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Effects of Rearing Environment on Adrenal Weights, Sexual Development, and Behavior in Gerbils: An Examination of Richter's Domestication Hypothesis

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Mongolian gerbils (*Meriones unguiculatus*) reared and maintained in standard laboratory cages exhibited accelerated eye opening, more rapid growth, earlier sexual maturity, and marked reduction in adrenal gland size in comparison with gerbils reared in more natural cages providing access to shelter. Gerbils reared in standard laboratory cages were also easier to handle and less responsive to sudden stimulation than those reared in sheltered cages. Changes in phenotype resulting from rearing in environments lacking shelter parallel changes in phenotype resulting from the domestication process. The implications of the data for genetically oriented hypotheses of domestication are discussed.

Members of domesticated mammalian strains differ markedly from their wild progenitors in both behavior and morphology. Domesticated rats, for example, are invariably described as less "fierce, aggressive and suspicious" (Richter, 1949, p. 382) than wild conspecifics, and members of domesticated strains have smaller adrenal glands, grow more rapidly, exhibit eye opening at an earlier age, and achieve reproductive maturity sooner than do members of wild strains (Barnett, 1958; Boice, 1977; Donaldson, 1924; Galef, 1970; Richter, 1954).

In an influential series of publications, Richter (1949, 1950, 1952, 1954, 1959) argued that characteristic behavioral differences between wild and domesticated strains result from differences in the selective pressures acting on wild and captive populations. Richter suggested that while tame and docile animals are most likely to breed successfully in protected captive environments, the fierce and wary are more reproductively capable in wild environments. Thus, life in captivity over many generations would inevitably result in selection for the behavioral traits characteristic of domesticated strains. Because Richter assumed that reduced adrenal gland size underlay docility, selection for tameness was, within Richter's model, of necessity also selection for adrenal hypotrophy. Other investigators working within the same conceptual framework have suggested that increases in rates of sexual development in domesticated strains result from artificial selection in captivity for increased fecundity (Kretchmer & Fox, 1975; Hale, 1962).

While it is almost certain that maintenance of a population in captivity over many generations results in alterations in the frequency of various genes in captive as compared with relevant wild populations (Price & King, 1969), the extent to which such alterations in gene frequency are responsible for phenotypic differences between wild and domesticated strains remains open to question (Berry, 1969; Donaldson, 1924; Friedman, 1964; Henderson, 1970; Oortmerssen, 1971). Domesticated animals differ from wild conspecifics not only in genotype but also in the conditions under which they normally develop and live. It is at least possible that differences in experience during ontogeny rather than (or in addition to) differences in genotype underlie phenotypic differences between wild and domesticated strains.

The results of a recent series of studies in

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our laboratory indicate that at least some of the differences in temperament between wild and captive rodents may be the result of differences in the conditions under which the two strains are normally reared and maintained. We found that domesticated gerbils (*Meriones unguiculatus*) reared either in tunnel systems constructed by their parents or in laboratory cages providing shelter were difficult to capture, vocalized and bit the experimenter if held, and reacted vigorously to the sudden presentation of a visual stimulus. Members of the same strain reared in cages providing no access to shelter were far less responsive both to handling and to sudden stimulation (Clark & Galef, 1977, 1979). These findings suggest that members of a normally docile and placid domesticated strain possess a genetic substrate adequate to support ontogeny of behavior characteristic of wild, ancestral populations. They further suggest that gerbils reared in captivity may fail to express "wild-type" behaviors phenotypically because of failure of the physical environment usually provided in captivity to permit experiences necessary for development or maintenance of such behaviors (Clark & Galef, 1977, 1979). Reports in the literature of rapid reversion to wild-type behavior in both feralized populations (i.e., domesticated animals released into natural habitats) and experimental subjects released into seminatural environments offer support for the hypothesis that the different environments provided in nature and in captivity contribute to the development of strain-typical behavioral phenotypes (Beck, 1973; Boice, 1977, 1979; Crowcroft, 1966; Daly, 1971, 1973; Darwin, 1868; Donaldson, 1916; Freedman, King, & Elliot, 1961; Howard, 1959; Minckler & Pease, 1938; Scott & Causey, 1973; Thiessen, 1973; Thiessen & Yahr, 1977).

The present experiment was undertaken to determine whether rearing in environments adequate to maintain expression of wild-type behavior is also sufficient to produce wild-type morphology and rates of development. If the same aspects of the physical rearing environment that contribute to ontogeny of wild-type behavior in domesticated gerbils also contribute to expression of wild-type morphology and rates of development, then one would expect domesticated gerbils reared in cages providing shelter to exhibit adrenal hypertrophy and retarded development relative to members of the same strain reared without exposure to shelter.

Method

Subjects

Subjects were selected from 176 litters of Mongolian gerbils (*Meriones unguiculatus*) born in the McMaster colony to multiparous breeding pairs acquired from Tumblebrook Farm (Brookfield, Massachusetts). Breeding pairs were housed in polypropylene cages (35 × 30 × 15 cm), lidded with 1.27-cm hardware cloth and carpeted with a thin layer of wood-chip bedding. The colony was maintained on ad lib Purina Laboratory Chow and water in a temperature-controlled colony room, illuminated on a 12:12 hr light/dark cycle.

Procedure

Maintenance. Within 24 hr of birth, each litter and its parents were moved to a new cage which either provided or did not provide access to shelter. Each litter to be reared without shelter (open-reared subjects) was placed in a cage identical to that in which it was born, while each litter to be reared in a cage providing shelter (shelter-reared subjects) had a 28 × 17 × 9 cm closed wooden box with a single 5 × 5 cm entrance placed in its cage.

All litters were left undisturbed until completion of the experiment except for removal of parents at 30 days, cage cleaning every 14 days, and removal of subjects for testing as described below.

Experimental procedures. Sixteen independent groups of subjects were examined to determine the effects of open compared with shelter rearing on the behavior, morphology, and rate of development of domesticated gerbils. Twenty subjects (10 of each sex) from each of the two rearing environments (open and sheltered) were examined behaviorally and morphologically at each of eight ages (22, 26, 31, 45, 61, 91, 127, and 181 days of age). No more than two subjects from any litter were assigned to the same group.

The apparatus and procedures used in behavioral testing are described in detail in Clark and Galef (1979). Briefly, the behavior of subjects in response to sudden visual stimulation was observed by means of closed-circuit television in a 1.2 × 1.2 × .9 m enclosure containing a refuge (see Figure 1). Individual subjects were first allowed to become familiar with the enclosure and were then presented with a moving visual stimulus for 15 sec. During the 2-min period following stimulus presentation, the experimenter recorded each subject's latency to enter the refuge, latency to emerge from the refuge, and total time spent in concealment.

Within 1 hr of completion of behavioral testing, each subject was sacrificed by anesthetic overdose, weighed,

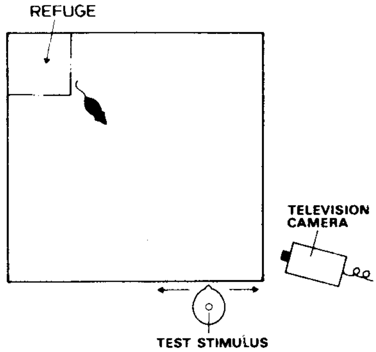

Figure 1. Overhead schematic view of the 1.2 × 1.2 m behavioral test enclosure.

and autopsied. Adrenal glands, testes or ovaries, and uteri were excised and weighed after determination of testes descension or vaginal opening had been made.

Twenty-six additional litters from each of the two rearing environments were examined twice daily from 15 to 22 days of age (day of birth equals Day 1) to determine each subject's age at eye opening (defined as the day on which both eyes were first fully open). To control for effects of litter size on rate of development (Elwood & Broom, 1978), we matched samples of shelter- and open-reared litters for size on the day of birth (4 litters of 3 pups, 4 of 4, 9 of 5, and 9 of 6).

Results

In general, the differences in development, morphology, and behavior found between populations of gerbils reared in cages providing or lacking shelter closely paralled the phenotypic differences that characteristically differentiate wild and domesticated mammalian strains. The experience of rearing and maintenance in cages lacking shelter resulted in accelerated development, adrenal hypotrophy, and enhanced docility relative to rearing in cages providing shelter.

Development

A variety of measures indicated that, in comparison with rearing in an environment lacking shelter, shelter rearing retarded development. As can be seen in Figure 2, which shows the distribution of ages at which eye opening occurred in open- and shelter-reared gerbils, open-reared gerbils had a significantly lower mean age at eye opening (18.2 ± .11 days) than did their shelter-reared conspecifics (18.8 ± .14 days), Kolmogorov-Smirnov test, $\chi^2(2) = 8.23$, $p < .02$. Further, as can be seen in panel A of Figure 3, which indicates the body weight of male and female open- and shelter-reared gerbils, open rearing accelerated growth in body weight in both males and females.

Most interesting, open rearing profoundly reduced the age of achievement of sexual maturity. The mean age at first parturition of the 9 of 10 open-reared females observed to 181 days of age that became pregnant by 181 days of age was 108.8 ± 7.0 days. Their shelter-reared comparison group showed a mean age at first parturition of 139.8 ± 4.6 days. The fact that shelter-reared females were more likely to cannibalize their litters immediately after parturition than were open-reared females may have introduced a bias into our observations of age at first parturition. However, the observations (a) that 6 of 10 open-reared females sacrificed at 91 days of age were pregnant while 0 of 10 shelter-reared females sacrificed at the same age were (Fisher's exact probability test, $.02 < p < .05$) and (b) that 8 of 10 open-reared females and only 3 of 10 shelter-reared females exhibited vaginal opening when sacrificed at 45 days of age (Fisher's exact probability test, $p = .10$) support the hypothesis that open rearing accelerates the achievement of sexual maturity in female gerbils.

Effects of open rearing on the rate of sexual maturation in male gerbils were similar to those observed in females. As can be seen in Figure 4, which shows the percentage of independent groups of males of various ages

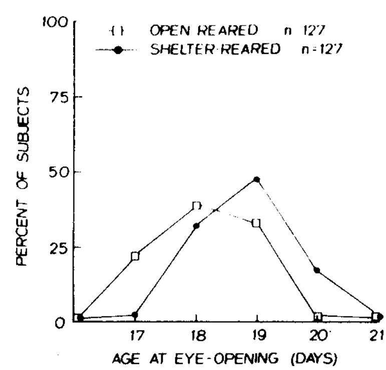

Figure 2. Percentage of open- and shelter-reared subjects with open eyes as a function of age.

with descended testes, open rearing considerably accelerated achievement of sexual maturity. Determination of the testes weights of open- and shelter-reared male gerbils supported the same conclusion. Open-reared gerbils exhibited significantly greater testes weights than their shelter-reared comparison animals at 31, 45, 61, and 91 days of age. While the finding of more rapid testes growth and testes descension in open-reared male subjects does not demonstrate that they become sexually active at an

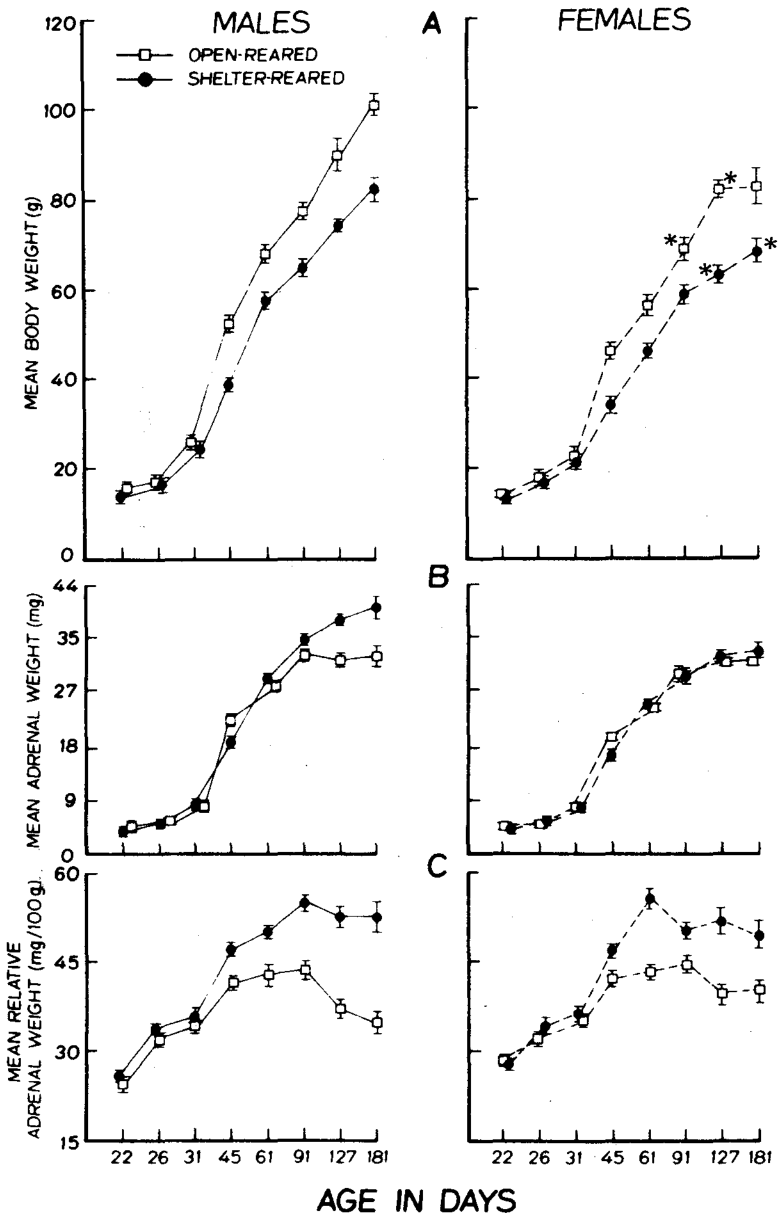

Figure 3. Body and adrenal gland weights of male and female open- and shelter-reared subjects. (A: Body weight as a function of age. At points marked with an asterisk, body weights were corrected for weight of gravid uteri. B: Mean absolute adrenal weights. C: Mean adrenal weight to body weight ratios. Flags indicate ± 1 *SE*.)

earlier age, it is surely consistent with such an interpretation.

Adrenal Weights

Panels B and C of Figure 3 show, respectively, the absolute adrenal weights and the adrenal weight to body weight ratios of open- and shelter-reared male and female gerbils. In terms of the more frequently employed measure of adrenal size, i.e., adrenal weight relative to body weight, open rearing profoundly reduced adrenal gland size in comparison with shelter rearing. The adrenal to body weight ratios of adult gerbils reared in cages providing shelter (M = 52.8 mg/100 g) fall at the lower end of the distribution of adrenal to body weight ratios reported for wild-caught *Meriones unguiculatus* by Benimetskii (1975).

Behavior

The results of the behavioral tests in the present experiment replicate those previously reported (Clark & Galef, 1979, Experiment 1). From 61 days of age to adulthood, both male and female gerbils reared and maintained in cages providing access to shelter exhibited responses to human handlers and sudden stimulation which were more like those of wild than domesticated animals. Shelter-reared subjects were much more difficult to capture and restrain, more likely to attempt to bite the experimenter, and fled and hid in response to sudden visual stimulation.

In the interests of brevity and because we

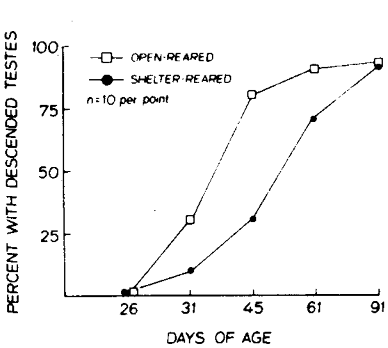

Figure 4. Percentage of open- and shelter-reared male subjects with descended testes.

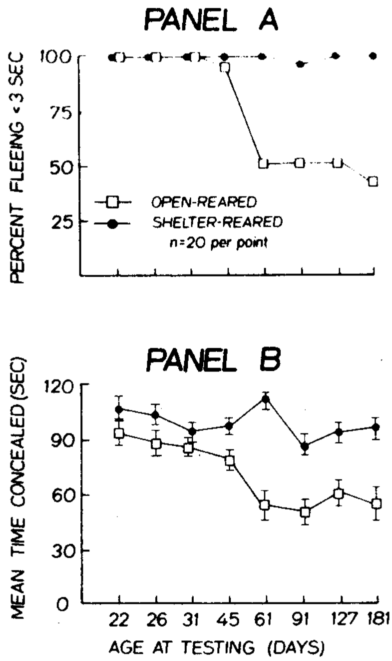

Figure 5. Behavior of open- and shelter-reared subjects in the behavioral test enclosure. (A: Percentage of subjects entering the refuge within 3 sec of stimulus presentation. B: Mean time spent in the refuge during the 120-sec test period. Flags indicate ± 1 *SE*.)

have presented similar data elsewhere (Clark & Galef, 1979), we present here only two indexes of behavioral response as a function of rearing condition. Figure 5A shows the percentage of open- and shelter-reared subjects fleeing to the refuge within 3 sec of stimulus presentation (a 3-sec criterion has been previously shown to be a valid and useful discriminator of responsive from nonresponsive subjects; Clark & Galef, 1977); Figure 5B shows the mean number of seconds that open- and shelter-reared subjects spent concealed during the 2 min following stimulus presentation. As is clear from examination of the figures, shelter-reared subjects were more responsive and wary than their open-reared counterparts.

Discussion

The results of the present study are consistent with the hypothesis that differences in the environmental conditions in which domesticated and wild populations of a species live can contribute to the development of those phenotypic characteristics that typically differentiate wild from domesticated individuals. Rapid maturation, hypotrophy of the adrenal glands, and behavioral docility are characteristics of members of a domesticated strain of gerbil reared and maintained in the absence of access to shelter and not of members of the same strain reared in more natural conditions providing access to shelter. These results suggest that the expression of domesticated phenotypes in some species may be dependent on specific experiences during ontogeny.

It might be argued that if members of a domesticated strain of gerbil can revert to a wild phenotype as the result of experience in a single generation, the strain was not domesticated to begin with. Price and King (1969, p. 43), for example, defined domestication as "an evolutionary process involving genotypic adaptation to the captive environment... the result of three phenomena: inbreeding, genetic drift and selection." To the extent that environmental factors contribute to changes in behavior in captive strains, such strains may not be domesticated in terms of the Price and King definition. We would suggest that attempts at definition of domestication may be somewhat premature. The empirical observations are clear; wild-living and captive populations of a variety of species differ from one another in similar ways along a number of dimensions. The problem is to determine the mechanism or mechanisms contributing to these phenotypic differences.

The data of the present study implicate environmental or experiential factors in the production of domesticated phenotypes in gerbils. However, it cannot be inferred from these data that changes in genotype resulting from inbreeding or selection in laboratory environments do not also contribute to phenotypic differences between laboratory and wild populations of gerbil. The influences of genotypic variation on morphology and behavior in domesticated and wild strains of species other than the Mongolian gerbil are amply attested to by the results of a multitude of studies in which members of various strains of a species are reared in similar environments and still exhibit marked phenotypic variability along wild–domesticated phenotypic continua (for examples, see Robinson, 1965, pp. 110–119, 164–190). There is no reason to suppose that similar processes have not attended the domestication of *Meriones unguiculatus*. The results of the present study do suggest, however, that domesticated strains of gerbil may have been selected so as to respond to rearing in certain environments by producing a domesticated phenotype. Development of the selected genotype in environments differing in critical ways from those in which selection occurred could, in this model, produce a wild phenotype.

Although the present experiments do not specifically address the question of the particular features of the sheltered environment promoting expression of wild-type morphology, previous studies indicate that wild-type behavior results from the experience of fleeing to shelter during maturation. Neither isolation from illumination nor isolation from human handlers during ontogeny produced observable effects on reactivity (Clark & Galef, 1977). Determination of experiences sufficient to produce wild-type morphology and rates of development requires further experimentation.

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