using alternative research designs. For example, MZTs are not markedly more similar in personality than MZAs. In the four published studies comparing the similarity of MZA and MZT twins on the two most fundamental dimensions of personality, extraversion and neuroticism, the weighted average MZA correlation is .39 for both factors. The comparable MZT averages are .56 for extraversion and .46 for neuroticism. Secondly, the correlation for nonbiologically related but reared together sibling pairs (i.e. adoptive siblings) provides a direct estimate of the effect of common rearing; in three adoption studies of adults (summarized by Loehlin 1992), the weighted average adoptive sibling correlation was $-.07$ for extraversion and $.09$ for neuroticism, while in a single adoption study of adolescents, the adoptive sibling correlation was $-.04$ for a measure of extraversion and $.00$ for a measure of neuroticism.

The minimal effect of common rearing appears to hold not only for personality factors but also for most major forms of psychopathology. Adoption studies of, for example, schizophrenia and alcoholism indicate that risk to the biological offspring of an affected parent is independent of whether the offspring is reared by the affected parent, while twin studies of most behavioral disorders reveal a greater than 2:1 ratio of MZT to DZT concordance (see above). There are, however, two noteworthy exceptions to the general finding of little shared environmental influence on behavioral characteristics: cognitive ability and juvenile delinquency. From a compilation of familial IQ correlations the following observations all support the existence of substantial shared environmental influences on general cognitive ability:

- a) the average MZT IQ correlation (.86) is less than double the corresponding average DZT correlation (.60);
- b) the average MZA correlation (.72) is moderately lower than the average MZT correlation; and
- c) the average adoptive sibling correlation (.32) is substantial. Taken together, these observations suggest that from 20% to 30% of the variance in IQ is associated with shared environmental effects (Chipuer et al 1990).

The overwhelming majority of the twin and adoptive sibling correlations for IQ are based on preadult samples, for which the effect of shared environmental factors may be maximal. As noted above, when twin IQ correlations are categorized according to the age of the twin sample, the ratio of MZT to DZT correlation is found to increase with age such that in adult samples the average MZT correlation (.83) exceeds the average DZT correlation (.39) by more than a factor of two, suggesting no shared environmental influence at this life stage. Moreover, the average adoptive sibling IQ correlation equals .32 in studies of children or adolescents but, as already noted, only .04 in studies of adults. The adoptive sibling correlation decreased with age in each of the three of these studies that involved longitudinal assessment of IQ. Shared environmental influences on IQ, although substantial in childhood, appear to decrease markedly in adulthood.

The pooled concordance rates for male juvenile delinquency are high and similar for MZT (91%) and DZT (73%), suggesting a substantial influence of shared environmental factors. Similarly, twin correlations for delinquency assessed quantitatively (e.g. as number of delinquent acts) rather than categorically find evidence for strong shared environmental effects. Like IQ, the influence of shared environmental factors on adolescent antisocial behavior may diminish in adulthood. In a sample of more than 3000 US veteran twin pairs, Lyons and colleagues (1995) reported that the heritability of antisocial behavior increased from .07 in adolescence to .43 in adulthood, while the proportion of variance associated with shared environmental effects decreased from .31 in adolescence to .05 in adulthood. The matter is not fully resolved; however, as a subsequent investigation of more than 2500 Australian twins (Slutske et al 1997) reported significant heritability (.71) and no shared environmental effect for retrospectively assessed adolescent conduct disorder.

The Heritability of Experience

The failure of behavioral geneticists to find much evidence of shared environmental influences appears inconsistent with an extensive empirical literature in developmental psychology demonstrating a strong association between rearing circumstances and psychological outcomes. For example, individuals with high IQs tend to have been reared in homes that were intellectually stimulating, aggressive individuals tend to have been reared by parents who were both punitive and arbitrary, and alcohol abusers tend to have been reared by parents with marital problems who used ineffective child-rearing methods. This inconsistency can be resolved by recognizing that environmental measures may reflect the influence of genetic factors (Plomin 1994). Rowe (1983) reported that adolescent MZT rated their rearing homes more similarly than adolescent DZT in warmth ($r = .63$ versus $.21$) but not permissiveness ($r = .44$ versus $.54$).

This finding of greater genetic influence on ratings of parental warmth than on ratings of control has been replicated in studies of reared together and reared apart adult twins who retrospectively rated their rearing homes and in a study of 707



sibling pairs that included MZT and DZT twins as well as full, half, and nonbiologically related siblings. Significantly, similar heritable effects are observed when aspects of the parent-offspring relationship are assessed directly through observational studies as well as indirectly through self-ratings. Moreover, the level of intellectual stimulation in the home, parental marital discord, exposure to psychological stress and trauma and access to support in one's social network all appear from twin studies to be partially heritable. The heritable nature of environmental exposure implicates genotype-environment correlational processes and the mechanisms by which genes and environments jointly influence the development of phenotypes, it also has significant implications for the methods psychologists use to identify environmental risk. The dominant paradigm within psychology for identifying environmental risk has involved the study of intact nuclear families, in which case an association between parental behaviors and offspring outcomes is characteristically interpreted as reflecting environmental mechanisms. Any association, however, may also reflect genetic mechanisms. Indeed, when the genetic basis of parent-offspring resemblance is controlled by studying adoptive families, the association between child-rearing strategies and offspring behavior and the relationship between home characteristics and intellectual achievement are nearly eliminated. Behavioral genetic research on the minimal effect of shared environmental factors and the heritability of experience challenges the validity of a vast amount of psychological research aimed at identifying environmental risk.

CONCLUSION

To examine the relative importance of genetic components of behavior while holding environmental components constant, two or more inbred strains may be used. Two different inbred strains that are different from each other can be assessed while holding the environment constant across both strains. Nonetheless, despite some effort, there are a limited number of confirmed linkages or gene associations for behavioral traits. There are, however, many promising leads. The failure to identify the genes underlying specific human behavioral phenotypes may indicate that we have been misled by the twin and adoption study findings. Alternatively, and we believe more plausibly, the current failure may simply reflect the difficulty of gene identification with complex and heterogeneous phenotypes. Additional molecular genetics research should provide the necessary observations to resolve these two possibilities. Behavioral genetic research is also consistent in indicating that nonshared rather than shared environmental factors constitute the major source of environmental influence on behavior. The adoptive sibling correlation provides a direct estimate of shared environmental influences, and for many psychological traits this correlation is near zero, especially when assessed in adulthood. Despite their apparent importance, little progress has been made in identifying the specific nonshared factors that contribute to individual differences in behavior; a failure that may reflect the random, idiosyncratic, and micro nature of nonshared environmental effects.

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