

THE ROLE OF THE PHYSICAL REARING ENVIRONMENT IN THE DOMESTICATION OF THE MONGOLIAN GERBIL (*MERIONES UNGUICULATUS*)

BY MERTICE M. CLARK & BENNETT G. GALEF, JR
Department of Psychology, McMaster University, Hamilton, Ontario L8S 4K1

Abstract. Gerbils reared in tunnel systems responded to a visual stimulus by fleeing, foot-thumping and remaining concealed, whereas many gerbils reared in laboratory cages responded in the same situation by approaching the stimulus. The critical factor in tunnel-rearing was the opportunity to flee to shelter during maturation. Neither isolation from illumination nor isolation from stimuli associated with human handlers produced the observed effect. Gerbils reared in laboratory cages exhibit the pattern of flight and concealment in response to stimulation following 24-hr experience in a tunnel system. The data are discussed in terms of their implications for models of the ontogeny of the behaviour characteristic of domesticated, as compared with wild, strains.

Comparison of the behaviour of wild and domesticated strains of a number of mammalian species reveals consistent differences. In particular, descendants of domesticated strains appear far less responsive to a variety of types of stimulation than do descendants of wild strains (Barnett 1958; Hafez 1962; Huck & Price 1975; Price 1970, 1973). Perhaps in consequence, members of domesticated populations have often been characterized by observers as less emotional, timid and savage than their wild progenitors (King & Donaldson 1929; Stone 1932; Richter 1954; Galef 1970).

The vast majority of accounts of the underlying cause of such differences in wild and domesticated animals have assumed that they are the direct results of differences in the genetic composition of compared populations (Castle 1947; Richter 1954; Spurway 1955; Connor 1971; Mayr 1974). In terms of the most frequently employed genetic hypothesis of the domestication process, some behaviour pattern that is adaptive in the wild (for example, intraspecific aggression and flight from or attack of man) is maladaptive in captivity and is consistently selected against (Lockard 1968; Price & King 1968). The hypothesized result of this artificial selection is the evolution of a new strain (Lockard 1968) that resembles its wild progenitor, both behaviourally and morphologically, less and less with the passage of time, until it eventually becomes unsuited to life in its original habitat (Hale 1962). On this hypothesis, the domestication process is, at least potentially, an irreversible event in the history of a population.

It is, of course, almost certain that the process of domestication produces measurable differences in the frequency of various genes in domesticated, as compared with relevant, ancestral wild populations. However, the extent to which such alterations in gene frequency are responsible for observed differences in the behaviour of domesticated and wild strains remains open to question (Donaldson 1912; Berry 1969; Henderson 1970; Oortmersen 1971). As Friedman (1964) has proposed, it is possible that members of domesticated strains are tamed anew in each generation as the result of critical experiences during ontogeny. On this hypothesis, domesticated strains possess the genetic substrate necessary to support the ontogeny of behaviour characteristic of wild ancestral populations, but fail to express them phenotypically because of alterations in development resulting from the experience of rearing in captivity.

Genetic and experientially oriented hypotheses of the domestication process are, of course, not mutually exclusive. It is, a priori, perhaps even probable that some features of the behavioural phenotype of domesticated strains reflect divergence in genotype from wild strains, whereas others reflect divergence in experience during ontogeny, or interactions between the two (Smith & Connor 1974).

Should individual experience in captivity be responsible, at least in part, for observed differences in the behaviour of wild and domesticated strains, then one would expect that wild individuals could be rendered less responsive to stimulation in a single generation, and there is a wealth of data, both anecdotal (Moore

1954) and experimental (Woolpy & Ginsberg 1967; Hughes & Boice 1973) that demonstrates the possibility of taming genetically wild individuals.

Conversely, should individual experience be responsible for the relative tractability of domesticated animals, then one might expect a rapid reversion to behaviour typical of wild populations in domesticated animals returned to their natural habitats. Both observation of feral populations of a variety of species (Darwin 1868; Minckler & Pease 1938; Beck 1973; Randall 1973; Scott & Causey 1973) and experimental rearing of domesticated animals in semi-natural environments suggest that, as a result of wild rearing, domesticated animals commonly revert to patterns of behaviour typical of wild strains (Crowcroft 1966; Freedman, King & Elliot 1961; Scott & Fuller 1965; Boice 1974). Such data offer support for hypotheses emphasizing the role of early experience in the development of patterns of behaviour typical of domesticated strains.

Although there is little evidence implicating any particular aspect of the environment in the production of the tameness and docility of domesticated animals, it is interesting to note that the species most commonly studied in the behavioural laboratory (rat, mouse, gerbil and hamster) live in burrows in their natural habitat but are maintained in captivity in laboratory cages devoid of shelter. In an investigation of the effects of burrow and laboratory rearing on the behaviour of the golden hamster (*Mesocricetus auratus*), Daly (1971) concluded that one major effect of rearing environment was to render burrow-reared animals more cautious in approaching unfamiliar environments than cage-reared ones. Unfortunately, the results of this experiment are difficult to interpret because the experimental manipulation was only partially successful. Of five litters reared in enclosures permitting burrowing, only one was actually reared beneath the surface. The burrow systems of four litters collapsed, and the young were reared on the surface.

Thiessen (1973) had greater success in inducing behavioural change as a function of maintenance conditions. He released a number of Mongolian gerbils (*Meriones unguiculatus*) into a large outdoor enclosure and, although a high rate of predation and heavy rains considerably reduced their numbers, three or four surviving pairs were available for study for several months. These gerbils dug complex burrow

systems and once established in them, became wary and difficult to observe. Although it is possible that the individuals managing to survive predators had a different mean genotype than their deceased fellows, the observation that the experience of living in a burrow system was correlated with an increase in wariness is suggestive of an influence of the nature of the physical environment on behavioural phenotype.

In the present series of experiments, domesticated Mongolian gerbils were reared in the laboratory in open cage and tunnel environments in order to assess the effects of burrow rearing on their behaviour. Subsequent analysis was undertaken to determine those features of the tunnel environment responsible for observed effects of tunnel-rearing on behaviour.

Experiment 1

Like most domesticated strains, the domesticated gerbil is extremely docile, shows no fear of human handlers, and rarely flees from or bites them (Rich 1968; Schwentker 1961). However, reports of the behaviour of gerbils observed in their natural habitat indicate that wild gerbils differ markedly from their domesticated conspecifics in their response to humans. For example, Anderson (in Allen 1940) reports that he could only approach to within 2.4 m of wild gerbils before they would flee into their burrows and foot-thump (cf. Won 1961).

If the difference in the response of laboratory and wild strains of gerbils to the presence of humans reflects the effects of being reared in diverse physical environments, then one might expect gerbils reared in a laboratory environment that simulated their natural habitat to exhibit the flight, concealment and foot-thumping response to the presence of humans which is seen in wild gerbils. In the first experiment, gerbils of a common genetic background were reared either in standard laboratory cages or in tunnel systems constructed by their parents and their responsiveness to a novel, moving, human-like visual stimulus assessed at maturity.

Methods

Subjects were 64 Mongolian gerbil pups, the direct descendants of 16 breeding pairs acquired from Tumblebrook Farm, Brant Lake, New York. Each of the 16 breeding pairs reared one litter in each of the two rearing conditions (LDO and LDT) described below.

Upon arrival in the laboratory, multiparous female gerbils and their mates were established

in a temperature controlled colony room (22°C), illuminated by overhead fluorescent lights from 9.00 to 21.00 hours (EST); darkness prevailed for the remainder of the day, and food and water were available continuously.

Experimental rearing conditions. (i) *Group LDO.* Subjects were reared on a 12 hr light-dark cycle (LD) in open (O) laboratory cages, devoid of shelter. The cages used were formed of translucent plastic (35.56 × 30.48 × 15.24 cm) and contained wood shavings to a depth of 1.27 cm. The cover of each cage was constructed of 1.25-cm hardware cloth. Cages were inspected each morning for the birth of litters and to determine the date of eye-opening of young. A litter was weaned and its members individually marked for identification by shaving portions of their bodies 27 days after the median date of eye-opening of that litter (the first day on which half of the pups in that litter had both eyes fully open (\bar{x} = 18.5, SE = 1.7 days). Litters were handled only when wood shavings were changed, once on the day of median eye-opening and once again 27 days later.

(ii) *Group LDT.* Subjects were reared on a 12-hr light dark cycle (LD) in tunnel systems (T). Cages for tunnelling were constructed by filling a sheet-metal enclosure (0.91 × 0.91 × 1.22 m) to a depth of 0.46 m with wetted packed earth. Breeding pairs constructed complex tunnel systems within these cages 3 to 4 days following introduction into them. All litters were born and reared inside burrows and rarely were seen on the surface, making direct determination of the date of birth impossible. However, preliminary observation had revealed that shortly after giving birth to a litter, female gerbils, like other desert rodents (Kirmiz 1962) would block all entrances to the burrow with earth. Consequently, whenever entrances to the tunnels were blocked, it was assumed that a litter had been born. Confirmation of the birth of a litter was accomplished by placing "Hav-a-Hart" mouse live-traps inside the tunnelling enclosure on days 16 to 19 following closure of burrow entrances and trapping all enclosure inhabitants. In every instance in which a litter was thought to be inhabiting the tunnel, young pups were trapped. Immediately after the eyes of the trapped young had been checked for opening, they were released back into the tunnel system. Twenty-seven days after median eye-opening had occurred, each litter was permanently removed from its tunnel system, marked for identification purposes, and housed in a

translucent plastic cage (35.56 × 30.48 × 15.24 cm) containing a wooden box (17.78 × 27.94 × 15.24 cm) with one (5.08 × 5.08 cm) entrance hole.

General procedure. Thirty days after median eye-opening had occurred in a litter, subjects in that litter were tested on the visual-cliff, receiving one test trial a day for five consecutive days. (Methods of testing on the visual-cliff, data collected in this apparatus, and the rationale for its use will be discussed in experiment 3.) At the conclusion of visual-cliff testing, subjects were left undisturbed for 1 week and then were tested in the shelter-field apparatus. Subjects were 58 to 64 days postpartum at the time of initiation of shelter-field testing.

Testing was conducted in a 1.22 × 1.22-m enclosure with walls 0.91 m high. A wooden shelter (30.48 × 30.48 × 15.24 cm) with two (5.08 × 5.08 cm) entrance holes was located in one corner of the enclosure (see Fig. 1). Behaviour occurring in the shelter-field enclosure was monitored via closed-circuit television. A visual stimulus, consisting of a rubber mask of a male human face placed on a styro-foam wig-stand and mounted on a pole, was presented to subjects while in the enclosure.

Immediately prior to testing in the shelter-field enclosure, the wooden shelter in the cage of each LDT litter was removed and subjects permitted 20 min to light-adapt. In order to control for possible litter effects (Henderson 1963, 1967; King 1969), only two pups (when

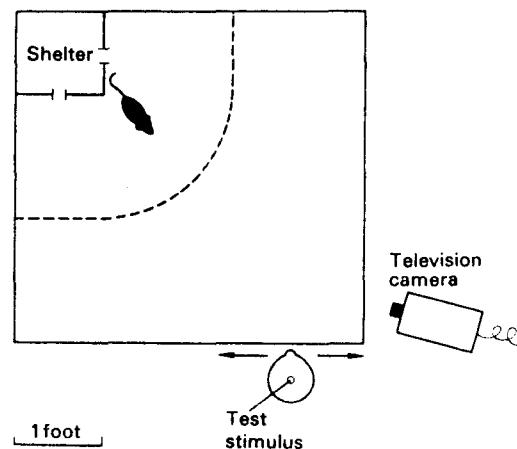


Fig. 1 Overhead schematic view of the shelter-field enclosure.

possible one male and one female) were randomly selected from each of the litters reared in each condition. Twenty-six of the subjects in each rearing condition were assigned to the experimental group and the remaining six subjects to the control group described below.

Basically, the shelter-field test consisted of two sub-tests to be referred to below as the pre-test and post-test periods. During the pre-test, individual subjects (experimental and control) were allowed to explore the open and sheltered portions of the enclosure. During the post-test, experimental subjects were presented with the visual test stimulus, while control subjects were permitted to continue to explore the enclosure undisturbed.

A. Pre-test (experimental and control groups). An individual subject was placed in one corner of the enclosure and the experimenter recorded the amount of time it spent inside the shelter during the 3-min period following that subject's initial exit from the shelter. Entry into or exit from the shelter was defined, respectively, as occurring when the subject had all four feet inside or outside of its entrance. Subjects failing to enter the shelter within 10 min following placement in the enclosure were removed from it and retested on the following day.

If a subject exhibited freezing behaviour during the 3-min pre-test period, recording was stopped and was restarted when the subject resumed locomotion. Freezing was defined as the assumption of a crouched posture accompanied by complete immobility (Doyle & Yule 1959).

B. Post-test (experimental group). Following the 3-min pre-test period, the visual stimulus described above was presented to each experimental subject when (1) that subject was within 45.7 cm of the wooden shelter, oriented away from it, and facing the corner of the enclosure in which the visual stimulus was to be presented (see Fig. 1) and (2) it had been moving throughout the preceding 5-s period (Fentress 1968a, b).

The test stimulus was introduced over one corner of the enclosure, moved slowly from left to right three times, and then held in an upright position. The total period of exposure of the test stimulus lasted 30 s. During the 2-min period subsequent to the presentation of the test stimulus, the experimenter recorded the time required for the subject to reach shelter, the time to first emergence from shelter, the total time spent in concealment, and instances of foot-thumping.

C. Post-test (control group). Subjects in the control group were treated identically to those in the experimental group except that no test stimulus was presented at the beginning of the post-test period.

Results

In the interest of brevity, analysis of a variety of measures (time to initial shelter entrance (pre-test) freezing, and sex differences in shelter-field performance) are not included in this paper, but are available in Clark (1974).

Pre-test. Six subjects in the LDT experimental group behaved so as to make both their pre- and post-testing impossible, and they were excluded from the experiment. On five consecutive days, two of these subjects remained immobile in the open portion of the enclosure, and four subjects entered the shelter and did not emerge for more than 10 min. We decided to exclude the behaviour of these six animals from further analysis and discussion because none of 42 other tunnel-reared gerbils tested using identical procedures (in studies not reported here) behaved in this fashion.

A Kruskal-Wallis One-Way Analysis of Variance of the pre-test data, presented in Table I, revealed no significant differences in the amount of time spent under shelter during the pre-test period by the subjects in the four groups ($H = 5.5$, $df = 3$, $P > 0.05$). This finding suggests that any differences in concealment behaviour during the post-test period cannot be attributed to differences in the tendency of open- and tunnel-reared subjects to seek shelter in the absence of stimulation.

Post-test. The main results of experiment 1 are presented in Table II, which describes the performance of both experimental and control groups of LDO and LDT on each of the four measures of post-test behaviour. The main effect of tunnel-rearing, as compared with open-rearing, is to be found in the comparison of the post-test behaviour of the LDT and LDO

Table I. Median Seconds Spent in the Shelter During the Pre-test Period by LDO and LDT Experimental and Control Subjects

	Experimental		Control	
	<i>N</i>	Median	<i>N</i>	Median
LDO	26	45.0	6	48.5
LDT	20	47.0	6	54.0

experimental subjects. As can be seen in Table II, all 20 of the LDT experimental subjects entered the shelter within 3 s following stimulus presentation, while only 15 of 26 LDO experimental subjects did so ($\chi^2 = 8.91$, Yates correction, $df = 1$, $P < 0.005$).

Furthermore, LDT experimental subjects spent significantly more time in the shelter before first emerging than did LDO experimental subjects (Mann-Whitney *U*-test, transformed *z* score = 2.84, $P < 0.01$), and spent more time concealed during the post-test period (Mann-Whitney *U*-test, transformed *z* score = 3.75, $P = 0.002$). Although there was a tendency for LDT experimental subjects to foot-thump more than LDO experimental subjects, this difference was not significant ($\chi^2 = 2.93$, Yates correction, $df = 1$, $P > 0.05$).

Comparison of the behaviour of LDO and LDT Control Groups, also presented in Table II, revealed no differences in latency to reach shelter, latency to emerge from shelter, or in total time spent in concealment (Mann-Whitney *U*-tests, all P 's > 0.05). This finding is consistent with the inference made from the pre-test data that simple differences in exploratory behaviour of LDO and LDT animals are not sufficient to explain differences in the post-test behaviour of these animals.

Comparison of the data from experimental and control subjects within both the LDO and LDT conditions revealed the robust effect of stimulus presentation on shelter-field behaviour. Experimental groups in both rearing conditions reached the shelter sooner, spent more time concealed before first emerging, and spent more total time in the shelter during the post-test period than did their respective controls.

Fleeing versus Non-fleeing subjects. Experimental subjects that took shelter in the first 3 s of the post-test period were considered to have 'fled' in response to the presentation of the test stimulus, whereas those requiring more than 3 s to reach shelter were considered not to have fled.

A criterion of 3 s to reach shelter following stimulus presentation was selected to differentiate fleeing from non-fleeing subjects because, as can be seen from the data in the fourth column of Table II, none of the control subjects reached shelter during the initial 3 s of the post-test period. Therefore, a 3-s criterion discriminated flight in response to stimulus presentation from random shelter entry.

To some extent differences in post-test performance of the LDO and LDT experimental groups reflected the fact that the LDO group consisted of two subgroups of subjects, those that fled immediately following stimulus presentation, and those that did not. The LDT group, on the other hand, consisted only of subjects that fled immediately following presentation of the test stimulus. Differences in post-test performance of the LDT and LDO experimental groups were somewhat attenuated, if analysis of post-test performance were based only on the data obtained from those subjects that fled in response to the test stimulus. Latency scores for the LDT experimental group during the post-test period remained unaffected, as all LDT subjects fled on presentation of the test stimulus, whereas latency scores to emerge from shelter and total time spent in shelter become 51.0 and 90.0 s respectively for the LDO group. Significant differences, however, still remained between LDT and LDO in time to first emergence (Mann-Whitney *U*-test, transformed *z* score = 2.79, $P < 0.05$) and total time spent in shelter (Mann-Whitney *U*-test, transformed *z* score = 1.98, $P < 0.01$). There were also significant differences in latency to first emergence and total time spent in shelter by fleeing and non-fleeing subgroups of group LDO (Mann-Whitney *U*-tests; both P 's < 0.05).

Discussion

The results of the present experiment indicate that the response of gerbils to the presentation of a visual stimulus varied in several important

Table II. Post-test Performance of Experimental and Control Groups

Group	Rearing condition	Median latency to reach shelter (s)	Median latency to first emerge from shelter (s)	Median total time spent in shelter (s)	Per cent entry < 3 (s) (flight)	Foot-thumping (per cent)
Experimental	LDO ($N = 26$)	2.0	11.0	60.5	57.6	15.4
	LDT ($N = 20$)	1.0	119.0	119.0	100.0	40.0
Control	LDO ($N = 6$)	13.0	6.5	29.5	00.0	00.0
	LDT ($N = 6$)	12.5	6.0	40.5	00.0	00.0

respects as a function of rearing conditions. First, gerbils reared in tunnel systems were more likely to respond to stimulus presentation by fleeing to shelter than were gerbils reared in standard laboratory cages. Second, following stimulus presentation, tunnel-reared gerbils showed increased latencies to leave shelter and spent a greater amount of time in concealment than did gerbils reared in open cages.

The fact that concealment behaviour in the absence of stimulus presentation did not differ between tunnel- and open-reared subjects in either the pre-test or the control condition suggests that differences between the groups in response to stimulus presentation cannot be attributed to differences in baseline exploratory behaviour.

It seems reasonable to conclude from the data of the present experiment that the physical environment in which gerbils are reared can influence the nature of their response to the sudden presentation of a human-like stimulus. The effects of rearing a domesticated strain of gerbils in a tunnel environment appear to be to establish the pattern of response to the appearance of humans normally seen in wild gerbils.

In experiment 2 we investigate features of the tunnel-rearing environment that might be responsible for the increased responsiveness of individuals reared in it. We focus attention on attributes of the tunnel-rearing experience specific to the presence of a tunnel, although the environment and experience of open- and tunnel-reared subjects differed in other respects as well.

Experiment 2

The tunnel system provided (1) a hole through which gerbils could flee, (2) an enclosed hiding place, and (3) a three-dimensional substrate. In contrast, the open-cage provided opportunity for neither flight nor concealment, and gerbils reared in laboratory cages were restricted in activity to a two-dimensional surface. In the present experiment these features, differentiating tunnel from open environments, were added to the basic open-cage design to allow assessment of their individual contribution to the differences in behaviour observed in open- and tunnel-reared animals.

Methods

Subjects were 128 gerbil pups selected, as in experiment 1, from 64 litters born and reared in the laboratory.

Experimental rearing conditions. Each breeding pair was established in a translucent plastic cage and maintained on a 12 hr light-dark cycle (LD). Marking, handling, and cage-cleaning procedures were those described in experiment 1. Nine days after the birth of a litter, 16 mothers and their young were randomly assigned to each of the four housing conditions described below.

As can be seen in Fig. 2, which illustrates the four housing conditions used, house-open cages (LDHO) provided a hole through which to run; cliff-open cages (LDCO), a three-dimensional substrate; house cages (LDH), a hole and an enclosed hiding place; and cliff-house (LDCH), a hole, enclosed hiding place, and experience with a three-dimensional substrate. Rearing pups in this array of environments and testing them in the shelter-field enclosure provided the opportunity to determine the contribution of each environmental feature to the difference in response of open- and tunnel-reared subjects to a novel, moving stimulus.

General procedure. Procedures for visual cliff and shelter-field testing were identical to those described in experiment 1. For the shelter-field test, two subjects were selected, as in experiment 1, from each of the 16 litters in each housing condition. Twenty-six of each group of 32 subjects were assigned to the experimental group and six subjects to the control group.

Results and Discussion

Data collected during the pre-test period in the present experiment were analysed with that collected during the pre-test period in experiment 1, and a Kruskal-Wallis One Way Analysis of Variance of the combined data revealed no significant differences in the amount of time spent in shelter by any of the 12 groups (six experimental and six control) during the pre-test ($H = 14.3$, $df = 11$, $P > 0.05$).

The main results of the present experiment are presented in Table III. Data obtained from the LDO and LDT groups of experiment 1 are included for purposes of comparison. Examination of Table III reveals that during the post-test period control subjects did not differ, as a function of rearing condition, in latency to reach shelter, in time to emerge from shelter or in total time spent in concealment (Kruskal-Wallis tests, all P 's > 0.05). Rearing condition did, however, significantly affect the responsiveness of experimental groups to stimulus presentation on all four measures of post-test performance (percentage fleeing, $\chi^2 = 14.5$,

$df = 3, P < 0.01$; extension of the median tests, latency to reach shelter, $\chi^2 = 10.5, df = 3, P < 0.025$; latency to emerge from shelter $\chi^2 = 12.5, df = 3, P < 0.01$; and total time spent in concealment, $\chi^2 = 11.75, df = 3, P < 0.01$). In general, the effect of rearing in environments providing shelter was to increase response to stimulus presentation. Although the percentage of subjects in the LDHO group (which had a hole to run through but no shelter available), fleeing in response to stimulus presentation, was somewhat greater than would be expected if provision of shelter were the only important aspect of tunnel-rearing in the potentiation of responsiveness to stimulation, the other two main measures of response showed a clear differentiation in behaviour between subjects reared with and without shelter.

Table IV presents data separately describing the behaviour of fleeing and non-fleeing subgroups. Among the fleeing subgroups there were overall significant differences, as a function of

rearing condition, in latency to emerge (extension of the median test, $\chi^2 = 14.5, df = 3, P < 0.025$) and in total time spent in concealment (extension of the median test $\chi^2 = 13.5, df = 3, P < 0.025$). However, there were no significant differences found in any measure of post-test behaviour among fleeing subjects having cover available during maturation (LDH, LDCH, LDT) or among fleeing subjects having no cover available during maturation (LDO, LDCO, LDH) (extension of the median tests, all P 's > 0.05).

These results indicate that the increased responsiveness to the presentation of the visual stimulus to be seen in tunnel-reared, as compared with open-reared subjects, resulted in large measure from the shelter which the tunnel system provided for gerbils reared in it. Neither provision of a cliff, nor of a hole through which to run, significantly increased responsiveness of fleeing subjects in the shelter-field enclosure, whereas the provision of shelter produced the entire behaviour pattern of flight and conceal-

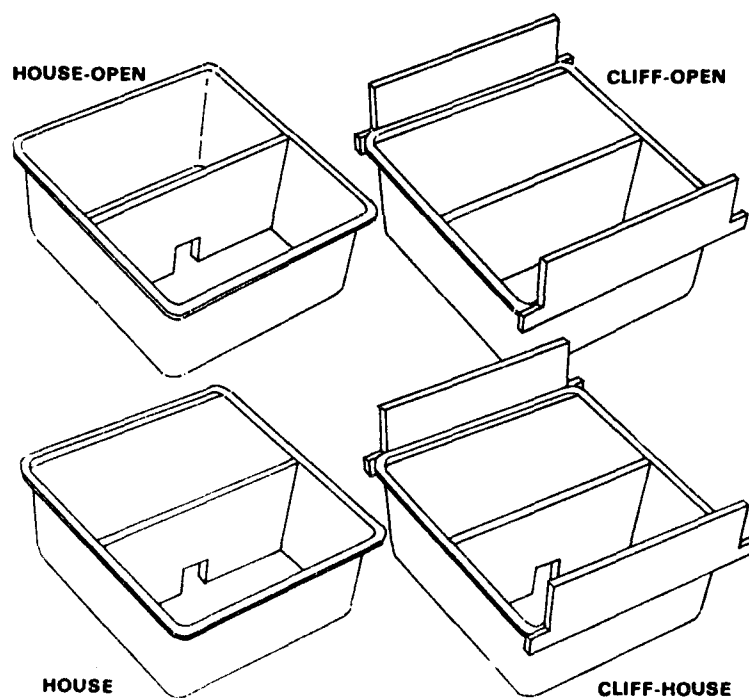


Fig. 2. Schematic diagrams of the house-open (HO), cliff-open (CO), house (H), and cliff-house (CH) cages used for rearing. The hardware cloth used to cover the tops of the cages is not shown. In H and HO cages, the hardware cloth was flush with the top edge of the plastic cages and in CO and CH cages, it was raised 12.7 cm above the plastic cage edge.

ment normally seen in tunnel-reared individuals.

Data from non-fleeing experimental subjects, also presented in Table IV, did not reveal any significant differences among groups in response as a function of rearing environment (Kruskal-Wallis One Way Analysis of Variance, df 's = 4, P 's > 0.05). However, comparison of the post-test performance of non-fleeing subjects (Table IV) with that of controls (Table III) revealed that non-fleeing individuals were not simply indifferent to stimulus presentation. There was a significant increase in latency to reach shelter on the part of non-fleeing experimental subjects (Mann-Whitney U -test, transformed z score = 2.18, P < 0.05), but no differences between non-fleeing experimental subjects and control subjects in latencies to emerge from shelter or in time spent in concealment (Mann-Whitney U -tests, transformed z scores both P 's > 0.05). Observation of the behaviour of non-fleeing subjects

revealed that their increased latency to enter shelter following stimulus presentation resulted from a marked tendency to approach and fixate the stimulus.

The observation (Table IV) that foot-thumping was exhibited only by fleeing subjects ($\chi^2 = 12.2$, Yates correction, $df = 4$, $P < 0.025$) suggests that fleeing animals were more highly aroused by stimulus presentation than non-fleeing ones (Routtenberg & Kramis 1967; Spatz & Granger 1970).

Experiment 3

It is implied in the discussions of experiments 1 and 2 that the increased responsiveness of animals reared in environments providing shelter in the shelter-field test is indicative of an increase in responsiveness or emotionality in these animals. The generality of the observed increased sensitivity to stimulation of shelter-reared

Table III. Post-test Performance of Experimental and Control Groups of Experiment 2

Group	Rearing condition	Per cent entry < 3 (s) (flight)	Median latency to reach first shelter (s)	Median latency to first emerge from shelter (s)	Median total time spent in shelter (s)	Foot-thumping (per cent)
Experimental	LDO ($N = 26$)	57.6	2.0	11.0	60.5	15.4
	LDCO ($N = 26$)	50.0	6.0	11.0	40.5	19.2
	LDHO ($N = 26$)	76.9	1.0	12.5	49.0	15.4
	LDH ($N = 26$)	84.6	1.0	85.0	109.5	19.2
	LDCH ($N = 26$)	92.3	1.0	85.0	111.0	30.0
	LDT ($N = 20$)	100.0	1.0	119.0	119.0	40.0
Control	LDO ($N = 6$)	00.0	13.0	6.5	29.5	00.0
	LDCO ($N = 6$)	00.0	7.5	3.5	30.5	00.0
	LDHO ($N = 6$)	00.0	22.0	7.0	31.0	00.0
	LDH ($N = 6$)	00.0	14.0	7.0	33.0	00.0
	LDCH ($N = 6$)	00.0	19.0	2.0	19.5	00.0
	LDT ($N = 6$)	00.0	12.5	6.0	40.5	00.0

Table IV. Post-test Performance of Fleeing and Non-fleeing Experimental Subjects in Experiment 2

Sub-group	Rearing condition	No. of subjects	Median latency to reach shelter (s)	Median latency to first emerge from shelter (s)	Median total time spent in shelter (s)	Foot-thumping (per cent)
Fleeing	LDO	15	1.0	51.0	90.0	26.6
	LDCO	13	1.0	45.0	80.0	38.5
	LDHO	20	1.0	31.0	68.0	20.0
	LDH	22	1.0	96.0	114.0	22.7
	LDCH	24	1.0	98.5	112.5	33.3
	LDT	20	1.0	119.0	119.0	40.0
Non-fleeing	LDO	11	26.0	7.0	32.0	00.0
	LDCO	13	18.0	2.0	25.0	00.0
	LDHO	6	20.5	5.5	21.5	00.0
	LDH	4	29.0	2.0	21.0	00.0
	LDCH	2	22.5	1.0	22.0	00.0
	LDT	0	—	—	—	—

animals is, of course, open to question. As many observers have indicated, animals described as emotional on the basis of one test are not necessarily the ones appearing emotional on a second measure (Anderson 1938).

The problem in the present series of experiments is, perhaps, particularly pressing in that there is a confounding of independent and dependent variables. Rearing in conditions providing cover provided experience with an environment very similar to that in which shelter-field testing was conducted, and it is possible that response-transfer on the part of shelter-reared animals underlies their increased probability of shelter entrance in the shelter-field test. It would be particularly helpful, therefore, to have available a second measure of reactivity, as disparate as possible from the shelter-field situation, to determine that the effects of rearing condition on behaviour in the shelter-field test are not unique to that testing situation.

As mentioned above, all subjects in the preceding experiments were tested on the visual-cliff prior to testing in the shelter-field enclosure. Although the visual-cliff has been primarily used as a measure of visual acuity, several investigators have suggested that visual-cliff performance is influenced by the emotionality of subjects (Routtenberg & Glickman 1964; Thiessen et al. 1968; Lore & Sawatski 1969). With particular reference to gerbils, Thiessen et al. (1968) have suggested that random performance and short latencies of choice behaviour on the visual-cliff may be the result of an emotional factor rather than visual deficits. Other investigators have reported short latency non-visually directed choice behaviour on the visual cliff, interpretable in terms of the reactivity of subjects, although these workers have not discussed the data in that framework (Walk & Gibson 1961; Rosenblum & Cross 1963).

In the present experiment, the behaviour of gerbils on the visual-cliff is described in terms of its relationship to their performance in the shelter-field enclosure to determine the validity of the shelter-field test as a measure of the effects of the physical rearing environment on behaviour. (A further discussion of the relationship of the data obtained in the shelter-field test situation to that obtained using other emotionality measures is to be found in Clark 1974.)

Methods

Subjects were 78 open-reared, 78 house-open reared, 78 house-reared, 78 cliff-house-reared and 20 tunnel-reared gerbils.

Procedure. Methods of rearing, handling and marking were as described in experiment 1.

A modified Model II visual-cliff (Walk & Gibson 1961) was constructed by suspending a Plexiglas plate (60.96 × 60.96 × 0.64 cm) 30.48 cm above the floor of a plywood box (60.96 × 60.96 × 91.44 cm). Blue and white checkered (2.54 × 2.54 cm) material was inserted directly below one-half of the Plexiglas plate (the shallow side) and 30.48 cm below the other half (the deep side). A wooden centreboard (60.96 × 9.52 × 7.62 cm) bisected the Plexiglas surface, concealing the junction of the deep and shallow sides. Illumination of the deep and shallow sides was equated so that the two sides appeared equally bright in Nikon photomic FT_N Finder. Behaviour in the visual-cliff apparatus was observed via closed-circuit television.

Prior to testing, all subjects reared in environments providing darkness were light-adapted for 20 min. Subjects were then tested individually on the visual-cliff in a quiet, well-illuminated room. Each subject was placed at one end of the centreboard, facing the opposite end, and left undisturbed until it either descended to the Plexiglas surface or had remained on the centreboard for 5 min, at which time it was returned to its home cage. The experimenter recorded each subject's latency to leave the platform and the side to which it descended. The centreboard and Plexiglas surface were cleaned with a moist cloth at the conclusion of each test trial.

Results

The main results of the present experiment are presented in Table V. Only data from the first visual-cliff test of each subject are described here, ensuring independence of observations. As is apparent from inspection of the data, the percentage of subjects descending from the centreboard varied as a function of rearing condition, with subjects reared with shelter available showing a greater probability of descending than those reared without shelter available ($\chi^2 = 25.5$, $df = 4$, $P < 0.01$). Furthermore, individual subjects, who fled in response to presentation of the test stimulus in the shelter-field enclosure, were far more likely to descend from the centreboard in the visual-cliff apparatus than those who did not flee.

Table VI presents data describing the latency to descend and choice of deep or shallow side by subjects on the visual-cliff. As can be seen by examination of the table, subjects in all groups showed a slight and, in most cases, significant preference for the shallow side. There were, however, no significant differences among groups in initial choices of the shallow or deep side as a function of rearing condition ($\chi^2 = 1.74$, $df = 4$, $P > 0.05$).

Comparison of latencies to descend and per cent shallow-side choices of subjects fleeing and not fleeing during the shelter-field post-test are presented in Table VII. Analysis of the data revealed that the latency of non-fleeing subjects in each group to descend from the centreboard on the visual cliff was significantly longer than

that of fleeing subjects (Mann-Whitney U -tests, all P 's < 0.05), and that non-fleeing subjects were somewhat more likely to choose the shallow side than fleeing subjects.

Discussion

The observations described above offer support for the hypothesis that the effects of the physical rearing environment on reactivity were not specific to the shelter-field test. Subjects reared in conditions providing shelter had both a greater probability of descending from the centreboard on the visual-cliff and a higher probability of fleeing in the shelter-field enclosure. This finding suggests that the increased responsiveness in the shelter-field enclosure of subjects reared in environments providing shelter

Table V. Analysis of the Relationship Between Descent on the Visual-Cliff and Flight in the Shelter-Field

Rearing condition	Percentage of subjects descending from visual-cliff platform	Percentage of subjects fleeing in the shelter-field enclosure	Fleeing		Not fleeing		Chi square
			Descend	Not descend	Descend	Not descend	
Open ($N = 78$)	57.7	41.0	29	3	16	30	21.9*
House-open ($N = 78$)	67.9	65.4	45	6	8	19	39.9*
House ($N = 78$)	84.6	92.3	63	9	3	3	†
Cliff-house ($N = 78$)	82.0	87.2	59	9	5	5	†
Tunnel ($N = 20$)	95.0	100.0	19	1	0	0	†

* $P < 0.001$, two-tailed test.

†Applicable statistical analysis not available.

Table VI. Percentage of Initial Descents to the Shallow Side and Latency for Subjects to Descend from the Visual-Cliff Platform

Rearing condition	Percentage of initial choices to the shallow side	z †	Latency (s)	
			\bar{x}	SE
Open ($N = 45$)	66.7	2.39*	71.3	12.5
House-open ($N = 53$)	71.2	2.75**	78.2	11.6
House ($N = 66$)	60.6	1.85 NS	41.3	7.5
Cliff-house ($N = 64$)	65.1	2.62**	72.0	10.2
Tunnel ($N = 19$)	62.7	†	19.6	3.7

†Transformed z score, binomial test.

‡Binomial probability value, $P = 0.36$ NS.

* $P < 0.05$, two-tailed test.

** $P < 0.01$, two-tailed test.

NS Not significant.

was not due to similarities between shelter-rearing environments and the shelter-field testing situation. On the contrary, rearing in environments providing shelter seems to produce a more general increment in reactivity in Mongolian gerbils.

The fact that subjects in every rearing condition showed a preference for the shallow side indicates that the choice of a side to which to descend on the visual-cliff was to some extent directed by visual cues. However, the observation that higher probabilities of shallow-side choice were associated with long latencies of descent and an absence of flight in the shelter-field enclosure suggests that subject reactivity is a factor in determining visual-cliff performance. The data suggest that reactive animals were less visually directed than non-reactive ones and may have been to some extent simply seeking to escape from the exposed centreboard.

Experiment 4

The results of the three experiments described above indicate that rearing gerbils in environments providing shelter results in an increment in their reactivity to stimulation. An organism maturing within an environment providing shelter may have a different range of experiences than one maturing in an open environment. The presence of a physical shelter enables an organism to modulate the amount of light to which it is exposed, to reduce its general ex-

posure to visual and auditory stimuli arising in the outside world, and to experience flight from an exposed area to one offering concealment. In the following three experiments an assessment is made of the contribution to reactivity in the shelter-field test of each of these three types of experience available only to shelter-reared subjects. The present experiment is concerned with the effects of illumination conditions during ontogeny on behaviour.

Immature animals living in environments providing shelter (LDH, LDCH, LDT) spend most of their time under that shelter, and hence, in the dark. Because dark-rearing has been demonstrated to have an effect on subsequent emotionality in a number of species (Gibson, Walk & Tighe 1959; Ganz & Fitch 1968), it is possible that the observed differences in behaviour between shelter- and open-reared subjects resulted from differences in the amount of illumination to which they were exposed during rearing. In the present experiment, groups of subjects were reared in darkness in open-cages (referred to below as group DDO) to assess the effects of low illumination levels during maturation on later behaviour.

Methods

Two subjects were randomly selected from each of 16 litters born and reared in the laboratory. Twenty-six of the subjects were assigned to the experimental group and six to the control group.

Table VII. Visual-Cliff Performance of Descending Subjects which Fled and Did Not Flee in the Shelter-Field Enclosure

Rearing condition	Fled in shelter-field test				Did not flee in shelter-field test			
	Percentage of initial choices to the shallow side	z †	Latency (s)		Percentage of initial choices to the shallow side	P ‡	Latency (s)	
			\bar{x}	SE			\bar{x}	SE
Open ($N = 45$)	55.2	0.56 NS	23.8	3.3	87.5	0.004**	158.0	20.5
House-open ($N = 53$)	71.1	2.98**	43.4	6.3	75.0	0.29 NS	225.9	12.1
House ($N = 66$)	60.3	1.76 NS	31.4	6.2	66.7	0.41 NS	233.0	30.2
Cliff-house ($N = 64$)	63.2	2.10*	50.9	7.5	80.0	0.38 NS	256.3	12.2
Tunnel ($N = 19$)	62.7	§	19.6	3.7	—	—	—	—

†Transformed z score.

‡Binomial probability value.

§Binomial probability value, $P = 0.36$ NS.

* $P < 0.05$, two-tailed test.

** $P < 0.01$, two-tailed test.

NS Not significant.

Procedure. Nine days following the birth of a litter, mother and young were removed from the breeding colony and transferred to a darkened room. No attempt was made to eliminate completely exposure of the pups to light, as rigorous light deprivation in infancy is known to produce severe visual deficits in a number of species (Riesen 1966). Instead, the dark colony room was kept in darkness but illumination was provided for several minutes a day when animals were fed, watered, cleaned, marked and observed for eye-opening.

All other maintenance and testing procedures were identical to those described in experiment 1.

Results

The main results of the present experiment are presented in Tables VIII and IX. Data from the LDO group of experiment 1 are included for purposes of comparison. As is evident from examination of the data, both from all subjects (Table VIII) and from fleeing subjects alone (Table IX), the effects of dark-rearing were generally to reduce responsiveness to stimulus presentation. Subjects reared on a 12-hr light-dark cycle (group LDO) fled significantly more frequently, showed longer latencies to emerge from shelter, and spent more total time in the shelter than did the dark-reared subjects (group DDO) (Mann-Whitney *U*-tests, all *P*'s < 0.05).

That these differences in the behaviour of dark and cyclic-reared experimental subjects

in response to stimulus presentation were not the result of changes in baseline levels of activity is indicated by the fact that corresponding effects were not to be found in the comparison of the behaviour of LDO and DDO control groups (Mann-Whitney *U*-tests, all *P*'s > 0.05).

Discussion

As was shown in experiment 2, the main effects of rearing in environments containing shelter were (1) to increase the percentage of subjects exhibiting flight behaviour, (2) to increase the latency to emerge from shelter, and (3) to increase total time spent in shelter in response to stimulus presentation.

Animals reared with cover available spent more time in the dark during ontogeny than those reared in open environments and, therefore, it seemed possible that differences in exposure to light during development might be responsible for the increased responsiveness to stimulus presentation observed in gerbils reared with cover available to them. The results of the present experiment, however, indicate that such an interpretation of the observed effects of rearing with cover available is an invalid one. Rearing in the dark served to reduce, rather than augment, responsiveness to sudden stimulus presentation.

Experiment 5

A second plausible explanation of the observed differences in behaviour between animals reared

Table VIII. Post-test Performance of Experimental and Control Groups in Experiment 4

Group	Rearing condition	Median latency to reach shelter (s)	Median latency to first emerge from shelter (s)	Median total time spent in shelter (s)
Experimental	LDO (<i>N</i> = 26)	2.0	11.0	60.5
	DDO (<i>N</i> = 26)	19.5	4.5	28.0
Control	LDO (<i>N</i> = 6)	13.0	6.5	29.5
	DDO (<i>N</i> = 6)	20.0	9.5	31.5

Table IX. Post-test Performance of Fleeing Subjects in Experiment 4

Rearing condition	Flight		Concealment		Foot-thumping (per cent)
	Per cent entry < 3 (s)	Median latency to reach shelter (s)	Median latency to first emerge from shelter (s)	Median total time spent in shelter (s)	
LDO (<i>N</i> = 26)	57.6	1.0	51.0	90.0	26.6
DDO (<i>N</i> = 26)	26.9	1.5	7.0	75.0	14.3

in cages providing cover and those reared in open-cages is in terms of differences in their relative exposure during development to environmental stimulation arising outside the cage. Animals reared in tunnel, house, and cliff-house environments spent much of their time within an enclosed space and, therefore, were exposed to less stimulation provided by activity in the colony room, than open-reared animals. It is possible that the differences in response to stimulus presentation of shelter- and open-reared animals in the test situation described in experiment 2 resulted from differences in habituation to extra-cage stimulation during rearing (Konrad & Bagshaw 1970).

To assess the effects of isolation from exposure to extra-cage stimulation during maturation on performance in the shelter-field test, the behaviour of gerbils reared in isolation was compared to that of individuals reared in a normal colony room. It was decided to rear animals in isolation under conditions of constant illumination, as pilot experiments had shown that animals reared in constantly illuminated open-cages were least likely to flee in response to presentation of a moving stimulus. Any effects of isolation on subsequent performance in the shelter-field test should, therefore, be most evident in animals reared in constantly illuminated open-cages.

Methods

Subjects were 58 gerbils selected from 29 litters. Twenty-four animals, randomly selected from 12 litters, were reared in open-cages in a constantly illuminated colony room and 34 animals from 17 litters were reared in open-cages in the constantly illuminated isolation enclosure described below.

The isolation enclosure was constructed of wood with fluorescent lighting fixtures mounted on its cover, and was subdivided internally by wooden partitions so as to contain four individual visually isolated cages. Ventilation was provided by an externally mounted exhaust fan.

Procedure. General maintenance, rearing and testing procedures were identical to those described in experiment 1, except that isolation-reared subjects were left totally undisturbed until they were marked for identification 27 days after median eye-opening (eye-opening was observed through peepholes in the top of the isolation-enclosure) and when they were removed from the isolation-enclosure for testing in the shelter-field.

Twelve animals in each group (isolation- and non-isolation-reared) were used as control subjects in the shelter-field test, and the remainder as experimental subjects. Testing in the shelter-field enclosure was conducted as in previous experiments, except that the visual stimulus was presented for 15 s rather than 30 s.

Results

As was mentioned in the introduction to the present experiment, subjects reared in constant-light in open-cages were selected for isolation-rearing because pilot observations had indicated that subjects reared in constant-light tended to show little response to stimulus presentation during the shelter-field post-test. Comparison of the post-test performance of non-isolation-reared experimental subjects with that of non-isolation-reared control subjects, presented in Table X revealed, as expected, that stimulus presentation did not significantly affect the behaviour of experimental subjects during the post-test period on any measure (Mann-Whitney *U*-tests, all *P*'s > 0.05).

Comparison of the data describing isolation-reared experimental and control subjects' post-test behaviour, also presented in Table X, revealed only small modifications in behaviour as a result of stimulus presentation. There was a significant increase in the experimental group's latency to emerge from shelter (Mann-Whitney *U*-test, transformed *z* score = 1.96, *P* = 0.05), but no significant effect of stimulus presentation on latency to reach shelter, or on total time spent in shelter (Mann-Whitney *U*-test, both *P*'s > 0.05).

Comparison of the post-test behaviour of isolation and non-isolation reared experimental subjects (Table X) revealed little effect of isolation-rearing on post-test behaviour. Isolation-rearing produced a significant increase in median latency to emerge from shelter (Mann-Whitney *U*-test, transformed *z* score = 2.12, *P* < 0.05), but no significant effect on latency to reach shelter or total time spent in concealment (Mann-Whitney *U*-test, both *P*'s > 0.05).

Analysis of the data obtained from fleeing subjects, presented in Table XI, revealed similarly that rearing in isolation had no significant effect on the percentage of experimental animals fleeing to shelter (Fisher's Exact Probability test, *P* = 0.52), or on total time spent in concealment (Mann-Whitney *U*-test, *U* = 5, *P* > 0.05) but did significantly increase latency to emerge

from shelter (Mann-Whitney U -test, $U = 0$, $P < 0.05$).

In general, the data reviewed thus far would seem to indicate that isolation-rearing acted to increase responsiveness to stimulus presentation, but not sufficiently to account for differences in behaviour observed in previous experiments between subjects reared in environments that either did or did not provide shelter. There were, in addition, two anomalous findings in the data from the present experiment that further reduce the likelihood that the relative isolation of subjects reared with shelter available was responsible for their increased responsiveness to stimulus presentation.

First, analysis of the pre-test behaviour of isolated, as compared with non-isolated, subjects revealed that isolation-reared subjects spent significantly more of the pre-test period in concealment than did non-isolation-reared subjects ($F = 8.15$, $df = 2/57$, $P < 0.01$). Second, comparison of the post-test behaviour of isolation- and non-isolation-reared control groups (Table X) revealed a significant increase in total time spent in concealment (Mann-Whitney U -test, $U = 35$, $P < 0.02$) on the part of the isolation-reared control group. Therefore, isolation-rearing produced changes in behaviour in the absence of stimulus presentation, while rearing in environments providing shelter did not do so.

Discussion

These findings suggest that the mechanism underlying differences in the responsiveness of isolated and non-isolated experimental subjects in the post-test period may be different from that responsible for differences in the responsiveness of open-reared and shelter-reared experimental animals discussed in experiment 2. In particular, the increase in concealment behaviour exhibited by isolation-reared subjects in response to stimulus presentation appears to be mediated by changes in exploratory behaviour in the shelter-field enclosure. Whereas the increased concealment behaviour of shelter-reared subjects does not. It therefore would seem reasonable to conclude that, although isolation-rearing can change responsiveness in the shelter-field test, rearing in relative isolation is not, in fact, responsible for the differences in the behaviour observed in the shelter- and open-reared subjects of experiment 2.

Experiment 6

In previous experiments data have been presented indicating that differences in the post-test performance of tunnel- and open-reared subjects are not the result of rearing in darkness or rearing in relative isolation from extra-cage stimulation. It remains possible, however, that the experience of moving into an enclosed area from an exposed one is sufficient in itself to potentiate response to

Table X. Post-test Performance of Experimental and Control Groups in Experiment 5

Group	Rearing condition	Median latency to reach shelter (s)	Median latency to first emerge from shelter (s)	Median total time spent in shelter (s)
Experimental	Isolation ($N = 22$)	9.5	38.5	58.5
	Non-isolation ($N = 12$)	11.0	7.5	35.0
Control	Isolation ($N = 12$)	11.0	9.0	42.0
	Non-isolation ($N = 12$)	7.5	4.5	27.5

Table XI. Post-test Performance of Isolated and Non-isolated Subjects Fleeing to Presentation of the Test Stimulus

Rearing condition	Flight		Concealment		Foot-thumping (per cent)
	Per cent entry < 3 (s)	Median latency to reach shelter (s)	Median latency to first emerge from shelter (s)	Median total time spent in shelter (s)	
Isolation ($N = 22$)	40.9	1.0	66.0	81.0	00.0
Non-isolation ($N = 12$)	33.3	2.0	24.5	62.0	00.0

stimulus presentation in the shelter-field test. If such experience be sufficient for the development of flight and concealment behaviour, then it is possible that even a brief exposure to an environment providing the opportunity for flight to shelter would be adequate to potentiate flight and concealment during the post-test period. In the present experiment, open-reared subjects were placed in a gerbil-constructed tunnel system for 24 hr prior to testing in the shelter-field enclosure to examine the effects of a brief experience with an area providing an opportunity for concealment on post-test performance.

Method

Subjects were 72 gerbil pups, 18 of which were randomly selected from six litters reared in tunnel-systems, and 54 of which were randomly selected from 18 litters reared in open-cages.

Procedure. Rearing, handling and testing procedures for open- and tunnel-reared gerbils were identical to those described in experiment 1 until visual-cliff testing had been completed. One week following visual-cliff testing, appropriately reared subjects were assigned to one of the four experimental or two control groups described below.

Experimental open-undisturbed ($N = 18$) and experimental tunnel-undisturbed ($N = 6$) subjects were left in the environment in which they

had been reared (open-cage or tunnel) for an additional 24 hr before being tested in the shelter-field enclosure. Experimental open-tunnel ($N = 18$) subjects were reared in open-cages and placed in an enclosure containing an uninhabited, gerbil-constructed tunnel system for 24 hr before being tested in the shelter-field enclosure, whereas experimental tunnel-open ($N = 6$) subjects were reared in tunnel systems and placed in an open-cage for 24 hr before shelter-field testing.

All experimental groups received a 15-s presentation of the visual stimulus at the end of the pre-test period in the shelter-field enclosure.

Control open-tunnel ($N = 18$) and control tunnel-open ($N = 6$) subjects were treated identically to their respective experimental groups (i.e. subjects reared in open-cages were given 24-hr experience in a tunnel system and subjects reared in tunnel-systems were given 24-hr experience in open-cages) except that they were not presented with the visual stimulus in the shelter-field enclosure at the beginning of the post-test period.

Results

Experimental open-undisturbed versus experimental open-tunnel. As is clear from examination of Table XII, which presents data describing the post-test behaviour of open-reared groups, placing open-reared subjects in a tunnel system

Table XII. Post-test Performance of the Open-Reared Groups in Experiment 6

Group	Manipulation	Median latency to reach shelter (s)	Median latency to first emerge from shelter (s)	Median total time spent in shelter (s)
Experimental open ($N = 18$)	Placed in tunnel	1.0	72.0	110.5
Experimental open ($N = 18$)	Undisturbed	19.0	11.5	45.0
Control open ($N = 18$)	Placed in tunnel	30.5	7.0	22.0

Table XIII. Post-test Performance of Fleeing Subjects in Open-Reared Groups in Experiment 6

Group	Manipulation	Flight		Concealment		
		Per cent entry < 3 (s)	Median latency to reach shelter (s)	Median latency to first emerge from shelter (s)	Median total time spent in shelter (s)	Foot-thumping (per cent)
Experimental open ($N = 18$)	Placed in tunnel	100.0	1.0	72.0	110.5	50.0
Experimental open ($N = 18$)	Undisturbed	33.3	2.0	42.0	75.0	33.3

for 24 hr prior to shelter-field testing markedly decreased the latency of experimental open-tunnel subjects to reach shelter (Mann-Whitney *U*-test, $U = 37$, $P < 0.002$), and significantly increased both their latency to emerge from shelter (Mann-Whitney *U*-test, $U = 48$, $P < 0.002$) and their total time spent in concealment (Mann-Whitney *U*-test, $U = 51$, $P < 0.002$) in comparison with experimental open-undisturbed subjects.

Examination of Table XIII, which presents data obtained from fleeing subjects only, reveals that placing open-reared subjects in a tunnel environment for 24 hr increased the percentage of open-reared subjects fleeing in response to stimulus presentation ($\chi^2 = 15.1$, $df = 1$, Yates correction, $P < 0.005$), had a marked effect on their latency to emerge from shelter (Mann-Whitney *U*-test, $U = 24$, $P < 0.05$) and on the total time which they spent in shelter (Mann-Whitney *U*-test, $U = 21$, $P < 0.05$).

A One-Way Analysis of Variance (Mendenhall & Ott 1970) of the pre-test data revealed no significant differences in the mean amount of time spent in shelter by the three open-reared groups ($F = 2.89$; $df = 2, 53$; $P > 0.05$).

Experimental tunnel-undisturbed versus experimental tunnel-open. Table XIV presents data from animals left undisturbed in the tunnel and those placed in an open-cage for 24 hr prior to shelter-field testing. As is evident from examination of the table, placing tunnel-reared animals in an open-cage for 24 hr had no observable effect on shelter-field behaviour. No significant differences were found in the number of experimental subjects fleeing from the test stimulus, in latency to emerge from shelter in the post-test period, in total time spent in concealment (Mann-Whitney *U*-tests all P 's

> 0.05) or in the number of subjects foot-thumping (Fisher's Exact Probability test, $P > 0.05$), as a result of the experimental manipulation. There were also no significant differences among pre-test concealment behaviour of the three tunnel-reared groups ($F = 2.41$; $df = 2, 17$; $P > 0.05$).

Discussion

The results of the present experiment indicate that the differences in behaviour between animals reared in open laboratory cages and those reared in tunnel systems could be produced by simply exposing open-reared subjects to a tunnel environment for 24 hr. The 24-hr experience of a tunnel system was sufficient to potentiate the entire behaviour pattern differentiating open-reared from tunnel-reared subjects. This finding has three implications: (1) It strengthens our earlier conclusions that neither rearing in relative darkness nor rearing in isolation from exposure to humans was a necessary condition for potentiating flight and concealment responses in tunnel-reared subjects; (2) it indicates that rearing in open-cages did not produce visual deficits resulting in lack of responsiveness to the visual stimulus presented in the shelter-field test; and (3) it offers support for the hypothesis that the experience of running into concealment was the critical factor in the ontogeny of the behavioural pattern shown by tunnel-reared gerbils in response to visual stimulation.

The finding that the effects of tunnel-rearing were not reversed by 24 hr spent in open-cages suggests that once the flight and concealment responses were established, as the result of experience in the appropriate environment,

Table XIV. Post-test Performance of Tunnel-Reared Groups

Group	Manipulation	Flight		Concealment		
		Per cent entry < 3 (s)	Median latency to reach shelter (s)	Median latency to first emerge from shelter (s)	Median total time spent in shelter (s)	Foot-thumping (per cent)
Experimental tunnel ($N = 6$)	Placed in open cages	100.0	1.0	118.0	118.0	66.7
Experimental tunnel ($N = 6$)	Undisturbed	100.0	1.0	105.0	116.0	50.0
Control tunnel ($N = 6$)	Placed in open cages	00.0	10.5	5.0	35.5	00.0

they were relatively resistant to reversal by experience in a more open environment.

General Discussion

Much of the support for genetic hypotheses of the domestication process has come from experiments failing to find robust effects of rearing environment on the behaviour of either wild or domesticated individuals (Galef 1970; Huck & Price 1975; Price 1970; Smith 1972; Boice 1974; Smith & Connor 1974). However, numerous less formal observations of feral animals and the results of the present experiment suggest that rearing environment may play a major role in the ontogeny of the behaviour characteristic of domesticated animals. Several possible reasons for the difference in outcome of the present and previous studies of the effect of rearing environment on the behaviour of domestic animals suggest themselves.

First, and perhaps least interesting, is the observation that the present experiment was performed using gerbils as subjects, while previous research has centered on the rat and mouse. It is possible that the underlying causes of reactivity are different in different species.

Second, failure to find an effect of one environmental feature on one behaviour pattern, or, for that matter, of a set of environmental features on a set of behaviour patterns does not imply that environmental influences on the development of reactivity are absent. As indicated above, in the present series of experiments, manipulation of only certain aspects of the early rearing environment were sufficient to influence reactivity in the test situation used. Furthermore, changes in behaviour as a function of rearing environment were not observable in other test situations. For example, in pilot experiments preceding the present series of studies, we found no difference in the locomotion, defecation, or wall-seeking scores of tunnel- and open-reared gerbils in the open-field, but the former animals were very difficult to capture and vocalized and bit the experimenter when held, while the latter were docile and tame. Similarly, wild and domesticated strains of rat (*R. norvegicus*) do not differ in open-field performance as measured by defecation and locomotion (Farris & Yeakel 1945; Broadhurst 1958), although all workers familiar with both strains would agree that there are considerable differences in their reactivity or responsiveness (Galef 1970). Therefore, there is some reason to question the adequacy of one of the most

frequently employed dependent variables in studies of domestication.

Third, subjects in several earlier studies of the effects of environment on reactivity have been exposed to environmental manipulation only after weaning had occurred. There is, however, reason to believe that organisms may be susceptible to environmental variables only during a restricted period in ontogeny (Smith 1966; Denenberg 1972; but see Daly 1973). Informal observations in the present series of experiments indicated that the sensitivity of gerbils to exposure to a tunnel system varied as a function of age. For example, the 36 pairs of mature males and females which constructed tunnels in which to rear their litters never became difficult to capture or handle in spite of extensive exposure to life in a tunnel system, while their young were very difficult to seize and hold. Although additional work is needed to specify the period during which such experience is maximally effective, there appear to be important interactions between the age of a subject and its susceptibility to experience.

Fourth, the finding in the present experiment of the sufficiency of a brief exposure to the appropriate environment to potentiate the reactivity pattern, and the relative irreversibility of the pattern once established, suggests that considerable care must be taken in order to deprive organisms capable of exhibiting high reactivity from the experiences necessary to potentiate such behaviour.

In conclusion, we would suggest that although there is considerable evidence that the relative docility and tameness of domesticated individuals may result from differences in the gene pool of domesticated as compared with wild strains, it may be premature to assume that behavioural features characteristic of domesticated strains are expressed independent of the rearing environment. The results of the present investigation indicate that aspects of individual experience consequent upon conditions of rearing in captivity may be, in some measure, responsible for the tameness and docility of domesticated strains.

It is possible that the process of domestication is not, in fact, unitary but can result from either of two mechanisms or their interaction. Both alterations in genetic substrate and reduction in responsiveness to stimulation resulting from rearing in captivity may be necessary to produce the tameness and docility characteristic of domesticated strains. On the basis of the

evidence currently available, it seems reasonable to hypothesize that domesticated strains may have been selected to respond to rearing in certain man-made environments by exhibiting characteristic low levels of responsivity to stimulation, while wild strains remain relatively resistant to environmental manipulation of responsiveness. In the case of the Mongolian gerbil, an adequate test of this hypothesis must be deferred until such time as wild members of the species are available for study.

Acknowledgments

This research was supported by Grant APA307 of the National Research Council of Canada to the second author. The report represents a portion of a dissertation submitted to the Faculty of Science of McMaster University in partial fulfilment of the requirements for the Ph.D. degree. The authors are indebted to Dr A. H. Black, Dr M. Daly, Dr D. M. Davies, Dr J. Hogan, Dr H. M. Jenkins, Dr M. Leon and Dr S. Siegel for their helpful comments and criticisms and to C. S. Day, D. Kuch and S. Nord for their technical assistance.

REFERENCES

- Allen, G. M. (1940). The mammals of China and Mongolia, Part 2. In: *Natural History of Central Asia* (Ed. by W. Granger), pp. 781-785. New York: American Museum of Natural History.
- Anderson, E. E. (1938). The interrelationships of drives in the male albino rat. III. Intercorrelations among measures of emotional, sexual and exploratory behavior. *J. genet. Psychol.*, **53**, 335-352.
- Barnett, S. A. (1958). Experiments on 'neophobia' in wild and laboratory rats. *Br. J. Psychol.*, **49**, 195-201.
- Beck, A. M. (1973). *The Ecology of Stray Dogs: A Study of Free Ranging Urban Animals*. Baltimore: York Press.
- Berry, R. J. (1969). The genetical implications of domestication in animals. In: *The Domestication and Exploitation of Plants and Animals* (Ed. by P. J. Ucko & G. W. Dimbleby), pp. 207-217. Chicago: Aldine.
- Boice, R. (1974). A test for degeneracy in laboratory rats: Indoor and outdoor burrowing by wild and domestic Norway rats. Paper presented at The Psychonomic Society, 15th annual meeting, Boston, Massachusetts.
- Broadhurst, P. L. (1958). Determinants of emotionality in the rat. III. Strain differences. *J. comp. physiol. Psychol.*, **51**, 55-59.
- Castle, W. E. (1947). The domestication of the rat. *Proc. natn. Acad. Sci. U.S.A.*, **33**, 109-117.
- Clark, M. M. (1974). The effects of the physical environment during maturation on subsequent reactivity to visual stimulation in Mongolian gerbils (*Meriones unguiculatus*). Ph.D. thesis, McMaster University.
- Connor, J. (1971). An experimental analysis of the domestication process in mice (*Mus musculus* L.). Dissertation Abstracts, 32, No. 3025-B.
- Crowcroft, P. (1960). *Mice All Over*. London: Foulis & Co. Ltd.
- Daly, M. (1971). Behavioural development, early experience and maternal behaviour in Golden hamsters (*Mesocricetus auratus*). Ph.D. thesis, University of Toronto.
- Daly, M. (1973). Early stimulation of rodents: A critical review of present interpretations. *Br. J. Psychol.*, **64**, 435-460.
- Darwin, C. (1868). *The Variation of Animals and Plants under Domestication*. Vol. 1 and 2. London: John Murray.
- Denenberg, V. H. (1972). *Readings in the Development of Behavior*. Stamford, Conn.: Sinauer.
- Donaldson, H. H. (1912). The history and zoological position of the albino rat. *J. Acad. Nat. Sci. Phil.*, **15**, 365-369.
- Doyle, G. A. & Yule, E. P. (1959). Grooming activities and freezing behaviour in relation to emotionality in albino rats. *Anim. Behav.*, **7**, 18-22.
- Farris, E. J. & Yeakel, E. H. (1945). Emotional behavior of gray Norway and Wistar albino rats. *J. comp. physiol. Psychol.*, **38**, 109-118.
- Fentress, J. C. (1968a). Interrupted ongoing behaviour in two species of vole (*Microtus agrestis* and *Clethrionomys britannicus*). I. Response as a function of preceding activity and the context of an apparently 'irrelevant' motor pattern. *Anim. Behav.*, **16**, 135-153.
- Fentress, J. C. (1968b). Interrupted ongoing behaviour in two species of vole (*Microtus agrestis* and *Clethrionomys britannicus*). II. Extended analysis of motivational variables underlying fleeing and grooming behaviour. *Anim. Behav.*, **16**, 154-167.
- Freedman, D. G., King, J. A. & Elliot, O. (1961). Critical period in the social development of dogs. *Science, N.Y.*, **133**, 1016-1017.
- Friedman, H. (1964). Taming of the Virginia opossum. *Nature, Lond.*, **210**, 323-324.
- Galef, B. G., Jr (1970). Aggression and timidity: Responses to novelty in feral Norway rats. *J. comp. physiol. Psychol.*, **70**, 370-381.
- Ganz, L. & Fitch, M. (1968). The effect of visual deprivation on perceptual behavior. *Exp. Neurol.*, **22**, 638-660.
- Gibson, E. J., Walk, R. D. & Tighe, T. J. (1959). Enhancement and deprivation of visual stimulation during rearing as factors in visual discrimination learning. *J. comp. physiol. Psychol.*, **52**, 74-81.
- Hafez, E. S. E. (1962). *The Behaviour of Domestic Animals*. Baltimore: Williams & Wilkins.
- Hale, E. B. (1962). Domestication and the evolution of behaviour. In: *The Behaviour of Domestic Animals* (Ed. by E. S. E. Hafez), pp. 21-53. Baltimore: Williams & Wilkins.
- Henderson, N. D. (1963). Methodological problems in measuring ambulation in the open field. *Psychol. Rep.*, **13**, 907-912.
- Henderson, N. D. (1967). Early shock effects in the BALB/C mouse. *J. comp. physiol. Psychol.*, **64**, 168-176.
- Henderson, N. D. (1970). Genetic influences on the behavior of mice can be obscured by laboratory rearing. *J. comp. physiol. Psychol.*, **72**, 505-511.

- Huck, U. W. & Price, E. O. (1975). Differential effects of environmental enrichment on the open-field behavior of wild and domestic Norway rats. *J. comp. physiol. Psychol.*, **89**, 892-898.
- Hughes, C. W. & Boice, R. (1973). Domestication sophistication and avoidance in Norway rats. *J. comp. physiol. Psychol.*, **84**, 408-413.
- King, D. A. (1969). The effect of early experience and litter on some weight and maturational variables. *Develop. Psychol.*, **1**, 576-584.
- King, H. D. & Donaldson, H. H. (1929). Life processes and size of the body and organs of the gray Norway rat during ten generations in captivity. *Am. Anat. Mem.*, No. 14.
- Kirmiz, J. P. (1962). *Adaptation to Desert Environment*. London: Butterworths.
- Konrad, K. W. & Bagshaw, M. (1970). Effects of novel stimuli on cats reared in a restricted environment. *J. comp. physiol. Psychol.*, **70**, 157-164.
- Lockard, R. B. (1968). The albino rat: A defensible choice or a bad habit. *Am. Psychol.*, **23**, 734-742.
- Lore, R. & Sawatski, D. (1969). Performance of binocular and monocular infant rats on the visual cliff. *J. comp. physiol. Psychol.*, **67**, 177-181.
- Mayr, E. (1974). Behavior programs and evolutionary strategies. *Am. Scient.*, **62**, 650-659.
- Mendenhall, W. & Ott, L. (1970). *Understanding Statistics*. Belmont, Cal.: Duxberry Press.
- Minckler, J. & Pease, F. D. (1938). A colony of albino rats existing under feral conditions. *Science, N.Y.*, **87**, 460-461.
- Moore, C. B. (1954). *The Book of Wild Pets*. Boston, Mass.: Charles T. Branford.
- Oortmerseen G. A. van (1971). Biological significance, genetics and evolutionary origin of variability in behaviour within and between inbred strains of mice (*Mus musculus*). *Behaviour*, **38**, 1-92.
- Price, E. O. (1970). Differential reactivity of wild and semi-domestic deer mice (*Peromyscus maniculatus*). *Anim. Behav.*, **18**, 747-752.
- Price, E. O. (1973). Some behavioral differences between wild and domestic Norway rats: Gnawing and platform jumping. *Anim. Learn. Behav.*, **1**, 312-316.
- Price, E. O. & King, J. A. (1968). Domestication and adaptation. In: *Adaptation of Domestic Animals* (Ed. by E. S. E. Hafez), pp. 34-45. Philadelphia: Lea & Febiger.
- Randall, R. E. (1973). The rabbit and the feral cat in the Monach Isles or Heisker National Nature Reserve. *Glasg. Nat.*, **19**, 13-16.
- Rich, S. T. (1968). The Mongolian gerbil (*Meriones unguiculatus*) in research. *Lab. Anim. Care*, **18**, 235-243.
- Richter, C. P. (1954). The effects of domestication and selection on the behavior of the Norway rat. *J. nat. Cancer Inst.*, **15**, 727-738.
- Riesen, A. H. (1966). Sensory deprivation. In: *Progress in Physiological Psychology* (Ed. by E. Stellar & J. M. Sprague), pp. 117-147. New York: Academic Press.
- Rosenblum, L. A. & Cross, H. A. (1963). Performance of neonatal monkeys in the visual cliff situation. *Am. J. Psychol.*, **76**, 318-320.
- Routtenberg, A. & Gluckman, S. E. (1964). Visual cliff behavior in albino and hooded rats. *J. comp. physiol. Psychol.*, **58**, 140-142.
- Routtenberg, A. & Kramis, R. C. (1967). 'Foot-stomping' in the gerbil: Rewarding brain stimulation, sexual behaviour and footshock. *Nature, Lond.*, **214**, 173-174.
- Schwentker, V. (1961). The gerbil, a new laboratory animal. *Illinois Vet.*, **5**, 5-9.
- Scott, J. P. & Fuller, J. L. (1965). *Dog Behavior: the Genetic Basis*. Chicago: University of Chicago Press.
- Scott, M. D. & Causey, K. (1973). Ecology of feral dogs in Alabama. *J. Wildl. Mgmt.*, **37**, 253-256.
- Smith, N. (1966). Adaptations to cliff-nesting in some Arctic gulls (*Larus*). *Ibis*, **108**, 68-83.
- Smith, R. H. (1972). Wildness and domestication in *Mus musculus*: A behavioral analysis. *J. comp. physiol. Psychol.*, **79**, 22-29.
- Smith, R. H. & Connor, J. L. (1974). The inheritance of behavioral wildness in house mice (*Mus musculus* L.). *Anim. Learn. Behav.*, **2**, 249-258.
- Spatz, C. & Granger, W. R. (1970). Foot-thumping in the gerbil: The effect of establishing a home cage. *Psychon. Sci.*, **19**, 53-54.
- Spurway, H. (1955). The causes of domestication: An attempt to integrate some ideas of Konrad Lorenz with evolution theory. *J. Genet.*, **53**, 325-362.
- Stone, C. P. (1932). Wildness and savageness in rats of different strains. In: *Studies in the Dynamics of Behavior* (Ed. by K. S. Lashley), pp. 3-55. Chicago: University of Chicago Press.
- Thiessen, D. D. (1973). Footholds for survival. *Am. Sci.*, **61**, 346-351.
- Thiessen, D. D., Lindzey, G., Blum, S., Tucker, A. & Friend, H. C. (1968). Visual behavior of the Mongolian gerbil (*Meriones unguiculatus*). *Psychon. Sci.*, **11**, 23-24.
- Walk, R. D. & Gibson, E. J. (1961). A comparative and analytical study of visual depth perception. *Psychol. Monogr.*, **75**, 1-44, No. 519.
- Won, P. H. (1961). *Studies on the Ecological Observation of Rodentia in Manchuria and Korea*. Seoul, Korea: Zoological Institute, Dong Kook University. Part II, 140-160.
- Woolpy, J. H. & Ginsberg, B. E. (1967). Wolf socialization: A study of temperament in a wild social species. *Am. Zool.*, **7**, 357-363.

(Received 17 March 1975; revised 5 August 1975;
MS. number: A1687)