ABSTRACT

BEHAVIORAL CHANGES IN THE DEERMOUSE, *PEROMYSCUS MANICULATUS BAIRDII*, AFTER SEVENTEEN YEARS OF DOMESTICATION: REACTION TO NOVEL STIMULI

by Edward O. Price

Body of Abstract

AN ABSTRACT OF A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1967

It was hypothesized that following seventeen years of laboratory breeding, a semi-domestic stock of deermice (Peromyscus maniculatus bairdii) would show decreased reactivity (sensitivity, responsivity) to novel or unfamiliar stimuli. Genetic modifications, resulting from the change in selection pressures accompanying the transition from nature to captivity, were postulated as the determinants of this change in behavior. A total of 360 subjects, including the semi-domestic stock and offspring of a representative sampling of wild-caught animals, were used in testing the behavioral responses to several selected novel situations. A first test measured the tendency to enter an unfamiliar arena (open-field) and approach a caged predator and a second test measured the effect of being placed in an unfamiliar environment (activity wheel) on body weight, food consumption and activity. This latter test was expanded to study the effect of total water deprivation on the body weight, food consumption, activity and survival time of the two strains. To determine the effect of early environmental experience upon reactivity to novel situations, young mice were reared by mothers of the opposite strain (maternal influence) or were reared in a semi-natural outdoor enclosure in contrast

to the laboratory (place of rearing influence).

The results indicated that the semi-domestic strain differed from the wild strain: (1) in its significantly shorter latencies to approach and investigate both the open field and the predator, (2) in its faster habituation to the open field and (3) in its unaltered food consumption when placed in unfamiliar living quarters.

The behavior of the wild strain tended to be consistent whether reared in the laboratory or in the outdoor enclosure. On the other hand, the behavior of the semi-domestic strain could be modified by experience. Given experience in the semi-natural environment of the species, the semi-domestic strain displayed "wild type" responses to novel stimuli.

Fostering wild offspring on semi-domestic females and vice versa had no effect on the behavior of either strain.

Total water deprivation produced no differential strain effect on body weight loss, food consumption, activity or survival. Enclosure-reared subjects and a control group for handling and isolation showed greater tolerance to water deprivation than mice reared in the laboratory by their own mothers.

It was postulated that the decreased reactivity of the semi-domestic strain to novel situations is a result of: (1) a relaxation of natural selection (present in nature), (2) decreased reproductive success among highly reactive animals and, (3) unconscious artificial selection by man. The genetic changes resulting from these selection phenomena may have favored an upward shift in the response threshold for reactivity to novel stimuli. Its modifiability following domestication may be due to a broadening of the range of environmental influence (decreased genetic control).

BEHAVIORAL CHANGES IN THE DEERMOUSE, *PEROMYSCUS MANICULATUS BAIRDII*, AFTER SEVENTEEN YEARS OF DOMESTICATION: REACTION TO NOVEL STIMULI

By

Edward O. Price

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1967

ACKNOWLEDGMENTS

Special thanks go to my major advisor, Dr. John King, whose encouragement and interest, critical evaluations and careful editing of this manuscript gave added impetus to my research endeavors. Appreciation is also expressed to Doctors Rollin Baker, Walter Blinn, William Cooper, and the late Phillip Clark, for their advice and interest in my degree program, and their careful editing of the following manuscript. Likewise, the contributions and encouragement of my wife, Mabell, and Mrs. B. Henderson were among my greatest assets. Lastly, the assistance and criticisms of my fellow graduate students in the Biology Research Center were of great value to me in my research program.

TABLE OF CONTENTS

TABLE OF CONTENTS
(Continued)

LIST OF TABLES

LIST OF TABLES
(Continued)

LIST OF TABLES
(Continued)

LIST OF TABLES
(Continued)

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS
(Continued)

INTRODUCTION

A shift in selective pressures accompanies the transition from nature to captivity resulting in profound modifications of the species gene pool during the domestication process (Darwin, 1875; Spurway, 1955; Lerner, 1958; Muntzing, 1959; and Hale, 1962). Climate, predation, food and water availability, for example, are no longer critical for survival, but psychological factors associated with a reduction in the quantity and quality of space, forced social groupings and human interference may determine fitness. This shift in selection pressures will, in time, result in genotypic and phenotypic modifications of many significant biological and psychological factors.

Whereas captive wild animals may acquire behavior patterns (Hediger, 1954), the process of domestication is an active evolutionary process (Lerner, 1958; Hale, 1962). The genetic changes accompanying domestication result, in part, from the interplay of three selective phenomena: (1) the relaxation of natural selection, (2) "natural

selection" in the laboratory (Lerner, 1958), and (3) artificial selection by man (Price & King, 1967). Genetic drift, the random loss or fixation of genes in small populations, and inbreeding may also influence the composition of the gene pool of captive populations.

Lerner (1958) points out that the term "natural selection" implies that certain genotypes leave more reproducing offspring than others. In contrast to artificial selection, its effects can only be measured "ex post facto." Natural selection does not purposefully bring about differences between individuals in their capacity to leave progeny but merely denotes this end result. On the other hand, artificial selection is a purposeful process. It can be the direct cause of differences between individuals in regard to their capacity to leave offspring when the criteria for "fitness" are determined by man.

Although artificial selection is excluded by definition from nature,natural selection almost always occurs in the captive environment along with artificial selection. Breeders may be chosen from a captive population solely for some morphological, physiological or behavioral characteristic; however, some of these selected individuals may be sterile or some may cannibalize their young. Others will

be culled out by disease and leave no progeny. Natural selection usually accompanies artificial selection and only when the fitness of the selected breeders does not vary can it be said that pure artificial selection has occurred.

Under artificial selection man's demands may be capricious and arbitrary and selection for a certain character may cause a reduction in fitness. Selection for the Rex hair color in rabbits has resulted in certain metabolic and endocrinic disturbances, increasing mortality and susceptibility to specific diseases (Muntzing, 1959). While selective advantage under artificial selection may be determined by the presence or absence of a certain visible or measurable phenotypic characteristic, under natural selection the totality of all phenotypic expressions determine selective advantage with subtle differences at the biochemical or physiological level often playing major roles.

Although the phenotypic changes in many of our common domestic animals have been well documented (Zeuner, 1963) little is known about the relative speed at which the domestication process works and what modifications are first seen in the animals involved. In one notable exception,

King (1939) reared over 25 generations of Norway rats in captivity to observe changes in morphology and reproduction. However, no systematic attempt was made to study behavior.

In studying the domestication process from an evolutionary standpoint, it is necessary to isolate the genetic and acquired components of the factors measured. All behaviors involve both genetic and experiential factors to some degree but by keeping the environment constant for all groups studied one can learn much about the influence of genetic factors. It is difficult to obtain a constant environment, particularly when social interactions are involved. For instance, the young of a captive wild-caught female may not receive the same maternal care as the young of a female (same species) which is many generations removed from the wild. The drastic change in the environment of the wild-caught female may affect her treatment of young. The semi-domestic female, coming from stock well adapted to conditions in captivity, may treat her offspring differently.

Genetic and experiential factors are also confounded when two populations behave similarly in one environment but differently in another. Animals born to wild-caught parents may behave the same regardless of the physical environment in which they were raised, whereas a domestic animal reared in nature might display extremely abnormal

behavior. Thus, the potentialities of a given population may not be completely tapped in any one environment. In the first case the behavior is relatively "fixed;" in the second, the behavior can be modified by experience.

One approach to the study of domestication is to record changes in a population of animals over successive generations in captivity (King, 1939). The other approach is to compare a long-captive strain with a group representing their wild ancestors (assuming living ancestors are not available). The present study used the latter approach by comparing the offspring of wild-caught Peromyscus manicula-tus bairdii with a semi-domestic stock approximately 20-25 generations and 17 years removed from the wild (Harris, 1952). It was hypothesized that this many generations of breeding in captivity coupled with the drastic shift in selection pressures has resulted in sufficient genetic change in the semi-domestic strain to modify their behavior.

Although all behavior may undergo some modification during domestication, the reaction to a strange or novel stimulus has been thoroughly investigated (Farris and Yaekal, 1945; Richter, 1953; Barnett, 1956 and 1958; Welker and King, 1962; Chitty and Shorten, 1946; Thompson, 1948 and 1953; and Chitty, 1954). Most investigations have

concluded (see Lit. Review) that domesticated varieties of rats and mice tend to investigate new or unfamiliar stimuli, whereas wild forms show a pronounced tendency to avoid novel stimuli (exhibit "neophobia") in a familiar environment.

The display of "neophobia" by wild animals in nature presumably has some significance. Obviously, total avoidance or total attraction to all novel stimuli would be maladaptive. Although acute "neophobia" would be advantageous in avoiding predation, it could be disadvantageous in locating mates, food or nesting sites. One can surmise that the greatest fitness will be ascribable to those individuals which regularly avoid potentially detrimental stimuli and approach stimuli favorable to their survival.

The present study is concerned with the reaction of deermice to unfamiliar stimuli. The reaction of animals to novel stimuli has been discussed in terms of sensitivity, attentiveness, emotionality, "neophobia," responsivity and a host of other behaviors and abstractions (see Lit. Review). These characteristics cannot be measured directly and must be described operationally. Broadhurst (1960) has used the term "reactivity" to describe the so-called "emotional" behaviors of rats. "Reactive" rats exhibited

decreased ambulation and increased fecal depositions in response to being placed in an unfamiliar environment. "Non-reactive" animals were less affected by changes in their environment and, thus, showed greater ambulation (investigatory behavior was not suppressed) and fewer fecal boluses per unit time. In the present study, "reactivity" is measured by such variables as the latency to enter, activity within, and habituation to an unfamiliar arena (open-field) and natural predator. In addition, the reactivity to being placed in a novel living environment (activity wheel) with no opportunity for escape is measured by changes in body weight, food consumption and activity. A reactive mouse will exhibit: long latencies, low activity, slow habituation, loss in body weight, and decreased food consumption. Thus, the non committal terms "reactive," "non-reactive" and "reactivity" will be used to describe the animals' response to novel stimuli in terms of the previously defined dependent variables.

One may postulate that a certain degree of reactivity to novel stimuli is selected for in nature. High reactivity could retard the ability to adapt to a changing environment. On the other hand, weak reactivity could increase the animal's vulnerability to predators, poisons, traps, etc. Each novel stimulus encountered, then, must

elicit both elements of approach and withdrawal (Schneirla, 1965). Certain stimuli such as the odor of a predator may elicit a strong degree of withdrawal or avoidance while other stimuli may be more neutral or positive (approach) in character (Sund, 1958; Roeder, 1963; Martin and Melvin, 1964). The experience gained at the initial encounter with a novel stimulus will influence the reaction to this stimulus on subsequent encounters. Therefore, by reinforcement of the approach or withdrawal responses (or habituation, as the case may dictate) an animal learns to respond appropriately.

In the laboratory, however, animals are seldom exposed to novel situations and even when provided, they usually have little or no survival value. Consequently, a relaxation of natural selection for reactivity to novel stimuli can be predicted during domestication (assuming that selection for this behavior occurs in nature).

Several behavioral characteristics are either directly or indirectly concerned with the reaction of an animal to novel stimuli: (1) reactivity to stimuli, including arousal levels and response thresholds, (2) physical capacity to perceive stimuli in the environment, (3) intensity of the exploratory or investigatory drive, and (4) general

activity. Of these four characteristics reactivity to novel stimuli would be most likely to be affected by "natural" and/or artificial selection in the laboratory, through decreased reproductive success of the more reactive individuals. The three other characteristics are more predisposed to change by the relaxation of natural selection present in the wild.

In the present study an attempt will be made to demonstrate the extent to which a semi-domestic stock has diverged from a wild strain in its reaction to novel stimuli. Two distinct test situations have been designed to measure this reaction: (1) the tendency to approach a novel stimulus when given a choice, and (2) the reaction to an unfamiliar living environment forced upon the animal.

The open-field apparatus is well suited to study this first reaction (Hall, 1934). An open-field is an enclosed (and in this case, unfamiliar) arena designed to test reactivity by an animal's defecation, activity and latency to enter responses. Since Peromyscus rarely defecates in an open-field the two primary dependent variables in this test were propensity to enter the open-field and activity therein. Reaction to the open-field, both initially and following 48 hours habituation, comprised the first

phase of the open-field tests. In the second phase both the initial and habituated reaction to a caged predator (least weasel) within the open-field was measured. The tests following habituation to the open-field and predator were administered to determine if the strains differ in latency to approach stimuli after equal opportunity to habituate to them.

In the second test the reaction to a novel living environment was measured by placing the mice in activity wheels and obtaining daily measures of body weight, food consumption and activity. Whereas, in the open-field test the animal was given the choice of either investigating the novel stimulus or remaining in a "safe" area, in this test the animal is placed within a strange environment with no means of escape.

In addition, the mice were totally deprived of water following the first five days in the activity wheel, in order to study strain differences in reaction to severe physiological stress. The rates of change in body weight, food consumption and activity were measured in addition to survival time in days.

Since the degree of reactivity to novel stimuli is relatively unimportant for survival in captivity and

reproductive success in a strange environment is enhanced by low reactivity, it was hypothesized that a strain of deermice bred in the laboratory for 17 years (approximately 20-25 generations) would be less reactive to unfamiliar stimuli than wild counterparts. Non-reactivity would favor decreased inhibition (disinhibition) of the investigatory response while reactive subjects would display stronger withdrawal responses and greater caution in approaching and investigating a novel stimulus. The tendency to approach and investigate an unfamiliar arena (open-field) was studied. When compared with wild deermice, the semi-domestic subjects were expected to exhibit the following: (1) a greater percentage of individuals entering the open-field during the two-minute test period; (2) shorter latencies to enter the open field; (3) greater investigatory activity within the open-field; (4) greater total time in the open-field during the two-minute test trial; and (5) fewer retreats to the start box per unit time in the open-field.

It was reasoned that once familiarization had occurred, withdrawal responses associated with a new environment would be extinguished. The following question was raised, "Would the two strains show a similar tendency to enter and investigate a relatively new environment once adequate

opportunity for habituation had been provided?" To answer the question, it was hypothesized that following 48 hours habituation, the more reactive wild strain would not differ from the semi-domestic subjects in regard to: (1) percentage of subjects entering the open-field; (2) latency to enter the open-field; (3) activity therein; (4) total time in the open-field during the two-minute test period; and (5) retreats to the start box per unit time in the open-field.

The reactivity of wild animals to novel physical stimuli is probably not as critical for survival as their reactivity to certain biological stimuli such as conspecifics and predators. Consequently, the response to a natural predator was measured following habituation to the open-field. The hypotheses tested were identical to those postulated for the initial reaction to the open-field

When forced to occupy an unfamiliar living environment the natural balance of approach-withdrawal tendencies is initially disrupted by the inability to show withdrawal. This conflict is often reflected in physiological mechanisms associated with appetite or hunger (see Lit. Review).

This conflict is reduced for non-reactive individuals and psychological distrubance in response to the above

treatment is minimal. It was postulated that the reactivity of the semi-domestic strain had become so reduced during domestication that only minimal stress was experienced when placed in an unfamiliar environment. More specifically, an initial drop in food consumption was predicted for the wild strain whereas no change in feeding behavior was expected for the semi-domestic subjects. Body weight was predicted to follow the same trend as food consumption.

Consideration was given to the fact that strain differential changes in food consumption and body weight could merely reflect differential changes in general activity. Running time in the activity wheels was measured. Since strain differences in regard to food consumption and body weight were believed due to genetic changes during domestication, no strain differential activity response was predicted.

Total water deprivation was administered to determine the extent to which the semi-domestic mice had diverged from their wild counterparts in response to severe physiological stress. Since a drop in food consumption and body weight was assured (see Lit. Review), attention was directed to the rate of decrease.

Although wild animals are seldom confronted with

total water deprivation, periods of severe drought are common in nature. Natural selection has favored those individuals best adapted for survival under minimal water rations. On the other hand, water had been readily available to the semi-domestic stock during its 17 years in captivity, allowing the relaxation of selection. It was hypothesized that the wild strain would be more tolerant of total water deprivation than the semi-domestic subjects. The wild strain was expected to show a slower rate of decrease in food consumption and body weight and longer survival time. In keeping with the literature, an initial increase in wheel-running time was predicted for both strains. Again, no strain-differential activity response was expected.

The effect of environmental factors on the behaviors tested were assessed by: (1) fostering within and between strains and (2) rearing in the laboratory versus the natural environment. In the present study the offspring of wild-caught individuals were used to represent the genotypically wild strain, since the early experience of the trapped parents was unknown. The importance of maternal care in shaping offspring behavior is a controversial subject at the present time (see Lit. Review). If the experimental

animals were influenced differently by the type of maternal care they received, these effects should be revealed by cross-fostering the offspring of wild-caught females on semi-domestic females and vice versa. Due to discrepancies in the literature and the fact that the major hypothesis points to genetic rather than environmental effects on behavior, no maternal influence was predicted.

A second factor which could affect the behavior of animals during domestication is the place of rearing (in nature versus the laboratory: see Price and King, 1967). If the gene pools of wild and domestic strains differ, wild animals might react differently to laboratory conditions than domestic animals and vice versa in the wild. The limitations imposed by the laboratory on the genetically-determined "wild" behavior of wild animals or their immediate descendents could lead to heightened reactivity to novel stimuli and slower adaptation to unfamiliar situations. The domestic animals, on the other hand, having been under selection for characteristics favorable to captivity should be less affected by laboratory induced restriction on behavior.

Both wild and semi-domestic deermice were given early experience (between 21 and 55 days of age) in a

semi-natural outdoor enclosure to test this variable. Few studies are available which test the place of rearing factor (see Lit. Review). Barnett (1963) notes that albino rats allowed to "run free" become more "savage" and "difficult to handle" than those maintained in close association with man. A laboratory stock of deermice will successfully choose the natural field environment of the species only when given early experience in the wild (Wecker, 1963).

The major hypothesis of this dissertation states that genetic change has reduced the reactivity of the semi-domestic strain to novel stimuli. The questions arise, "Can the level of reactivity be modified by the place of rearing?" and "Is the modification different in the two strains?" Although the modifiability of behavior is under genetic control, an answer of "yes" to only the second question points to strain differences in genotype. An answer of "yes" to either question indicates that reactivity to novel stimuli is not a genetically "fixed" character. For purposes of this study, it is hypothesized that the place of rearing has no influence on the responses studied, that reactivity to novel stimuli is a genetically "fixed" behavior.

LITERATURE REVIEW

The behavior patterns involved in the reaction of an animal to a novel stimulus contain many components considered characteristic of emotional behavior. Thus, a review of the literature in this general area will provide a foundation for subsequent discussion.

Changes in Emotionality

Emotional characteristics and their role in domestication. One character which seems easily disposed to genetic change under domestication is emotionality. The latter is a term used loosely and often synonomously with the term "temperament." The first studies on differences in emotionality between wild rodents and their domestic counterparts (Yerkes, 1913; Coburn, 1922; and Stone, 1932) were concerned with quantitative differences in so-called "wildness," "savageness" and "timidity" in rats and mice as determined by specific tests. Today, emotionality is used (as a convenient wastebasket) to categorize a complex of responses which occur in situations which the

experimenter deems stressful in character. Emotionality, in regard to the behavior of rats and mice, has often been measured operationally by differences in defecation and ambulation (Hall, 1934; Broadhurst, 1958; Denenberg and Whimbey, 1963), avoidance conditioning (Spence and Maher, 1962; Owen, 1963; Tobach and Schneirla, 1962; and Levine and Broadhurst, 1963), latency to approach an unfamiliar area or object (Barnett, 1958; Welker, 1959; Denenberg, Carlson and Stephans, 1962; Joslin, Fletcher and Emlen, 1964) and consummatory behavior following deprivation (Levine, 1957; Lindholm, 1962; Spence and Maher, 1962). The fact that different species or strains may react differently when under stress has tended to confuse our understanding of emotionality and made comparative work very difficult. Despite the pitfalls involved in the use of the term "emotionality," when operationally defined it is probably the best term available.

Keeler and King (1942) reported a rapid change in temperament associated with the genetic system controlling coat color. They state, "the tame albino rat, at least the strain studied, was probably not domesticated by selection over long periods of time, but was modified in behavior principally by the introduction (by mutation) of the black

gene (non-agouti) in which savageness and wildness have been considerably reduced." They also point out that from a survey of 18 stocks of domestic albino rats used in American scientific laboratories today, most have been derived from animals carrying the black gene, the coat color not expressed because of albinism.

In testing the Keeler-King hypothesis of coat-color gene effects on emotionality, Broadhurst (1958) subjected five pure strains of rats to an open-field test for emotional defecation. He failed to find any correlation between coat color and scores in this mildly stressful test. However, it is not certain that the open-field test adequately measures emotionality as it is involved in the domestication process (Tobach and Schneirla, 1962; Bindra and Thompson, 1953; Hunt and Otis, 1953). Another point which Broadhurst (1960) raises is that the Keeler-King hypothesis can only be properly investigated against a homogeneous background of other genetical characteristics, otherwise alternative genetical determinants of the behavioral response studied may mask or exaggerate the effect of the coat-color gene. To test this hypothesis, Broadhurst crossed two strains known to differ with respect to the agouti-nonagouti gene, bred the F_1 and F_2 generations and

observed the effect of the segregating gene among the latter. No coat-color effect was found in the open-field test (Broadhurst, 1960). He concluded, then, that docility in the rat, at least, is probably not due to a major gene effect operating through pleitropy but rather "a linkage effect of perhaps several major genes, probably in association with a polygenic system determining behavioral responses."

Artificial selection for emotional characteristics. Successful selection for emotional and non-emotional albino rats as measured by defecation and ambulation in Hall's open-field test has been obtained by Hall (1951) and Broadhurst (1960). Although selected specifically for maze learning, Tryon's maze bright rats were found to be more emotionally disturbed in non-maze situations and less emotionally disturbed in the maze proper than the maze-dull rats (Tryon, 1942). Not only does successful selection for emotional characters indicate that these traits are at least partially determined by heredity but it also provides an estimate of the differential response of emotional and non-emotional traits to selection pressures. Hall (1951) found that the maximum effects of selection for non-emotionality are realized in the first generation while it

took nine generations for the emotional strain to become stabilized. He also discovered that the hybrid offspring of emotional and non-emotional parents are usually non-emotional in behavior. These two factors led Hall to postulate that the genes for non-emotionality are dominant over those for emotionality. Likewise, Broadhurst found that selection for emotional non-reactivity was faster than selection for emotionally reactive characters. Ten generations of selection resulted in a mean increase of one unit of ambulation in the reactive strain while the non-reactive line showed a mean decrease of 2.29 units. To the extent that defecation and ambulatory scores in the open-field are valid indices of emotionality, the greater responsiveness of non-emotional characters to selection, at least in the rat, and the increasing docility usually accompanying domestication suggests that non-emotionality is a character selected for in captivity. I propose that this reduction in emotionality results principally from a change in selection pressures associated with the transition from the natural environment into captivity.

Natural selection for non-emotionality in the laboratory. It is well known that psychological stress can severely reduce reproductive success (Southwick, 1955;

Jenkins, 1961; Eleftheriou, Bronson & Zarrow, 1962; and Christian and Davis, 1964) by means of pregnancy blockage, greater loss of embryos, smaller litter size and an increase in cannibalism. If wild animals experience some sort of stress when brought into the laboratory one would expect lowered reproductive success (relative to their domestic counterparts) to accompany any attempts at breeding.

The stress experienced by a wild animal in captivity is probably influenced by its general emotionality. To the extent that greater emotionality results in greater stress following this environmental change any reduction in reproductive success in captivity is a result, at least in part, of the emotional characteristics of that species. It follows, then, that probably the less emotional individuals of a species, which are stressed less by captivity, will leave the bulk of the offspring for the wild-caught generation and in essence selection for non-emotionality will have occurred. Furthermore, the greater the stress of confinement the more intense will be selection for non-emotional characteristics. Consequently, in a highly emotional species strong selection for non-emotionality can be expected, particularly among the wild-caught animals

themselves.

The information obtained by King (1939) on changes in reproductive success of the Norway rat over successive generations of laboratory breeding has given credence to the latter hypothesis. Of 20 wild-caught female rats, only six bred in captivity and only one female successfully reared her offspring. The other five breeders either cannibalized or neglected their young. In the second generation the majority of females were fertile and successfully reared their progeny. During the first eight generations sterility in females decreased from 37.3 to 5.9 percent and by the tenth generation sterility and low fertility of females ascribable to the effects of captivity had all but disappeared. Only five of 161 females reared in the tenth to the twelfth generations did not breed and in these cases sterility was caused by diseases of the reproductive organs.

The average number of litters produced by each female during her reproductive life increased from 3.5 litters in the first generation to 10.2 litters in the nineteenth generation. This was partially due to an eight month increase in the average length of the reproductive period by the twenty-fifth generation (also reported by Richter in 1959). In this time, however, litter size had

not changed.

The failure of wild pintail ducks to breed in captivity led Phillips and Tienhoven (1960) to study the gonadal development of ducks caught as young in the wild and of ducks reared from the eggs of wild parents. The arresting of gonadal development in the wild-caught birds was found to be due to a lack of gonadotrophic hormones from the pituitary. This was confirmed by the fact that injections of chicken pituitaries produced normal ovarian development. Furthermore, gonadal development and pituitary gonadotrophin content was greater in birds handreared from eggs of wild parents than in the wild-caught birds, indicating that early behavioral experiences may be involved in the reproductive failure of the captives.

Leopold (1944) found that in captivity the wild turkey is much less tolerant of disturbances than either domestic or hybrid birds. Although the three genotypes did not differ in regard to clutch size, egg fertility or hatching success, the domestic turkey, like the domestic rat and hand-reared pintail duck, is a more precocious breeder than the more emotional wild bird. Wild turkeys seldom breed in their first year while first-year domestic birds are considered the most vigorous breeders.

Furthermore, the domestic birds start breeding activities in the spring two months before their wild counterparts.

These examples serve to illustrate that the failure of wild animals to breed in captivity or the reduced reproductive success experienced is in essence natural selection for those individuals best able to tolerate the captive environment. If such toleration capacity is proportional to the relative non-emotional characteristics of an individual, it follows that domestication for most species necessarily will be accompanied by natural selection for high emotional thresholds.

General Dependent Variables

Reaction to novel stimuli. As stated previously, the behaviors involved in reaction to novel stimuli to a great extent reflect the general emotionality of the animals involved. The tendency of domesticated strains of rats and mice to investigate new or unfamiliar stimuli is well documented (Farris and Yaekel, 1945; Richter, 1953; Barnett, 1956 & 1958; Welker, 1957; Welker and King, 1962). On the other hand, wild rats have been found to consistently avoid novel stimuli in a familiar environment. Farris and Yaekel (1945) showed that rats 43 generations removed from the wild were significantly more emotional or fearful

in an open-field test than an established domestic strain of albinos. Chitty and Shorten (1946) found that wild Norway rats exhibited a pronounced "neophobia" to strange objects in a familiar situation such as a block of wood placed between a home site and an established feeding area. Automatic recorders showed that this avoidance of novel stimuli occurred even in complete darkness. Thompson (1948), studying the feeding habits of wild rats, discovered that prolonged fasting would often preclude the approach of an unfamiliar stimulus at a feeding site. Other rats would run out, seize a mouthful of food and return to cover to consume it. Barnett (1956) employing first generation laboratory and albino rats in a test for food preference found that the initial activity of the wild genotype animals was inhibited by the presence of unfamiliar food and food containers. The laboratory albinos investigated the new food and commenced eating as soon as it was available, whereas the movements of the wild animals were determined by the two opposing forces of investigation and avoidance. Barnett (1958) further reported that food consumption in wild rats would cease or decrease drastically for several days when the position of food or its container was changed. In every case, the wild animals initially

avoided the unfamiliar stimulus and the laboratory albinos immediately began to explore or investigate it.

Richter (1953) showed that wild Norway rats (but not domestic albinos) will develop a "refusal response" to poisoned food by consuming food containing the toxic substance in sub-lethal doses. Both odor and taste aided the wild rats in detecting the poisoned food which apparently had become associated with the deleterious effects of the sub-lethal doses consumed previously. When the poison was placed at random in one of two food receptacles, a number of rats showing refusal responses literally starved to death while others often displayed a catatonic-like behavior. An interesting fact uncovered in this study was that young rats develop "toxiphobia" more rapidly than the adults.

Howard (1949) estimates that in nature only one out of five deermice born will reach sexual maturity and that the heaviest losses occur on dispersal from the nest. If selection is most severe on the juveniles during dispersal and the latter is the time when animals are exposed to many stimuli in their environment for the first time, then it seems reasonable that selective factors would favor those individuals which, at this young age, most readily

discriminate between beneficial and harmful stimuli in their environment and make the appropriate approach or withdrawal responses to them. Thus, if the capacity to make (or learn to make) appropriate responses to novel stimuli is important for survival, the findings of Howard give special significance to Richter's discovery that young rats develop "toxiphobia" more rapidly than adults.

Activity. The influence of general activity on an animal's behavior is nearly as all-pervading as its general emotionality. Often in animal behavior studies it is difficult to determine whether or not quantitative differences in scores on a given test are truly representative of the behavior measured or merely reflect differences between individuals and groups in regard to activity. In order to assess the influence of general activity on the tests administered in the present study, "spontaneous" activity in running-wheel cages was measured to specifically investigate: (1) strain and treatment differences in activity, and (2) changes in activity due to terminal water deprivation.

Genotype-correlated activity in the Norway rat has been studied by both Rundquist (1933) and Brody (1942). The former established two strains on the basis of high and

low activity in running wheels. Brody, using the high and low activity strains of Rundquist, concluded that selection for low activity was more easily obtained than selection for high activity. The extremely active individuals from the low strain had virtually been removed by the sixth generation but in the active strain a few inactive individuals were found in each generation. Brody was of the opinion that the two strains were separated primarily by single gene differences although this conclusion has been challenged by Robinson (1965). Price (1963) found that wild-trapped Peromyscus maniculatus bairdii were significantly less active in a tilt box than both their own offspring, born and reared in the laboratory, and the semi-domestic stock used in the present study. No difference in activity was found between the latter two groups, however, suggesting that the differences observed were due to environmental rather than genetic effects. Richter and Rice (1954) reported that the normal running-wheel activity in laboratory and wild Norway rats was similar but that the activity of wild rats was significantly higher under conditions of fasting.

The effects of total water deprivation on activity is a somewhat controversial subject. Wald and Jackson

(1944), Campbell (1964), Stevenson and Rixon (1957) claim that lack of water increases activity in a running-wheel while Treichler and Hall (1962) found no change. When activity was measured in stabilimeter cages, Campbell and Cicala (1962) and French (1956) found no change and a decrease in activity, respectively, in rats and mice deprived of water. A subsequent study by Campbell (1964) showed that while activity in a stabilimeter normally did not change when water was removed, if the stabilimeter was raised so as to wobble excessively with movement of the subject, activity increased as it did in running-wheels. Campbell, consequently, suggested that some sort of response-produced feedback system produced the increase in activity.

The relationship between wheel running and body weight has received attention by several investigators. Brobeck (1945) found a negative correlation between running wheel activity and body weight in rats. Active rats lost as much as five grams in five days. By locking or unlocking the wheels, Brobeck was able to control weight gain or loss. Premack and Premack (1963) noted that the daily food intake of rats was temporarily reduced by the introduction of an activity wheel and later increased by removal of the

wheel. Perhaps, this could, at least partially, account for the loss in body weight with increased wheel running noted by Brobeck. Spear and Hill (1962) showed that rats placed on a 24 hour feeding schedule lost more weight living in activity wheels than in normal living cages. Thus, one can conclude from these studies that running-wheel activity may result in a decline in body weight either by an increase in normal activity or by a decrease in food consumption.

The effects of water deprivation. In the present experiment, survival time under terminal water deprivation together with activity and food consumption was measured for mice housed in activity wheels and a control group deprived in their home cages (activity was not measured in this group).

The physiological variables and behavioral adaptations of animals to severe water shortage have been reviewed by Schmidt-Nielson (1952) and Chew (1961). Although these reviews adequately cover the genetic determination of water-related behavior at the species level, within-species adaptations have been seldom explored (O'Kelly, 1963). One exception to this is Lindeborg (1952) who examined the water requirements of closely related species

and subspecies within the genus Peromyscus. In southern Michigan periods of nearly 50 days with only 0.25 inches or less of rainfall sometimes occur. Lindeborg found that only approximately 50 percent of the P. m. bairdii tested could survive this length of time on severely reduced water rations. The lull in the breeding activity of this mouse during the summer months could, thus, be adaptive in that the increased water requirements (2 fold) of nursing P. m. bairdii females could easily bring about a negative water balance. It is a possibility, then, that selection favors those animals which are best able to survive periods of water shortage and which restrict breeding activity to the months when temperature is lower and moisture is higher. Furthermore, Lindeborg noted a significant difference in water consumption between two stocks of Peromyscus maniculatus gracilis captured in similar habitats only 65 miles apart in upper Michigan. If selection for water requirements does occur among populations of Peromyscus in Michigan, a relaxation of such selection could be expected in the laboratory. Consequently, it would not be surprising to find that genotypically wild mice would show longer survival times under conditions of severe water deprivation than their semi-domestic counterparts. Under conditions of

stress, however, this phenomenon could be reversed.

The decrease in food consumption during severe water deprivation has been well documented (Chew, 1951; Chew and Hinegardner, 1957; Beck, 1964; Bing and Mendel, 1931; Kleitman, 1927; Lepkovsky, et. al., 1957; and Strominger, 1947). Chew (1951) found that when suddenly deprived of water, Peromyscus leucopus would exhibit a 63 percent drop in food intake during the first 24 hours together with a 14.6% loss of body weight. This 14.6% loss may be due to a small tissue water loss plus a reduction in contents of the alimentary tract but as Chevillard (1935) has pointed out, in the white mouse body weight may vary from 6 to 12% in one day simply to alimentation. For this reason body weight determinations in the present study were made at approximately the same time each day at the end of the inactive period. French (1956) showed that Peromyscus maniculatus sonoriensis, a desert species, reduced its food consumption to about 50% normal intake on the first 24 hours of total water deprivation. He suggested that the decreased food intake may be due to lack of saliva and digestive secretions for the ingestion and digestion of the dry food available. Adolph (1947) in a study employing the domestic rat, noted that food intake declined progressively

with days of total water deprivation and after the third day was less than one-tenth the normal intake. On the other hand, Chew and Hinegardner (1957) found a sharp drop in food consumption of white mice on the first day of total water deprivation followed by a relatively constant intake thereafter, at this low level until death, despite the progressive decrease in body weight. The authors concluded that the drive to eat had not been reduced but rather that the lack of water interfered with swallowing because of insufficient saliva.

Naturally, with a decrease in food intake during terminal water deprivation, body weight will show a progressive decline. Chew and Hinegardner (1957) determined that the amount of weight lost prior to death (when totally deprived) was largely determined by the initial weight of the animal (on ad lib intake), according to the equation $Y = 15.517$ plus $0.166X$ with $r = 0.612$ and $C = 7.4\%$ (Y = minimum weight; X = initial weight; r = correlation coefficient; C = coefficient of variation). Variation was greater among females than among males but no apparent differences in variation due to age were discovered.

Chew and Hinegardner (1957) cite references to the physiological effects of inadequate water intake or excessive

water loss. Their findings in regard to lipid content, body water content, and blood water content are particularly informative. When deprived of water, white mice will utilize body fat to make up the deficit resulting from decreased intake of food and water. Because fat reserves are completely exhausted at death, it was suggested that starvation plays an important part as a causative factor. Body water content expressed as percent of fat-free body weight (fat does not store water) showed a statistically significant decrease during terminal water deprivation, indicating a progressive dehydration of body tissues. Likewise, the water content of whole blood was significantly reduced, a change restricted to the blood cells but not the plasma.

Lindeborg (1952) found that P. m. bairdii on a daily water ration of only 0.2 cc. (normal is 2.66 cc. per day) lost an average of 43% of its initial body weight by the time of death, which occurred at an average 24 days after initiating the test. Although Chew and Hinegardner (1957) report survival times of 3-8 days for white mice without water, no data have been found comparing the survival times of wild and semi-domestic strains of the same species in regard to total water deprivation. Richter and

Rice (1954) found no difference in average survival time for wild and domestic Norway rats placed on total food deprivation, but water deprivation was apparently not studied.

Independent Environmental Variables Tested

Maternal influence. The importance of controlling for pre- and postnatal maternal influences in studies on genotypically-correlated behavior in rats and mice has been stressed by Thompson (1957), Broadhurst (1961), Denenberg, Ottinger and Stephans (1962), Barnett (1963), Ottinger (1963), Ressler (1963) and others. In the present study prenatal effects were not studied but laboratory-reared subjects were cross-fostered to test for a possible postnatal maternal influence.

The data available regarding postnatal maternal effects have been somewhat contradictory. Broadhurst (1961) failed to find significant effects on open-field behavior from cross-fostering emotional and non-emotional rats. Likewise, negative results were found in mice for aggressive behavior (Fredericson, 1952) and social dominance (Ginsburg and Allee, 1942). Foster (1959), in comparing the reciprocal F_1 hybrids between the field-dwelling Peromyscus maniculatus bairdii and the semi-arboreal P.

maniculatus gracilis and their reciprocal backcrosses, failed to find a maternal influence of either parent on the behavior of its offspring. On the other hand, Denenberg and Whimbey (1963) have shown that the behavior of rats may be modified by the experiences their mothers had while infants. Similarly, Ottinger, Denenberg and Stephans (1963) report that both rotation of mothers and cross-fostering between low and high emotional strains have demonstrable effects on the open-field behavior of offspring. They conclude that "offspring emotionality is directly related to both pre-natal and post-natal emotionality of the mothers." Ressler (1963), likewise, found a significant post-natal maternal effect between two inbred strains of mice in regard to visual exploration, weight at weaning and at 60 days, and survival to weaning. These results may be correlated with differential parental handling (Ressler, 1962) influenced both by the strain of parents and the strain of young. Finally, Griesel (1964) reports that rats reared by inactive foster mothers were significantly more active in an activity wheel than those reared by active foster mothers. However, a comparison of these two groups in the open-field did not reveal consistent differences in ambulation or defecation.

The rearing environment (laboratory versus nature). Although the differences between wild and domestic strains under constant laboratory conditions has been explored (Yerkes, 1913; Coburn, 1922; Richter, 1954; and Barnet, 1963), practically no one has made similar comparisons on wild and domestic strains born and reared in nature. One exception is a study by Wecker (1964) in which it was found that Peromyscus maniculatus bairdii born to parents some 15-20 generations removed from the wild, would successfully choose a field over a woods-type environment only after early experience in the field, whereas their wild counterparts chose the field environment even when born and reared in the laboratory. Thus, domestication had, in this case, resulted in the loss of an innate propensity for habitat selection.

GENERAL METHODS

Subjects

Wild genotype. The 180 wild genotype subjects employed were the offspring of wild-caught deermice trapped in the vicinity of East Lansing, Michigan, from three separate, non-isolated areas. Some 50 pairs of wild-caught individuals were mated following capture in November of 1964 and April of 1965. To avoid inbreeding, an effort was made not to mate those individuals caught in close proximity.

Semi-domestic genotype. The ancestors of the 180 semi-domestic mice to be employed were trapped in the vicinity of Ann Arbor, Michigan (approximately 60 miles from East Lansing) in 1948 by Van T. Harris (1952). They were first maintained by Harris at the University of Michigan and later kept at the Detroit Cancer Institute by William Prychodko. In 1955, John King transferred about 12 pairs to the Roscoe Jackson Laboratory at Bar Harbor, Maine, and in 1962 brought a breeding stock of about 50 pairs to Michigan State University where the present stock

is approximately 20-25 generations removed from the wild. During the period since 1948, no conscious inbreeding has been practiced and in most cases a conscious effort to avoid inbreeding has been made. The only selection employed has been selection for fast and slow eye-opening which is now in its fifth generation. Provided that selection for eye-opening speed has exerted no pleiotropic effect on the factors determining reactivity to novel stimuli, it may be said that no conscious selection for this behavior has been made during 17 years in captivity. In reality, little is known about the genetic constitution of the mice in either stock. The extent of inbreeding in the wild for P. m. bairdii has been estimated at 4-10% (186 litters - Howard, 1949) but still little can be said regarding the relative heterozygosity of the gene pool for either strain employed. Furthermore, the intensity of natural and unconscious artificial selection on the semi-domestic strain is unknown.

Evidence is available that individuals of a population differ in their capturability (Young, et. al., 1952; Wiegirt and Mayenshein, 1966). It is conceivable that the wild-caught parents of the first generation stock were not truly representative of the native stock. However, if some

selection for trapability occurred in obtaining the wild stock, it probably occurred when the ancestors of the semi-domestic stock were trapped in 1948. It is assumed that the founder populations of both stocks were equally representative of the native populations from which they were derived.

Treatment Groups

In the present study wild and semi-domestic mice were used as the basic experimental groups (genetic effects) while subgroups were differently treated to provide tests for maternal influence and place of rearing experience (environmental effects). The experimental and control groups employed in the present study are diagramatically represented in Table 1.

Treatments for maternal influence. The literature reviewed on the subject of maternal influence points out the discrepancies found in this area. A test for the effects of this variable in the present study was made possible by fostering wild-genotype offspring on semi-domestic mothers and vice versa. The effect of fostering, itself, was determined by exchanging litters within a strain. Fostering was only employed with laboratory reared animals. Mice given early experience (five weeks) in the outdoor enclosure were

Table 1. Basic experimental and control groups employed, tests taken separately.

Test One (Open-field)

Wild Genotype
- A. Born and reared in the laboratory
  - 1. Natural mother (N = 10 ♂♂ and 10 ♀♀)
  - 2. Within-fostered (N = 20)
  - 3. Cross-fostered (N = 20)
- B. Early experience in outdoor enclosure
  - 1. Natural mother (N = 20)

Semi-Domestic Genotype
- A. Born and reared in the laboratory
  - 1. Natural mother (N = 10 ♂♂ and 10 ♀♀)
  - 2. Within-fostered (N = 20)
  - 3. Cross-fostered (N = 20)
- B. Early experience in outdoor enclosure
  - 1. Natural mother (N = 20)

Test Two (Unfamiliar living environment)

Wild Genotype
- A. Born and reared in the laboratory
  - 1. Natural mother (experimental) (N = 10 ♂♂ and 10 ♀♀)
  - 2. Within-fostered (N = 20)
  - 3. Cross-fostered (N = 20)
  - 4. Natural mother (Control) (N = 20)
- B. Early experience in outdoor enclosure
  - 1. Natural mother (N = 20)

Semi-Domestic Genotype
- A. Born and reared in the laboratory
  - 1. Natural mother (experimental) (N = 10 ♂♂ and 10 ♀♀)
  - 2. Within-fostered (N = 20)
  - 3. Cross-fostered (N = 20)
  - 4. Natural mother (control) (N = 20)
- B. Early experience in outdoor enclosure
  - 1. Natural mother (N = 20)

---

all reared by their own mothers (see section on care and handling).

Treatments for place of rearing. As stated previously it is conceivable that the place of early rearing experience may be of great importance in determining subsequent behavior. A test for this factor was provided by comparing laboratory reared animals of both wild and semi-domestic strains with those given five weeks of experience (following weaning) in an outdoor enclosure (see section on care and handling).

Numbers Employed

Twenty animals, ten males and ten females, were tested in each of the experimental and control groups employed. A total of 80 animals per strain were used in the open-field test while 100 subjects of each strain were employed in the second test measuring the reaction to a novel environment forced upon the subjects. Thus, a total of 360 animals were used as subjects in both tests combined.

Care and Handling

All mice (including those given early experience in the outdoor enclosure) were born in the laboratory in clear plastic cages (5" x 11" x 6" deep) with removable

wire lids. Wood shavings were used to cover the bottom of the cages and cotton was provided for nesting material. Food (Purina Mouse Breeder Chow) and water were provided ad libitum.

Litters containing less than three young were rejected for testing purposes and all litters consisting of more than four young were reduced to four (2 males and 2 females, when possible). When a 2:2 sex ratio was not obtained two mice of the predominant sex were saved at weaning, and the others discarded in that only siblings of the same sex were raised together. All fostering was completed at three days of age or younger.

Litters were weaned at 21 days of age, and the mice to be used as subjects were numbered by a system of toe and ear clipping and placed either by groups of two (keeping sexes separate) into standard laboratory cages or, in the case of the mice to be given early experience in nature, by groups of four (same sex) into one of the 16 areas in the outdoor enclosure.

Following weaning the animals in both the outdoor enclosure and laboratory were left undisturbed except for periodic cleaning of the laboratory cages. After five weeks' experience in the outdoor enclosure the mice were

removed by live trapping and brought into the laboratory where they were maintained in standard cages in groups of two (like sex) until the day of testing.

All handling prior to testing (except where otherwise stated) was accomplished by grasping the tail with 12" metal forceps (tips covered with rubber hose). The handling technique is described more fully in the sections discussing procedure.

Outdoor Enclosure

The outdoor enclosure was located on the MSU farm approximately 1/4 mile SE of the horse barns. As indicated in the photo (Figure 1) the enclosure was located in an abandoned section of grassland similar to the natural habitat of the species employed. The outside dimensions were 100 feet by 25 feet with internal partitions dividing the pen into 16 equal areas 12½ feet square in size. One-fourth inch mesh hardware cloth fastened along its length to 14 inch aluminum flashing provided the escape-proof walls. The free side of the hardware cloth was folded over along its length about four inches to form a perpendicular shelf. This shelf side was buried in the soil about 4-6 inches deep so that the shelf projected toward the inside, thus, preventing the mice from digging out. The walls were

Figure 1. Outdoor enclosure used in testing for effects of place of early rearing experience.

strengthened around the periphery by wooden 2 x 4 posts.

Each area in the enclosure was equipped with a nest area made from a 12" piece of 4" drain tile buried in the ground and covered with a piece of 1" pine. Standard laboratory food plus ear corn was provided to supplement the natural foods present in each area and water was provided ad lib. during the dry months.

TEST-SPECIFIC MATERIALS AND METHODS

Open-Field Test

Subjects and Treatment groups. The eight treatment groups outlined in Table 1 were employed in this test, together comprising 160 subjects. The laboratory reared subjects were tested in ten blocks of 12 animals each, with two animals of like sex from each treatment group comprising a block. Tests began when the mice in a given block averaged 60 days of age. Due to heavy mortality from local predators, at first, the testing of the enclosure-reared subjects was delayed until most of the tests on laboratory reared subjects had been completed. Tests on the former began five days following removal from the outdoor enclosure, at approximately 60 days of age.

Apparatus.

Open-Field - Six open-field boxes, 10" wide, 30" long and 22" deep, were constructed with plywood sides (natural finish) and hardware cloth floors. The floor was divided by colored wire into 5 equal sections of 6 inches each. Midway along the long (30") side, a 1¼" hole was

made which served as the point of entry for the mice being tested. A 7¼ watt bulb placed over each open-field provided light from 6:00 a.m. to 6:00 p.m. daily. A blind concealed the experimenter during the tests.

Nest box - During habituation the entry hole in each open-field led to a nest box with inside dimensions of 4" x 4" x 4" constructed of plywood with a removable Plexiglas lid and a hardware cloth floor. A wooden plunger was constructed as a false side to the nest box to facilitate removal from the latter with a minimum of handling. Each nest box was fitted with an interlocking device permitting easy attachment and detachment from the open-field. Food pellets were strung on a thin wire across the front of the nest box and water was provided by means of a spout projecting through the Plexiglas lid.

Start box - A start box was constructed for each open-field having inside dimensions of 2½" x 2½" x 5" high. The sides and top were made of plywood and the bottom masonite. A sliding sheet metal door formed the front side and an interlocking device permitted easy attachment and detachment from the open-field.

Predator - A least weasel (Mustela nivalis) was placed in each open-field in a plywood and hardware

cloth cage of dimensions 4" x 8" x 6" high. The cages containing weasels were placed directly opposite the entrance hole so that the shortest distance from the entrance hole to the cage was 6 inches. During the tests the weasels were generally active but did not elicit any audible sounds or sudden movements. However, they usually would watch the mouse as it moved about the open-field. The predators were well fed when employed in the tests.

Procedure. One day before the beginning of testing, nest boxes were placed in the home cages of each of the six pairs of mice in a given block. On the initial test day the nest box was removed from the home cage and one of the two animals was prodded into its respective start box by means of the wooden plunger described previously. The start box was then placed in front of the entrance hole of the open-field and after 8 minutes of habituation, the door on the start box was raised and the time clock started. The door to the start box remained open during the test. During the two minute test period the following data were obtained: (1) percent of subjects entering the open-field within the two minute test period, (2) latency to enter the open-field (when all four feet are outside the entrance hole, (3) activity as measured by the number of sections

crossed per unit time in the open-field, (4) total time in the open-field during the test period, and (5) the average time spent in the open-field per entry (total time in the OF divided by the number of retreats to the start box). All time measurements were obtained with stop-clocks and counters located outside the experimental room which the experimenter controlled by a silent manually operated mercury switch keyboard. After testing, the animal was forced to return to the start box by means of movable partitions.

Each pair of littermates was tested in the same open-field and they alone remained in that OF for the remainder of the 6 day test period. Before beginning tests on any given day all mice were removed from the experimental room (while in their nest boxes) to an adjacent room where they remained until all tests had been completed for that day. Mice of each pair were tested in their respective open-field to keep room cues and odors as nearly constant as possible. The tests were conducted at approximately the same time each day (1:00 - 3:00 p.m.) and neither strains nor litters were mixed during the test period to eliminate the influence of differential strain or treatment effects (if any) on subsequent behavior.

Two relatively sound-proof rooms were employed in the test administration. Three open-fields were placed in each room making it possible to have one subject in starting position while another was being tested in the other room. This alternation of rooms for testing purposes allowed the mice 8 minutes without disturbance immediately before testing as opposed to a maximum of 4 minutes if only a single room had been used. At approximately one and one-half minutes before each test the next subject to be tested was placed in starting position before its respective open-field in the adjacent test room. The only disturbance, if any, during the 8 minute pre-test period occurred when the experimenter entered the test room approximately one minute prior to test administration.

The test sequence is summarized diagrammatically in Table 2. Each subject was administered all four tests in the sequence described.

It was hypothesized that as a result of 17 years of laboratory breeding the reactivity of the semi-domestic strain to novel stimuli had declined so that, when compared with the genetically wild strain, they showed: (1) a greater proportion of subjects entering the open-field during the time alloted, (2) faster latencies to enter, (3)

Table 2. Basic experimental procedure of the open-field test including test sequence, days administered and measurements involved.

Test	Day	Measurement	Dependent Variables (Each Test)
1	0	Initial Reaction to Open-Field	1. Whether or not O.F. was entered.
2	2	Habituated Reaction to Open-Field	2. Latency to enter open-field
3	3	Initial Reaction to O.F. plus Weasel	3. Activity (no. of blocks crossed)
4	5	Habituated Reaction to O.F. plus Weasel	4. Total time in O.F. (2 min. trial)
			5. Number retreats to start box.

greater activity, (4) more total time in the open-field, and (5) fewer retreats to the start box. Furthermore, it was postulated that the presence of the least weasel would bring about a greater change in the behavior of the wild strain than the semi-domestics.

Unfamiliar Living Environment Test

Subjects and treatment groups. The eight treatment groups outlined in Table 1 were employed, including a control group (reared by their natural mothers in the laboratory) for each strain making a total of ten groups or 200

subjects. The animals used in the eight basic experimental groups were all adult naive subjects which had not been handled or disturbed for at least three weeks prior to testing and which ranged from 90 to 110 days of age. Body weight and food consumption of the control animals were measured four days prior to testing to obtain a base line response for these variables. Likewise, these subjects ranged from 90 to 111 days of age.

Apparatus.

Activity wheels - Twelve 8" activity wheels were custom-made by the metal shop at Michigan State University and each consisted of a single circular backing disc of heavy galvanized sheet metal to which was attached the runway made of perforated sheet metal 3" wide, leaving one side of the wheel open. One end of a bicycle hub was attached to the backing disc of the wheel and the other end was fastened to a flat sheet metal plate 12" x 12" so that approximately ¼" clearance was obtained between the plate and the edge of the runway on the open side, thus, allowing the wheel to run freely but not permitting the animal to escape. A water bottle was attached to the back of the main plate so that the metal spout projected through a hole in the plate into the wheel. Food was provided by

stringing blocks of Purina lab chow (1/64" holes drilled through the center of each block) on fine wire and looping the free end of the wire around the bicycle hub so that the food remained stationary as the wheel turned.

Activity records were obtained by pen deflections on an Esterline Angus Event Recorder running at 3" per hour. Magnetic reed switches were attached to a piece of heavy Plexiglas fastened in a stationary manner to the bicycle hub. A magnet was glued to the backing disc of each activity wheel 2" from the center and closed the reed switch at each revolution, thus, completing the electrical circuit to the event recorder. Because of the slow speed at which the paper drive was set, continuous wheel-running appeared as a solid block of pen deflections.

Procedure.

Experimental groups - On the initial day of testing the subjects were removed from their home cages, weighed and placed in activity wheels where they remained throughout the test period. Each day between 2:00 and 6:00 p.m. (usually between 4:00 and 5:30 p.m.) the animals were removed from the wheels (detaching wheels from plates) and weighed. At the same time food consumption for the 24 hours previous was determined by weighing the food remaining

and subtracting from the previous weight. A small percentage of the food handled was lost through the wheel as crumbs. The food wasted by ten animals from each of three treatment groups per strain (within fostered and control groups excepted) was determined by twice collecting the crumbs lost on paper toweling beneath the wheels and expressing this wastage as a percent of the total food handled during the previous 24 hour period. Food consumption data adjusted for wastage could, thus, be obtained for all subjects.

The mice were maintained on this schedule for 5 days during which food and water were provided ad libitum. After five days the water was removed from the water bottles of all subjects reared by their normal mothers, and the resulting change in body weight, food consumption and activity was measured until death in addition to survival time in days. Fostered animals were not tested for survival. During this phase a check was made at 9:00 a.m. each day to obtain greater accuracy in determining survival time.

Gross activity data collected by the Esterline Angus event recorder were quantified by taking each daily 20 hour period, from 6:00 p.m. to 2:00 p.m., and determining the number of ten minute periods (6 per hour, 120 in all) in

which the animal was active.

Control group - Because of the confounding effects of handling and being isolated from their rearing partner on the response to a novel stimulus (activity wheel) and the confounding effect of being placed in a strange environment on survival time during water deprivation, a control group containing mice reared by their own mothers was set up for both strains. To start, the subjects were moved in their home cages from the colony room to the adjacent test chamber where the activity wheels and experimental animals were found. To get a base-line for food consumption and body weight, a record was kept of these variables for four days while the animals were still paired. Two strings of food were placed in each cage to prevent competition between the individuals of a pair. Because there was no way to determine how much food each mouse of the pair consumed, the total amount consumed by both was used as a base-line for any given pair. On the fifth day the mice were isolated from one another into cages containing bedding material from the original home cage. The effects of isolation on body weight were determined for each mouse and the effects on food consumption were found for each pair. Following five days under this

regime water was removed from the water bottles, bedding was removed from the cages (to correspond to the lack of bedding in the activity wheels) and food consumption and body weight were measured until death. No measure of activity was taken with this group.

All test animals were maintained in a relatively soundproof room at 70-72° F. (air conditioned) and on a 12:12 light-dark cycle (6:00 a.m. to 6:00 p.m.). The Esterline Angus recorder was kept outside the test room in order to keep sound within to a bare minimum and to enable one to examine the activity record without disturbing the mice.

The following tables (3 and 4) indicate the basic testing procedure employed along with the principle dependent variables measured. Due to the loss in reactivity of the semi-domestic strain to unfamiliar stimuli, it was hypothesized that this strain would show no change in body weight, food consumption and activity upon being placed in an unfamiliar environment. Food consumption and, therefore, body weight were expected to be below normal for the genetically wild subjects during the period immediately following placement in the activity-wheel cages. Wheel-running activity of the wild and semi-domestic strains was

Table 3. Basic experimental procedure of the "unfamiliar living-environment" test including test sequence and days administered. NM = natural mother, WF = within-fostered, CF = cross-fostered, OP = outdoor enclosure, C = control.

Days	Wild					Semi-Domestic				
	C	NM	WF	CF	OP	C	NM	WF	CF	OP
A	x					x				
B	x					x				
C	x					x				
D	x					x				
1	x	x	x	x	x	x	x	x	x	x
2	x	x	x	x	x	x	x	x	x	x
3	x	x	x	x	x	x	x x	x	x	x
4	x	x	x	x	x	x	x	x	x	x
5	x	x	x	x	x	x	x	x	x	x
				Water Deprivation Begins						
6	x	x			x	x	x			x
7	x	x			x	x	x			x

Table 4. Dependent variables tested in the unfamiliar living-environment test in relation to test days.

Variable	A-D	1-5	6-7	7 Plus
1. Body weight	x	x	x	x
2. Food consumption/ gram body weight	x	x	x	x
3. Activity		x (Controls excepted)	x	x
4. Days until death				x

expected to be similar prior to deprivation. Following total water deprivation both strains were postulated to exhibit increased activity (based on literature). The semi-domestic subjects were expected to show a faster decline in food consumption and body weight during water deprivation than the wild mice and, thereby, a shorter survival period.

RESULTS

Test One - Open Field

In order to facilitate statistical analysis (for reasons discussed later), the data were divided into two parts: (1) a comparison of the responses of the laboratory reared subjects over test days, and (2) a comparison of those natural-mothered groups reared in the laboratory versus the outdoor enclosure (test day one only). Of the five dependent variables measured (see Table 2) three were discarded in the statistical analysis. The variable "number of retreats into the start box" was discarded due to the large number of zero scores resulting from non-entries and because it was difficult to determine if the subjects re-entered the start box to explore the latter or escape from the open-field. The "total time spent in the open-field" variable was discarded in that, in most cases, it merely represented the inverse of the latency to enter since most subjects remained in the open-field once they had entered. Activity, taken as the number of blocks crossed per unit time in the open-field, was invalid. Some subjects, once

having entered the apparatus, ran around in a frenzied manner and then quickly returned to the start box, amassing extremely high activity scores.

Laboratory reared groups only. Since a much higher than expected proportion of subjects did not enter the open-field during the two minute test trial the "entry versus non-entry" variable, in many respects, answered the biological questions asked in this test. The nature of the data, however, did not lend these scores to adequate statistical analysis. Nevertheless, the percentage of entries were plotted in Figure 2 for all four test days with treatment groups combined. A simple X^2 test for "entry versus non-entry" with treatment groups combined indicated that on all four test days the semi-domestic strain showed a significantly higher proportion of entries than did the wild strain. The percent entries and X^2 values are presented in Table 5.

The scores for latency to enter, being parametric in nature, were more amenable to statistical analysis. A three-factor analysis of variance was conducted involving strains, treatments and days. In this analysis sexes were combined, since they obviously did not differ. Test day four (habituation to the weasel) was not included because

Figure 2. The percentage of laboratory reared subjects (treatments combined) which entered the open-field (test days taken separately).

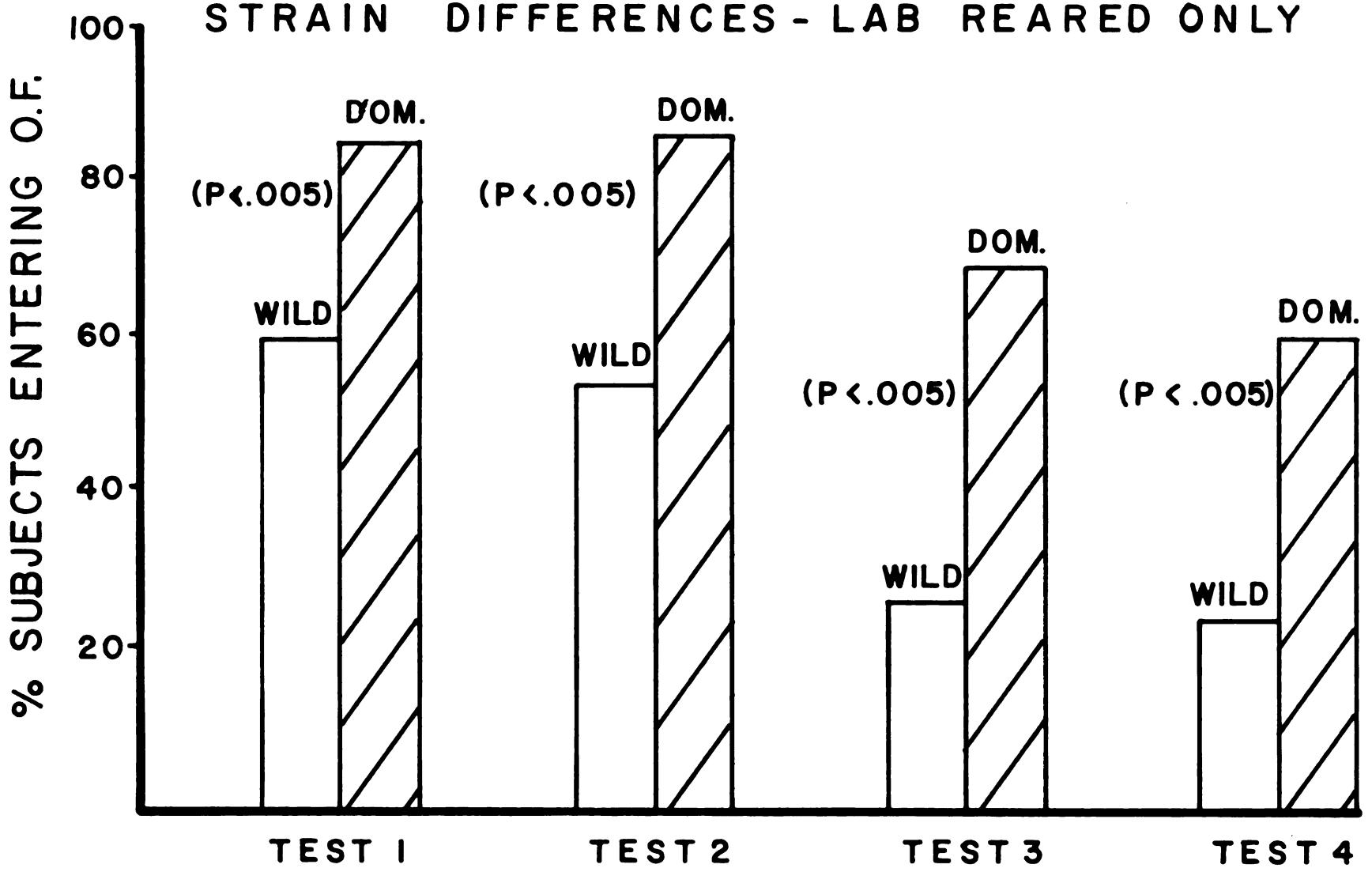

STRAIN DIFFERENCES - LAB REARED ONLY
% SUBJECTS ENTERING O.F.
100
80
60
40
20
DOM.
(P<.005)
WILD
DOM.
(P<.005)
WILD
DOM.
(P<.005)
WILD
DOM.
(P<.005)
WILD
TEST 1
TEST 2
TEST 3
TEST 4

FIGURE 2

Table 5. The percentage of laboratory reared subjects (treatments combined) which entered the open-field and the results of the statistical analysis (test days taken separately).

Test Day	Strain		X^2	d.f.	Prob.
	Wild	Domestic			
1	60.0%	85.0%	8.19	1	.005
2	55.0%	86.7%	15.50	1	.005
3	26.7%	68.3%	20.88	1	.005
4	24.3%	60.0%	9.42	1	.005

the within-fostered subjects were not given this test and an equal number of scores were desired for each subsample. The latency scores were transformed to logs in order to meet the assumption of homogeneity of variance. Because of the large number of maximum (120 sec.) scores obtained in some groups due to non-entries, the within-group variability was lower than normal in these groups and the probability of rejection was, thus, increased. In order to reduce this chance of error, the probability needed for rejection was set at the .01 level.

Table 6 includes the log mean latency to enter scores for the first three test days. Figure 3 presents the median latency to enter (non-log) scores for the six groups over the four test days even though only the first three test days were included in the analysis. The "F"

Figure 3. Median latency (seconds) to enter the open-field for all laboratory-reared groups.

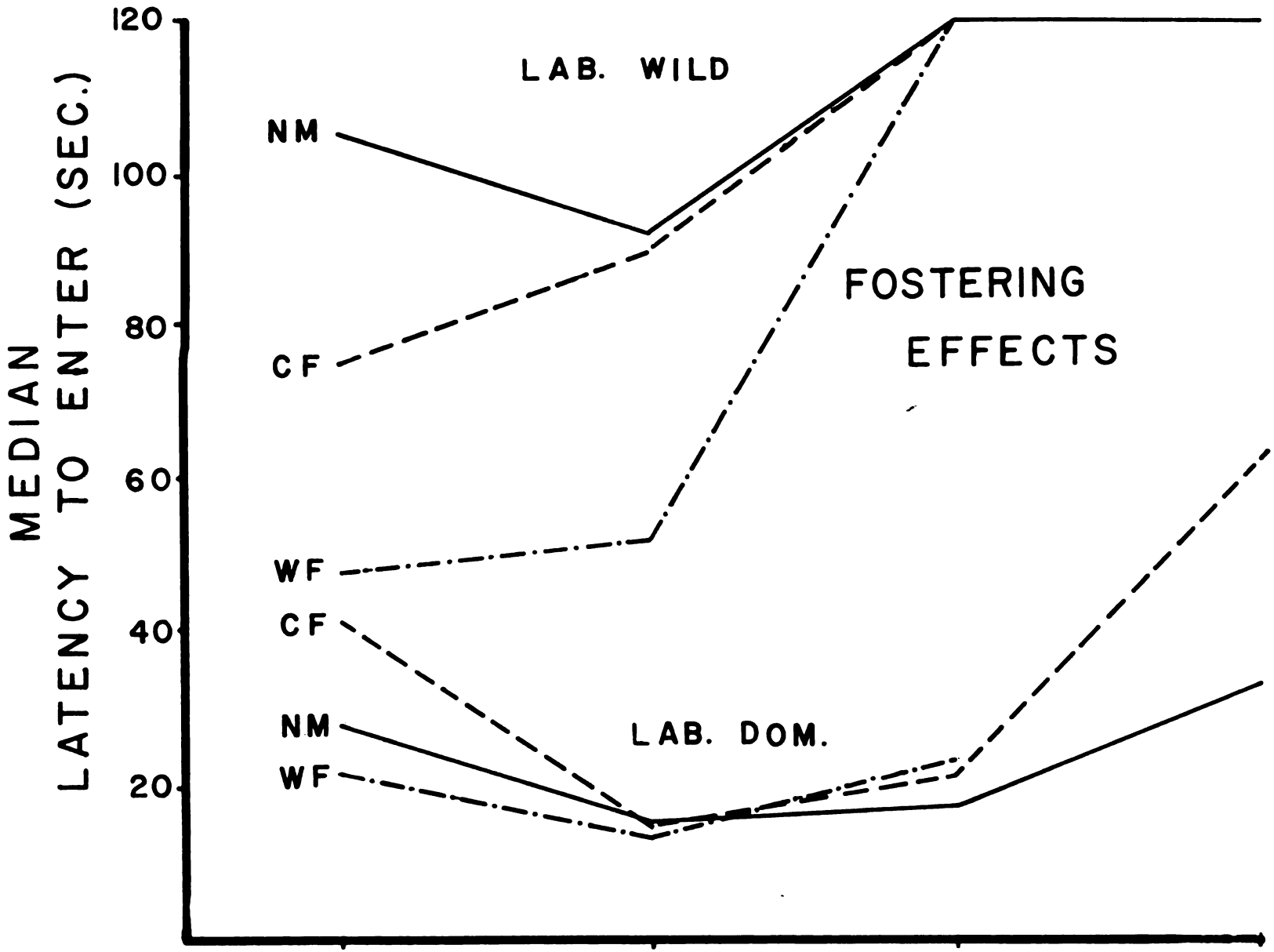

120
100
80
60
40
20
MEDIAN
LATENCY TO ENTER (SEC.)
LAB. WILD
NM
CF
FOSTERING
EFFECTS
WF
CF
NM
LAB. DOM.
WF
1
2
3
4
TEST

FIGURE 3

Table 6. Long mean scores for latency (seconds) to enter the open-field for all laboratory-reared groups (test day four excepted).

	Natural Mother		Within Fostered		Cross Fostered	
Test Day	Wild	Domestic	Wild	Domestic	Wild	Domestic
1	1.76	1.51	1.69	1.35	1.78	1.59
2	1.65	1.29	1.71	1.15	1.74	1.33
3	1.84	1.37	1.92	1.46	1.94	1.46

values and associated probabilities obtained for the three factors tested and their possible interactions are summarized in Table 7.

Table 7. Results of the statistical analysis of the latency to enter data (laboratory-reared subjects only).

Factor	Sum Sq.	d.f.	Mean Sq. V.	F	Prob.
Strain	13.74	1/342	13.74	68.57	.005
Treatment	0.54	2/342	0.27	1.36	N.S.
Days	2.22	2/342	1.11	5.54	.005
Strain x days	0.80	2/342	0.40	1.99	N.S.
Strain x treatment	0.17	2/342	0.08	.42	N.S.
Treatment x days	0.31	4/342	0.08	.39	N.S.
Strain x treatment x days	0.33	4/342	0.08	.41	N.S.
Error	68.53	342	0.20		

As pointed out in Table 7, significant strain and day effects were obtained. The wild strain exhibited significantly longer latencies to enter the open-field whereas no significant differences were obtained between those subjects reared by their own mothers and those fostered both within and between strains. A multiple range test conducted on the day factor with treatments combined indicated that at the .01 level of significance, the semi-domestic strain significantly habituated to the open-field (Test 2) whereas the wild strain did not. In addition, the latency scores of both strains increased in response to the weasel (Test 3) although the absolute increase in latency seconds was more than seven times greater for the wild strain than for the semi-domestics.

Rearing in the laboratory versus the outdoor enclosure. After tests on the fall enclosure-reared subjects had been completed it was evident that a slight sex difference had been obtained among the semi-domestic animals. In order to determine the reliability of this result and since mortality or dissertion was extremely high among these enclosure-reared samples (76% in the semi-domestic strain and 64% in the wild strain) a second sample of outdoor enclosure-reared animals was made, this time in the

early spring. The loss of animals was considerably less in this sample (19% for the semi-domestics and 18% for the wilds), providing for greater confidence in the samples from these groups. However, only the initial reaction (day 1) to the open-field was tested with the latter samples.

It was found that the behavior of the spring-reared semi-domestic mice did not differ significantly from that of the fall sample and the sex difference was repeated. However, the fall and spring samples of wild subjects showed significantly different behaviors ($X^2 = 6.46$; d.f. = 1; $P < .02$). Unfortunately, a third sampling of wild individuals was not possible in order to determine which of the two previous samples was not representative. But since the spring sample suffered fewer losses in the outdoor enclosure this group was used in preference to the fall sample in determining the effects of the physical rearing environment. Therefore, the fall sample of enclosure-reared semi-domestic subjects (chosen to keep an equal subsample number for analysis) and the spring sample of wild subjects were compared in regard to their initial reaction to the open-field. These groups, in turn, were compared with comparable groups of animals given no experience in

the outdoor enclosure (reared in the laboratory).

The genotypically wild subjects displayed the same "wild type" behavior regardless of their place of rearing. The percentage of entries for the enclosure-reared wild subjects was nearly identical to that of the wild laboratory-reared animals. On the other hand, only 40% of the enclosure-reared semi-domestic males entered the open-field during test one as compared to an 80% entry for the laboratory-reared males ($X^2 = 5.15$; d.f. = 1; $P < .05$). Seventy percent of the enclosure-reared semi-domestic females entered during the two minute trial, a 20% reduction from the 90% entry for the laboratory-reared females. This difference was not significant, however ($X^2 = 1.04$; d.f. = 1). The sex difference obtained in the enclosure-reared semi-domestic animals was not significant ($X^2 = .808$; d.f. = 1), therefore, sexes were combined in a comparison of enclosure-reared wild and semi-domestic strains. In this comparison, 60% of the wild subjects had entered the open-field whereas a 55% entry was obtained by the enclosure-reared semi-domestics. This non-significant difference obviously points to the conclusion that the semi-domestic deermice had reverted to a typical "wild-type" behavior when given early experience in the natural environment of

the species.

Table 8 presents the mean latency to enter scores on initial encounter with the open-field (sexes separate).

A three way analysis of variance of latency to enter scores enabled tests for strains, sexes, treatments and interactions. Table 9 summarizes the results of this analysis. No significant main or interaction effects were found.

Table 8. Mean latency to enter scores (seconds) on initial presentation of open-field for laboratory and enclosure-reared subjects (sexes separate).

	Male		Female	
	Laboratory	Outdoor Enclosure	Laboratory	Outdoor Enclosure
Wild	68.2	69.0	92.4	87.8
Domestic	58.6	83.9	41.2	67.3

As determined previously in the entry versus non-entry comparison, once having been given early experience in its natural environment the semi-domestic strain displayed behavior comparable to the genotypically wild subjects. Failure of the main effect of treatment to be significant in this analysis was difficult to interpret. The fact that the behavior of the wild strain did not differ under the

Table 9. Results of the statistical analysis of the latency to enter data (Lab. versus outdoor enclosure rearing).

Factor	Sum Sq.	d.f.	Mean Sq. V.	F	Prob.
Strain	5,491.30	1/72	5,491.30	2.79	N.S.
Sex	103.52	1/72	103.52	.05	N.S.
Treatment	2,832.20	1/72	2,832.20	1.45	N.S.
Strain x Sex	7,411.24	1/72	7,411.24	3.77	N.S.
Strain x Treat.	3,795.02	1/72	3,795.02	1.93	N.S.
Sex x Treatment	24.64	1/72	24.65	.01	N.S.
Strain x Sex x Treatment	47.74	1/72	47.74	.02	N.S.
Error	141,646.72	72	1,967.32		

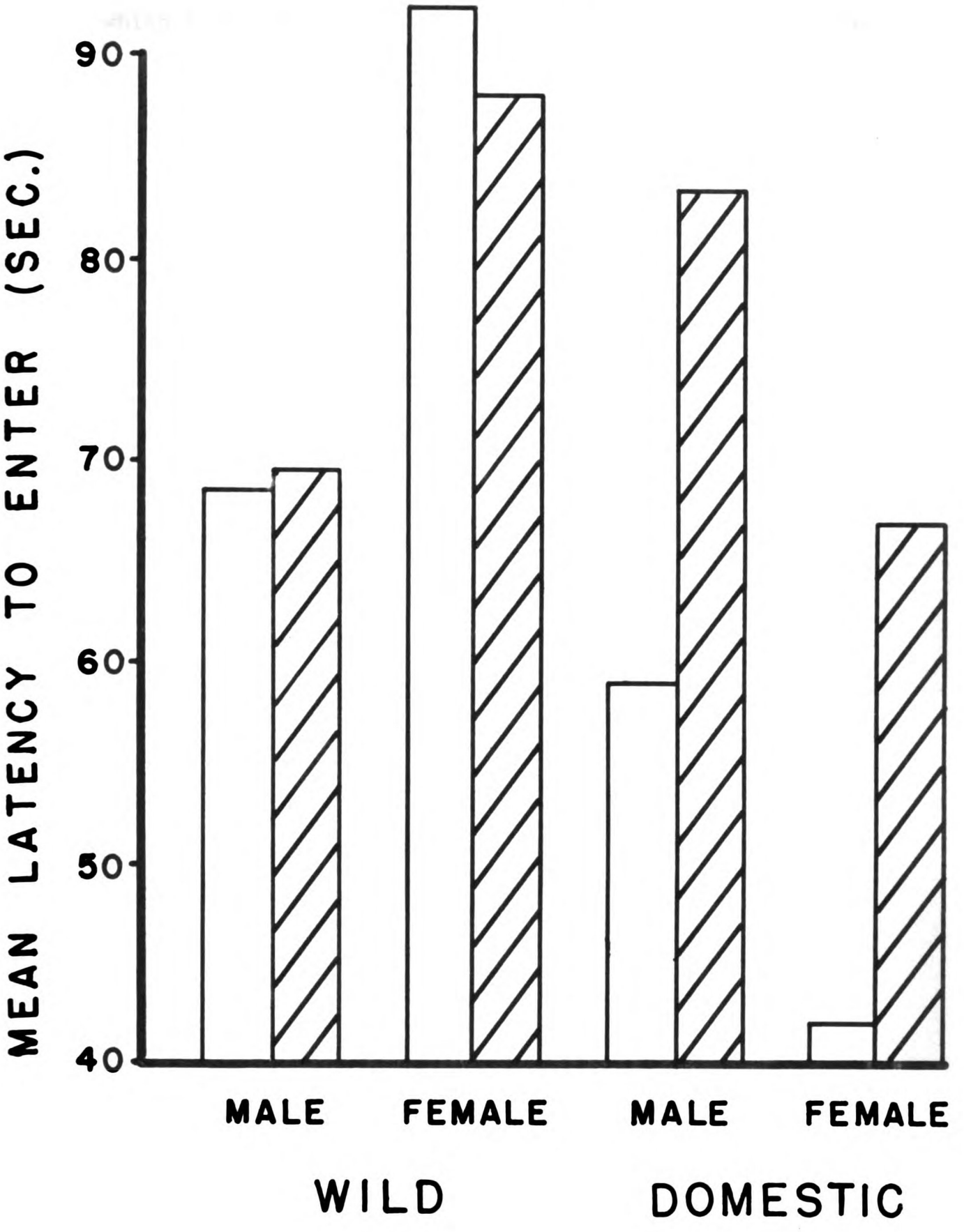
two rearing conditions could partially account for this result. A strain-treatment interaction was certainly not a causal factor. These relationships can be seen more clearly in Figure 4.

Test Two - Unfamiliar Living Environment

Preliminary analyses. Two preliminary analyses, initial body weight and food wastage, were conducted before testing the major dependent variables involved in this test. The initial body weight of all groups employed in this section was treated in regard to sex, strain and treatment in a three factor analysis of variance. This was done in order to obtain a base line for the various groups on

Figure 4. Mean latency (seconds) to enter the open-field for natural-mothered groups reared in the laboratory (open columns) and a semi-natural outdoor enclosure (striped columns).

FIGURE 4


MEAN LATENCY TO ENTER (SEC.)
90
80
70
60
50
40
MALE
FEMALE
MALE
FEMALE
WILD
DOMESTIC

which to assess future changes in body weight and the validity of food consumption per gram body weight (rather than absolute food consumption) as a measure of food ingested. Secondly, a test of body weight over days using the same animals violates the assumption of independence of data in analysis of variance treatments, making an accurate comparison of body weights somewhat unreliable. Table 10 gives the mean initial body weights for all groups employed. The results of the analysis of initial body weight are presented in Table 11. As expected the males were significantly heavier than the females ($P<.005$). Since this relationship is a regular occurrence, in future comparisons of body weight over days the sexes will be treated separately. The semi-domestic strain was found to be significantly heavier than the wild strain ($P<.01$). Since food consumption per gram body weight was still higher in the semi-domestic mice, greater significance was given to the use of a food consumption measure that was adjusted for body weight. Body weight was not affected by treatments, however, even though treatments interacted significantly with strains ($P<.025$).

The data on food wastage, expressed as a percentage of the total food handled (chewed off the string of food

Table 10. Mean initial body weight (grms). (C = control; NM = natural mother; WF = within fostered; CF = cross-fostered; OP = outdoor enclosure)

		C	NM	WF	CF	OP
Wild	Male	16.7	16.2	17.9	17.6	18.6
	Female	15.0	15.1	14.6	16.0	14.3
Domestic	Male	17.0	19.0	18.2	16.9	18.3
	Female	15.2	16.0	16.7	15.1	17.5

Table 11. Results of the statistical analysis of initial body weight.

Factor	Sum Sq.	d.f.	Mean Sq. V.	F	Prob.
Strain	30.73	1/180	30.73	7.95	.01
Sex	217.99	1/180	217.99	56.39	.005
Treatment	32.18	4/180	8.04	2.08	N.S.
Strain x Sex	4.93	1/180	4.93	1.28	N.S.
Strain x Treat.	45.86	4/180	11.46	2.97	.025
Sex x Treatment	6.08	4/180	1.52	.39	N.S.
Strain x Sex x Treatment	43.70	4/180	10.92	2.83	.025
Error	695.81	180	3.87		

blocks), were subjected to a two factor analysis of variance, treating strains and treatments (within-fostered animals excluded). The data were transformed to common logs in order to meet the assumption of variance homogeneity. The log mean percent food wasted for the various groups is presented in Table 12. The transformed data are presented in Figure 5, and the results of the statistical analysis, in Table 13. The main effect for strains was significant ($P<.005$) with the semi-domestic animals wasting more food than the wild subjects. Treatment, itself, did not significantly influence this variable but it did interact with strains in a significant manner ($P<.01$). As a result of this finding the absolute food consumption for each strain was corrected for wastage by subtracting the mean percent wastage for each strain from the absolute amounts handled.

Table 12. Long mean percent of food wasted (NM = natural mother; CF = cross-fostered; OP = outdoor enclosure.).

	NM	CF	OP
Wild	4.77	4.65	6.13
Domestic	6.60	7.92	6.01

Table 13. Results of the statistical analysis of food wastage.

Factor	Sum Sq.	d.f.	Mean Sq. V.	F	Prob.
Strain	.413	1/54	.413	22.23	.005
Treatment	.037	2/54	.019	1.01	N.S.
Strain x Treatment	.290	2/54	.145	7.79	.01
Error	1.004	54	.019		

Handling and isolation. To determine the effect of handling and isolation (from rearing partner) on body weight and food consumption per gram body weight, two control groups were employed (wild and semi-domestic) and a two-factor analysis of variance was conducted on these variables using strains and days as the factors tested. The means and results of the statistical analysis are presented in Tables 14 and 15, respectively. The means are presented diagrammatically in Figures 6 and 7 (body weight and food consumption, respectively).

Despite the slight increase in body weight following isolation, no significant day effect in regard to body weight was obtained for either the males or females.

Figure 5. Log mean percent food wasted (NM = natural mother; CF = cross-fostered; OP = outdoor enclosure-reared).

FIGURE 5

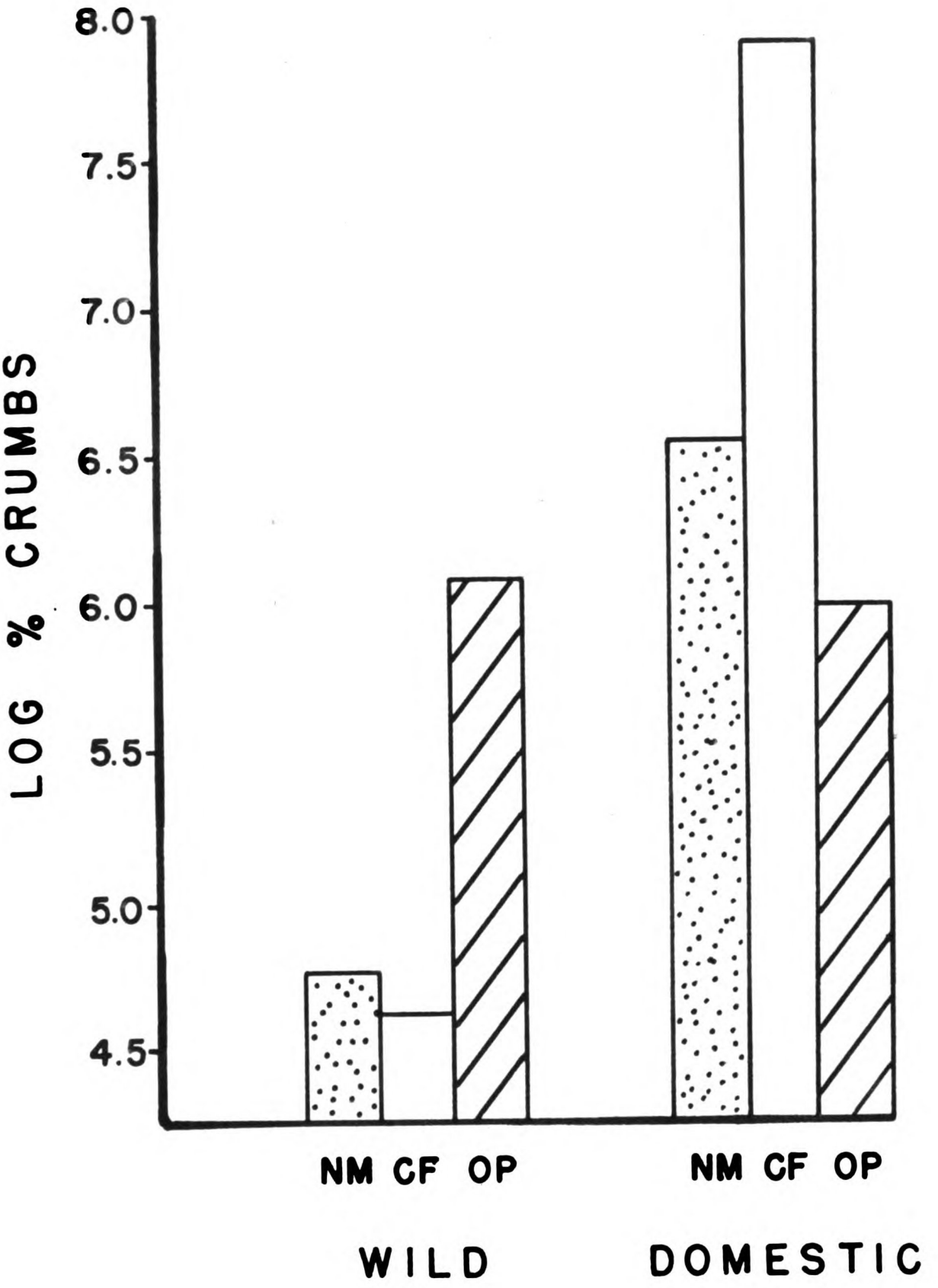


Figure 6. Mean body weight (grms.) of control groups for handling and isolation (Open circles = domestic strain; solid circles = wild strain; solid line = males; broken line = females; I = initial wt.; letters = days pre-isolation; numbers = days post isolation).

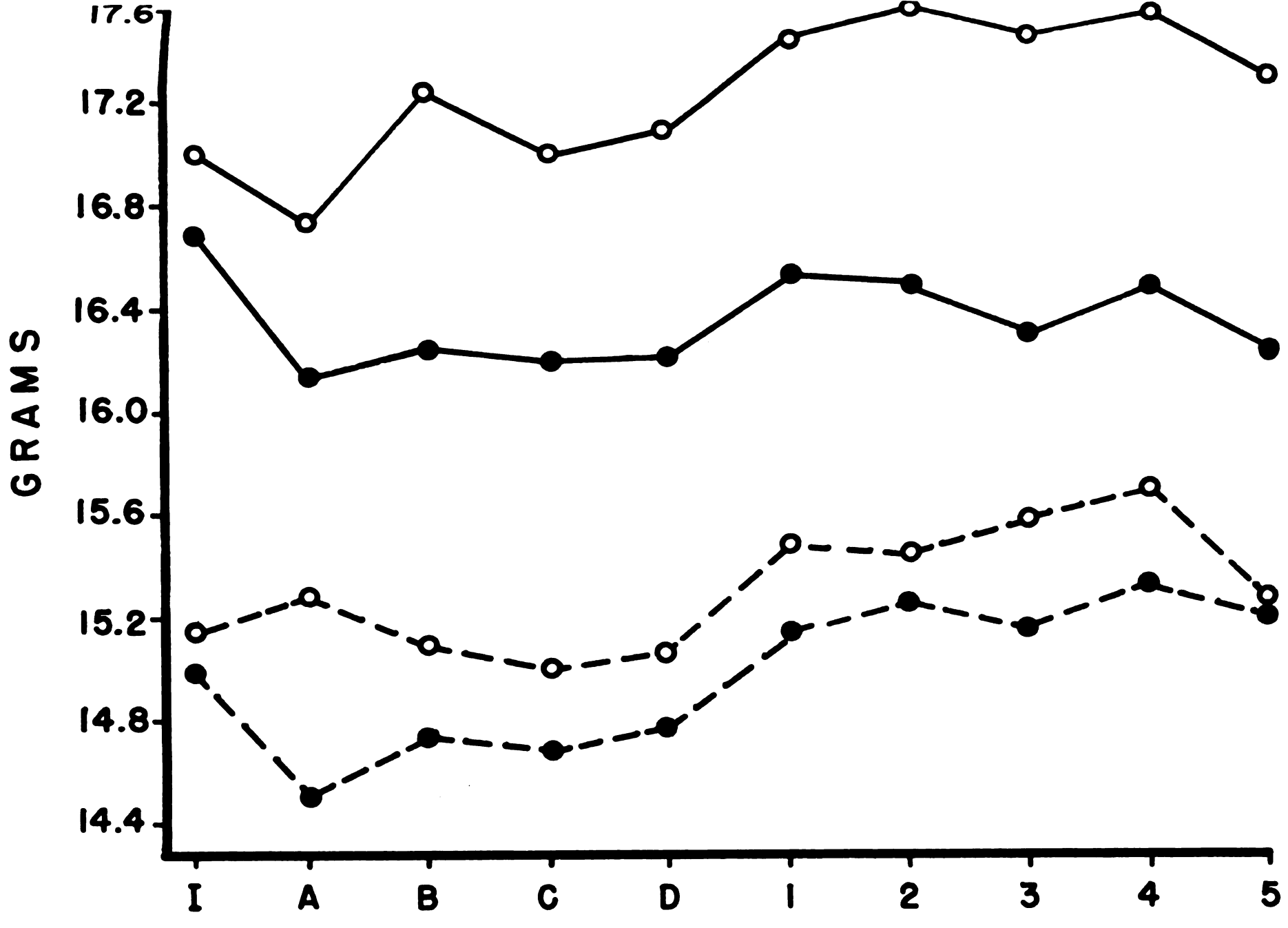


FIGURE 6

Figure 7. Mean food consumption (grms. food/grm. body weight) of control groups for handling and isolation (open circles = domestic strain; solid circles = wild strain; letters = days pre-isolation; numbers = days post isolation).

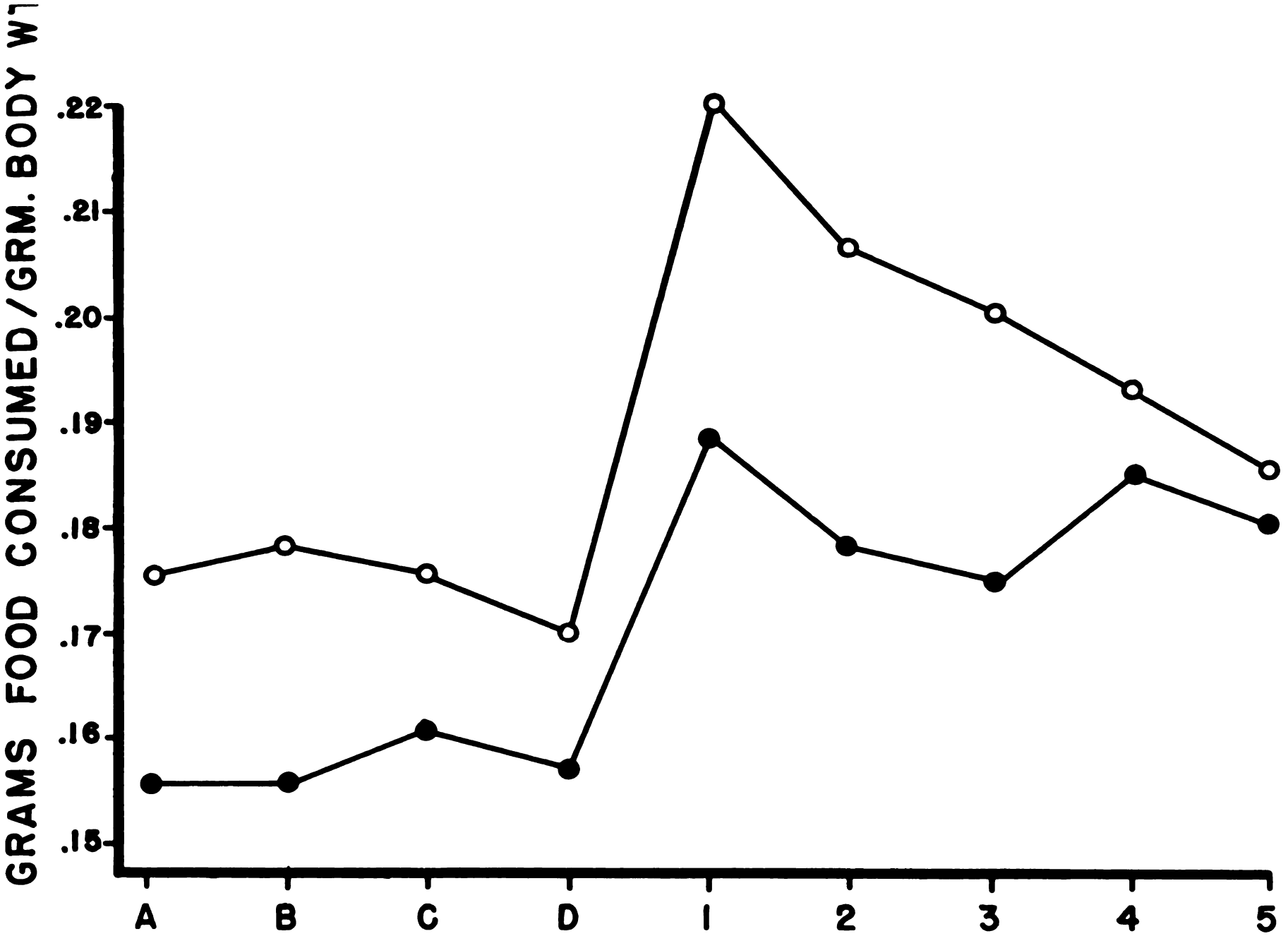

GRAMS FOOD CONSUMED/GRM. BODY WT
.22
.21
.20
.19
.18
.17
.16
.15
A
B
C
D
1
2
3
4
5
DAYS

FIGURE 7

Table 14. Mean body weight (grms.) and food consumption (grms. food/ grm. body weight) of control groups for handling and isolation. (I = initial weight; letters = days pre-isolation; numbers = days post-isolation.)

A. Body Weight

		Days									
		I	A	B	C	D	1	2	3	4	5
Males	Wild	16.7	16.2	16.2	16.2	16.2	16.5	16.4	16.3	16.5	16.2
	Domestic	17.0	16.8	17.2	17.0	17.1	17.4	17.6	17.4	17.6	17.3
Females	Wild	15.0	14.5	14.8	14.6	14.8	15.2	15.3	15.2	15.4	15.3
	Domestic	15.2	15.3	15.1	15.0	15.1	15.5	15.4	15.6	15.7	15.2

B. Food Consumption

	Days								
	A	B	C	C	1	2	3	4	5
Wild	.156	.156	.161	.156	.188	.179	.174	.186	.179
Domestic	.176	.180	.178	.170	.221	.208	.201	.193	.185

Table 15. Results of the statistical analysis of body weight and food consumption (control for handling and isolation).

Factor	Sum Sq.	d.f.	Mean Sq. V.	F	Prob.
A. Body Weight					
1. Males					
Strain	41.86	1/180	41.86	41.86	.005
Days	6.95	9/180	.77	.77	N.S.
Strain x Days	3.39	9/180	.38	.38	N.S.
Error	498.96	180	2.77		
2. Females					
Strain	5.35	1/180	5.35	5.35	N.S.
Days	11.34	9/180	1.26	1.26	N.S.
Strain x Days	2.07	9/180	.23	.23	N.S.
Error	365.08	180	2.03		
B. Food Consumption					
Strain	.017	1/162	.017	22.50	.005
Days	.034	8/162	.004	5.55	.005
Strain x Days	.004	8/162	.0005	.63	N.S.
Error	.123	162	.0008		

Nevertheless, in keeping with the results discussed earlier, the semi-domestics tended to be heavier than the wilds. Food consumption was a different situation in that a significant day effect was obtained ($P<.005$). The new multiple range test showed that a significant increase ($P<.01$) in food consumption was experienced by both strains on

being brought into the experimental chamber and isolated from their rearing partner for the first time. Despite the corrections for greater food wastage and body weight in the semi-domestic strain, the latter still showed a significantly greater ($P<.005$) level of food consumption than the wilds.

Reactivity to unfamiliar living environment. Body weight and food consumption were measured for all experimental groups. Three factor analyses of variance, employing days, strains and treatments, were conducted for the body weight data (sexes separate) whereas a four factor analysis involving days, sexes, treatments and strains treated the food consumption data. The mean scores are presented in Tables 16 and 17 (body weight and food consumption, respectively). The results of the analyses are summarized in Tables 18 and 19 (body weight and food consumption, respectively) and represented diagrammatically in Figures 8, 9 (body weight) and 10 (food consumption). No significant change in body weight was observed over the five test days in response to being placed in the unfamiliar environment. Significant effects were obtained, however, for both strains (♂♂ - $P<.005$; ♀♀ - $P<.005$) and treatments (♂♂ - $P<.005$; ♀♀ - $P<.05$) as well as the strain

Table 16. Mean body weight (grms.) for test days (sexes taken separately). (NM = natural mother; WF = within fostered; CF = cross fostered; OP = outdoor enclosure)

A. Males

		Days					
		0	1	2	3	4	5
Wild	NM	16.2	15.9	15.7	15.9	16.0	16.1
	WF	17.9	17.4	17.3	17.5	17.5	17.5
	CF	17.6	16.4	17.2	17.4	17.2	17.3
	OP	18.6	18.2	18.2	18.2	18.2	18.1
Domestic	NM	19.0	18.9	19.2	19.2	19.1	19.2
	WF	18.2	17.8	18.2	18.3	18.3	18.3
	CF	16.9	16.7	17.0	17.2	17.0	17.2
	OP	18.3	18.1	17.8	18.2	18.1	18.2

B. Females

		Days					
		0	1	2	3	4	5
Wild	NM	15.1	14.8	14.9	15.1	15.0	14.9
	WF	14.6	14.4	14.3	14.6	14.6	15.0
	CF	16.0	15.9	15.7	15.8	15.7	15.6
	OP	14.3	14.2	14.4	14.4	14.5	14.6
Domestic	NM	16.0	16.0	16.2	16.2	16.1	16.2
	WF	16.7	16.8	16.6	16.8	16.7	16.7
	CF	15.1	14.9	14.9	15.1	15.0	15.0
	OP	17.5	17.7	17.5	17.5	17.2	17.7

treatment interactions (♂♂ - $P<.005$; ♀♀ - $P<.005$). The new multiple range test on treatments indicated that the wild male group reared in the laboratory by their own mothers weighed significantly less ($P<.05$) than the wild male

Table 17. Mean food consumption (grms. food/grm. body wt.) during 24 hour test intervals (sexes combined). (NM = natural mother; WF = within fostered; CF = cross-fostered; OP = outdoor enclosure).

		Days				
		1	2	3	4	5
Wild	NM	.194	.201	.223	.228	.232
	WF	.201	.217	.245	.242	.236
	CF	.190	.234	.249	.227	.231
	OP	.185	.205	.218	.208	.217
Domestic	NM	.247	.242	.242	.234	.251
	WF	.245	.232	.248	.251	.254
	CF	.256	.260	.259	.252	.256
	OP	.225	.198	.212	.220	.210

group reared in the outdoor enclosure. In addition, the male domestic cross-fostered group weighed significantly less ($P<.05$) than the domestic strain reared in the laboratory by their natural mothers. In the case of females, no wild treatment groups differed at the 0.05 probability level whereas the semi-domestic cross-fostered individuals weighed significantly less ($P<.01$) than outdoor-enclosure-reared animals of the same strain. All possible within-strain comparisons not mentioned did not reach the .05 level of significance.

Table 18. Results of the statistical analysis of body weight for all experimental groups in response to an unfamiliar living environment.

Factor	Sum Sq.	d.f.	Mean Sq.V.	F	Prob.
1. Males					
Strain	92.84	1/432	92.84	23.96	.005
Treatment	79.89	3/432	26.63	6.87	.005
Days	8.29	5/432	1.66	.43	N.S.
Strain x Treatment	221.05	3/432	73.68	19.01	.005
Strain x Days	3.36	5/432	.67	.17	N.S.
Treatment x Days	4.18	15/432	.28	.07	N.S.
Strain x Treatment x Days	3.22	15/432	.22	.06	N.S.
Error	1674.17	432	3.88		
2. Females					
Strain	236.74	1/432	236.74	89.23	.005
Treatment	21.26	3/432	7.09	2.67	.05
Days	1.14	5/432	.23	.09	N.S.
Strain x Treatment	253.36	3/432	84.45	31.83	.005
Strain x Days	.97	5/432	.19	.07	N.S.
Treatment x Days	3.44	15/432	.23	.09	N.S.
Strain x Treat.x Days	3.05	15/432	.20	.08	N.S.
Error	1146.07	432	2.65		

Table 19. Results of the statistical analysis of food consumption for all experimental groups in response to an unfamiliar living environment.

Factor	Sum Sq.	d.f.	Mean Sq.V.	F	Prob.
Days	.044	4/720	.011	4.62	.005
Sex	.058	1/720	.058	24.00	.005
Treatment	.117	3/720	.039	16.29	.005
Strain	.085	1/720	.085	35.58	.005
Days x Sex	.017	4/720	.004	1.75	N.S.
Days x Treatment	.019	12/720	.002	.67	N.S.
Days x Strain	.049	4/720	.012	5.12	.005
Sex x Treatment	.010	3/720	.003	1.33	N.S.
Sex x Strain	.002	1/720	.002	.62	N.S.
Treatment x Strain	.017	3/720	.006	2.38	N.S.
Days x Sex x Treat.	.019	12/720	.002	.67	N.S.
Days x Sex x Strain	.003	4/720	.001	.33	N.S.
Sex x Treatment x Strain	.008	3/720	.002	1.04	N.S.
Day x Treatment x Strain	.010	12/720	.001	.33	N.S.
Day x Sex x Treatment x Strain	.055	12/720	.005	1.92	.05
Error	1.70	720	.002		

Figure 8. Mean body weight (grms.) of male subjects of all experimental groups for days in an unfamiliar living environment. (Open circles = domestic strain; solid circles = wild strain; solid line = natural mother; dotted line = within fostered; dash-dot line = cross-fostered; broken line = outdoor enclosure.)

FIGURE 8

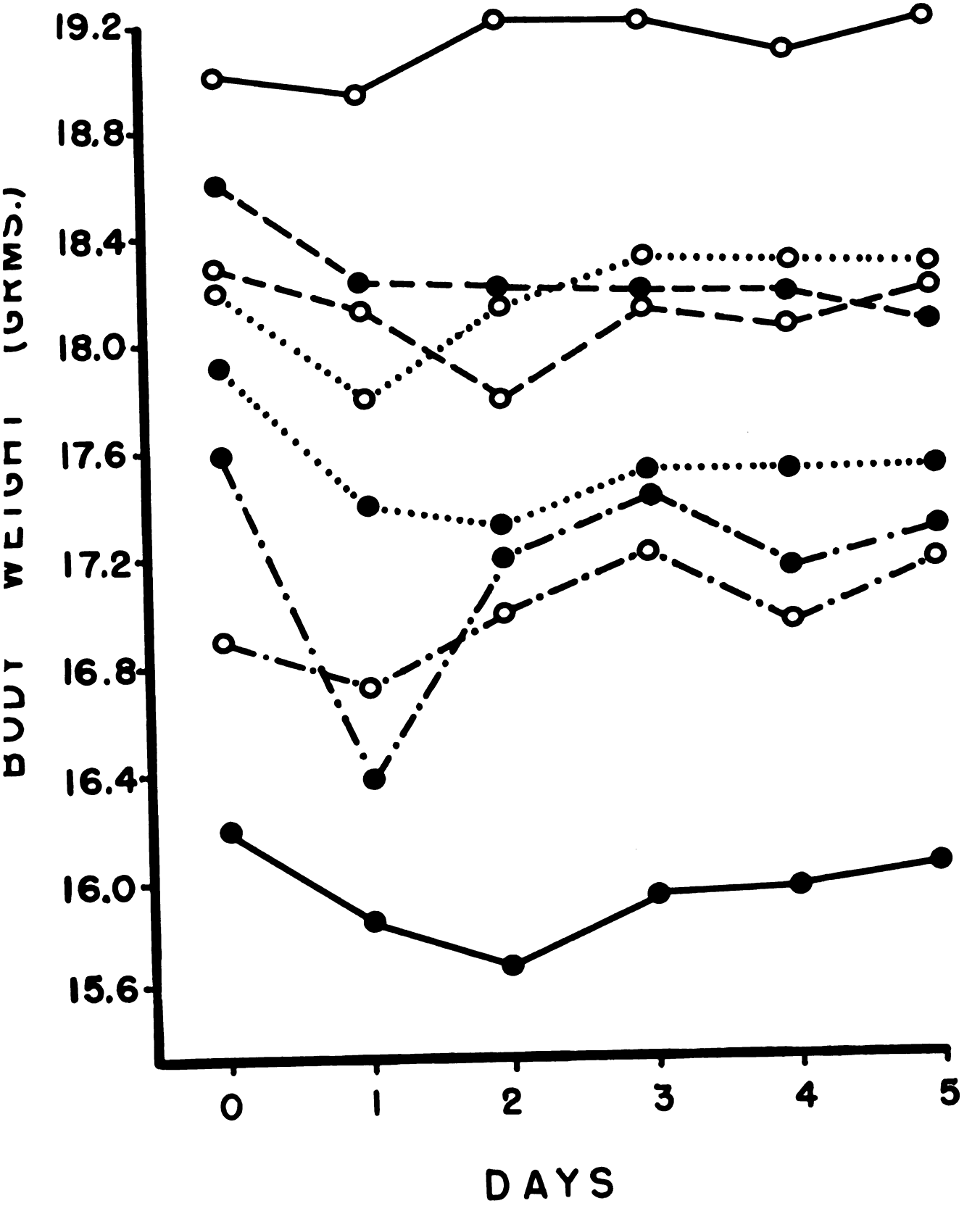


Figure 9. Mean body weight (grms.) of female subjects of all experimental groups for days in an unfamiliar living environment. (Open circles = domestic strain; solid circles = wild strain; solid line = natural mother; dotted line = within fostered; dash-dot line = cross-fostered; broken line = outdoor enclosure.)

FIGURE 9

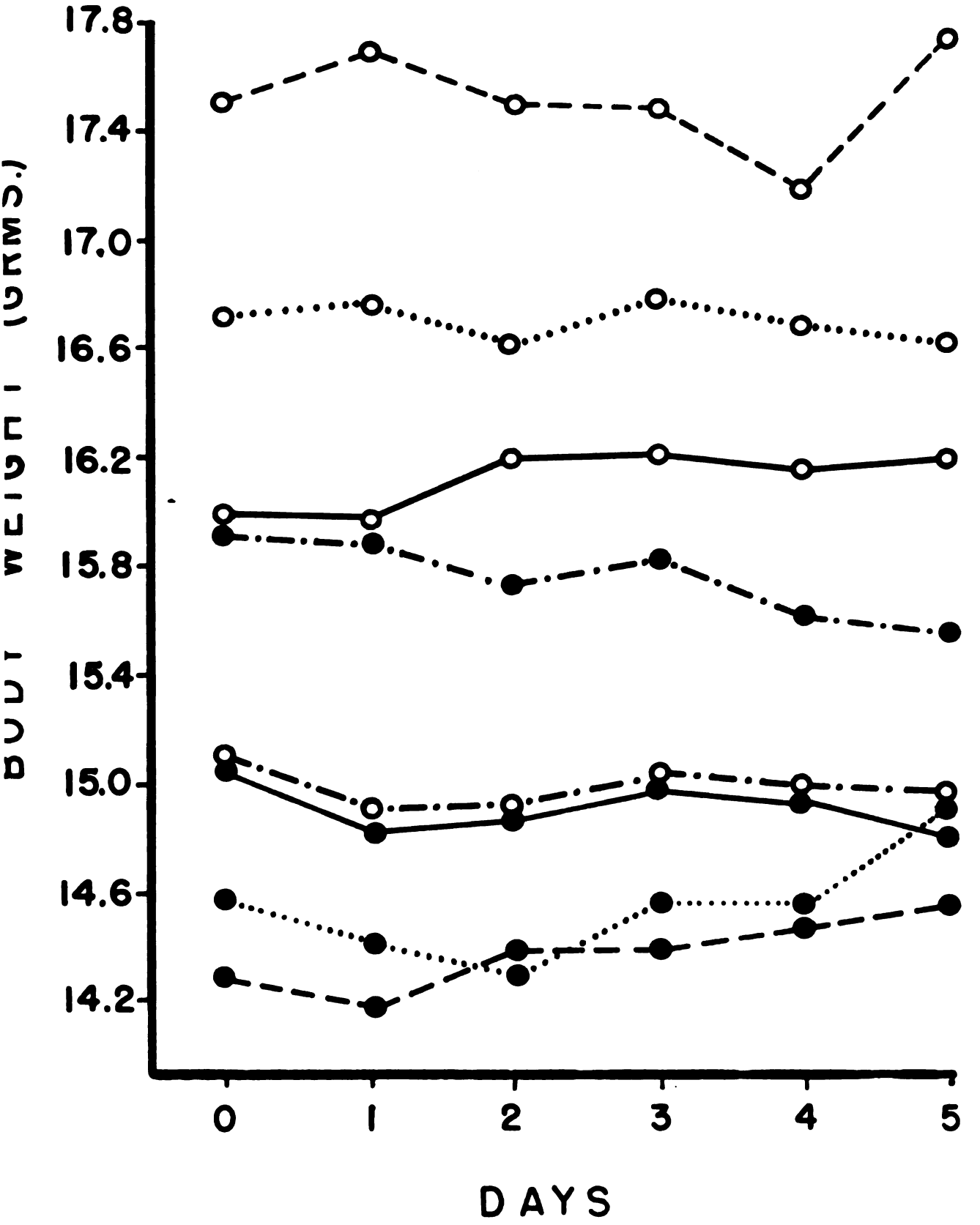
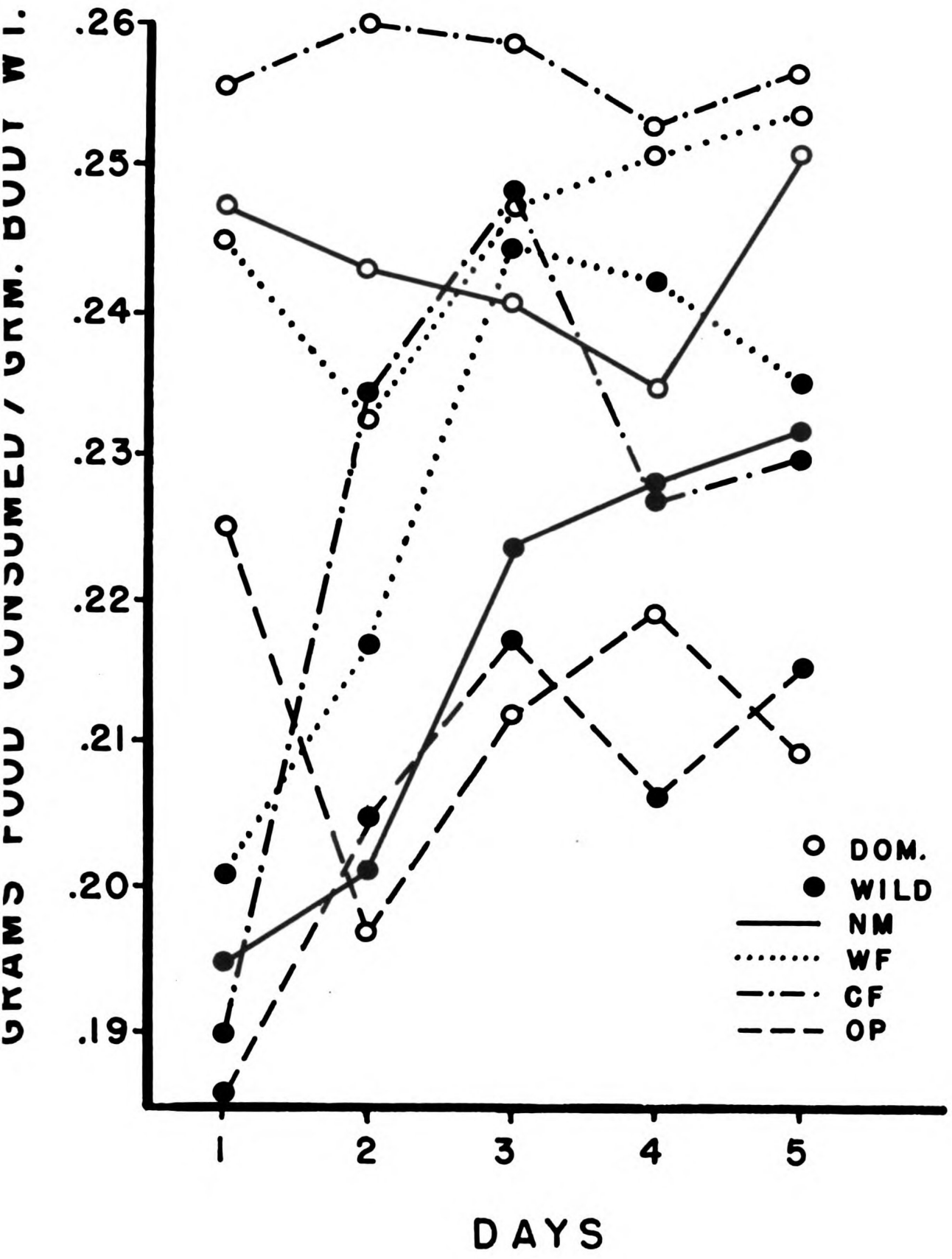


Figure 10. Mean food consumption (grms food/grm. body weight) of all experimental groups for successive 24 hour intervals in a novel living environment (NM = natural mother; WF = within fostered; CF = cross fostered; OP = outdoor enclosure).

FIGURE 10


GRAMS FOOD CONSUMED / GRM. BODY WT.
.26
.25
.24
.23
.22
.21
.20
.19
1
2
3
4
5
DAYS
DOM.
WILD
NM
WF
CF
OP

As indicated in Table 19, all the major effects tested in regard to food consumption were significant at the .005 level of probability. The only interaction declared significant was that of strains versus days ($P<.005$). The two most significant findings in this test were: (1) food consumption among all groups of wild subjects was considerably lower during the first 48 hours in the novel environment than thereafter (whereas it did not differ over days in the semi-domestic strain) and (2) of the various treatment groups employed, food consumption was lowest in the enclosure-reared animals of both strains.

The multiple range test indicated that food consumption in the semi-domestic stocks did not differ in regard to days. In fact, in this strain, mean food consumption was highest during the first 24 hours. Food consumption by the wild strain, on the other hand, was significantly lower ($P<.01$) during the first 24 hour period than for any other day. The second 24 hour period of food consumption was still significantly lower ($P<.05$) than that of the third day in this strain. Thus, being placed in an unfamiliar environment with no escape had a depressing effect on food consumption in the genotypically wild animals (a result similar to that found by Barnett in

wild Norway rats) while this "neophobic" response had been lost during 20-25 generations of breeding in captivity.

In regard to treatments the multiple range test indicated that in the semi-domestic strain, the group given early experience in the outdoor enclosure showed a significantly lower ($P<.01$) food consumption level (days combined) than the other three domestic experimental groups. Likewise, the outdoor enclosure group of the wild strain ate significantly less ($P<.01$) than both wild fostered groups. Although early depression of food consumption was not obtained in the semi-domestic outdoor enclosure group, the general depression of food consumption in this group, when compared to the laboratory-reared groups of the same strain, suggests, as in the open-field tests, that early experience in nature causes genotypically domestic animals to display "wild type" behavior.

Due to a flaw in the event recorder a large amount of activity data had to be discarded. In order to obtain equality of sub-sample numbers, valid data were randomly discarded, in some cases, so that each treatment group had a sampling of eleven scores (instead of the intended twenty). The mean activity units for the first five days in the activity wheels are presented in Table 20.

Table 20. Mean activity units for all experimental groups during the first five days in the unfamiliar living environment (sexes combined). (NM = natural mother; WF = within fostered; CF = cross fostered; OP = outdoor enclosure.

		Days				
		1	2	3	4	5
Wild	NM	70.5	62.7	66.4	66.2	70.1
	WF	78.5	72.6	69.6	65.3	70.4
	CF	80.5	74.5	70.5	61.9	65.5
	OP	72.3	60.9	56.8	54.5	51.5
Domestic	NM	77.5	66.5	69.8	67.5	65.4
	WF	76.5	72.5	66.2	76.9	70.0
	CF	68.5	69.5	67.8	71.5	70.9
	OP	70.7	60.1	67.8	64.9	64.5

These data were analyzed by a three factor analysis of variance treating strains, days (pre-deprivation) and treatments. The results of this analysis (Table 21) point out that the activity of the two strains did not differ in response to being placed in an unfamiliar environment with no opportunity for escape. Significant day and treatment effects (both $P<.005$) were obtained, however, despite the lack of significant interaction factors (see Figure 11). Multiple range tests indicated that both strains were significantly more active ($P<.01$) during the first 24 hour period in the activity wheels than on the other days (which

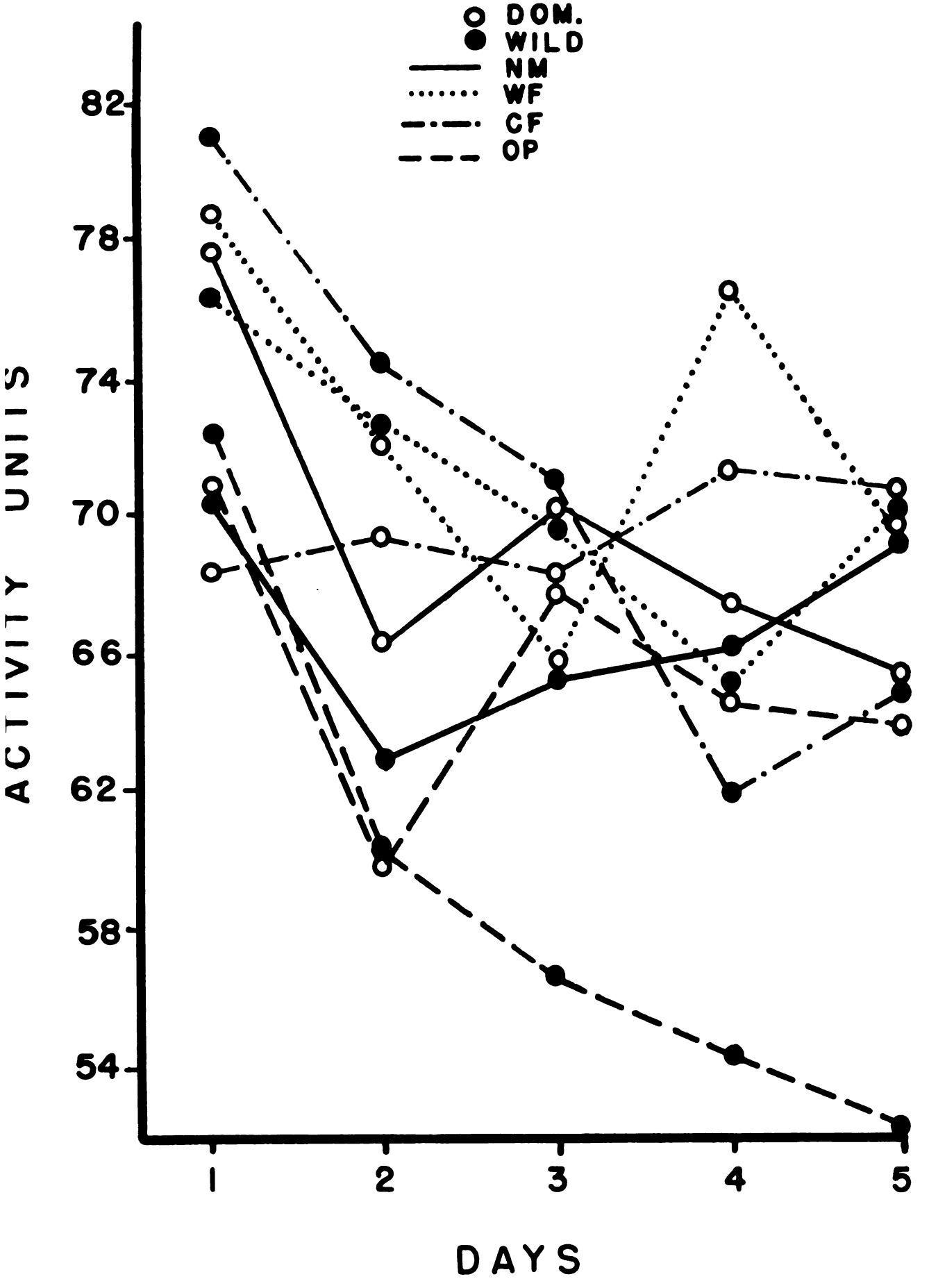
Table 21. Results of the statistical analysis of wheel-running activity for all experimental groups prior to water deprivation.

Factor	Sum Sq.	d.f.	Mean Sq.V.	F	Prob.
Days	4365.52	4/400	1091.38	4.38	.005
Strains	525.82	1/400	525.82	2.11	N.S.
Treatments	5577.89	3/400	1859.30	7.46	.005
Days x Strains	1421.95	4/400	355.49	1.43	N.S.
Days x Treatments	1168.99	12/400	97.42	.39	N.S.
Strains x Treatments	788.84	3/400	262.95	1.06	N.S.
Days x Strains x Treatments	2472.53	12/400	206.04	.83	N.S.
Error	99632.00	400	249.08		

did not differ among themselves). Likewise, in regard to treatments, the subjects of both strains given early experience in the outdoor enclosure were significantly less active ($P<.01$) than the laboratory-reared treatment groups (which did not differ among themselves). Thus, while activity may be used to explain the longer latencies of the outdoor enclosure-reared semi-domestic animals in entering the open-field, it cannot account for the

Figure 11. Mean activity (wheel-running) units for all experimental groups during the first five days in the unfamiliar living environment. (NM = natural mother; WF = within fostered; CF = cross-fostered; OP = outdoor enclosure.)

FIGURE 11


DOM.
WILD
NM
WF
CF
OP
82
78
74
70
66
62
58
54
ACTIVITY UNITS
1
2
3
4
5
DAYS

differential initial food consumption of the two strains in response to the strange environment.

Effect of total water deprivation. As stated in the section on procedure, following five days exposure to the novel environment, all but the fostered animals were totally deprived of water until death. Since the subjects began to die 48 hours after deprivation, the effects of water deprivation on body weight, food consumption and activity were considered for these two 24 hour periods only. In this manner constant subsample numbers were maintained for purposes of statistical analysis.

Since a drop in body weight and food consumption is inevitable during total water deprivation, these measures were expressed as a percentage drop (from the pre-deprivation levels) for purposes of strain comparison. In the case of body weight, the value obtained for each animal immediately prior to deprivation (Day 5) was considered 100%. The body weight following 24 hours of deprivation was expressed as a percentage of this predeprivation weight and so on for the second day of deprivation. Since body weight would be expected to drop with successive days of deprivation, days post-deprivation were treated separately in the analysis. Fostered groups are excluded from this

and all subsequent analyses.

The mean percent body weight and food consumption of the pre-deprivation level (100%) and activity scores for the first two days of total water deprivation are presented in Tables 22, 23, and 24 and Figures 12, 13, and 14, respectively. The results of the statistical analyses of the data for these variables are given in Tables 25 (body weight), 26 (food consumption) and 27 (activity). As Table 25 indicates, a significant treatment effect for body weight was obtained on both days (both $P<.001$) whereas the

Table 22. Body weight for the two days following total water deprivation expressed as the mean percent of the pre-deprivation level (NM = natural mother; OP = outdoor enclosure; C = control).

		Day	
		6	7
Wild			
	NM	79.5	69.9
	OP	82.7	73.1
	C	84.3	75.3
Domestic			
	NM	79.5	69.6
	OP	80.9	71.4
	C	84.0	73.7

Table 23. Food consumption for the two days following total water deprivation expressed as the mean percent of the pre-deprivation level (NM = natural mother; OP = outdoor enclosure; C = control.

		Day	
		6	7
Wild			
	NM	40.9	28.6
	OP	90.2	62.4
	C	47.6	33.9
Domestic			
	NM	45.6	19.9
	OP	49.9	26.2
	C	50.7	25.5

Table 24. Mean wheel-running activity units on test days 5 (pre-deprivation), 6 and 7 (2 days following total water deprivation). (NM = natural mother; OP = outdoor enclosure).

		Day		
		5	6	7
Wild				
	NM	69.6	65.7	56.8
	OP	52.2	57.2	57.3
Domestic				
	NM	66.4	72.3	67.9
	OP	64.1	65.3	55.0

Figure 12. Mean percent of the pre-deprivation body weight for the two days following total water deprivation. (Open circle = semi-domestic strain; solid circle = wild strain; solid line = natural mother; broken line = outdoor enclosure; dash-dot line = control group)

FIGURE 12

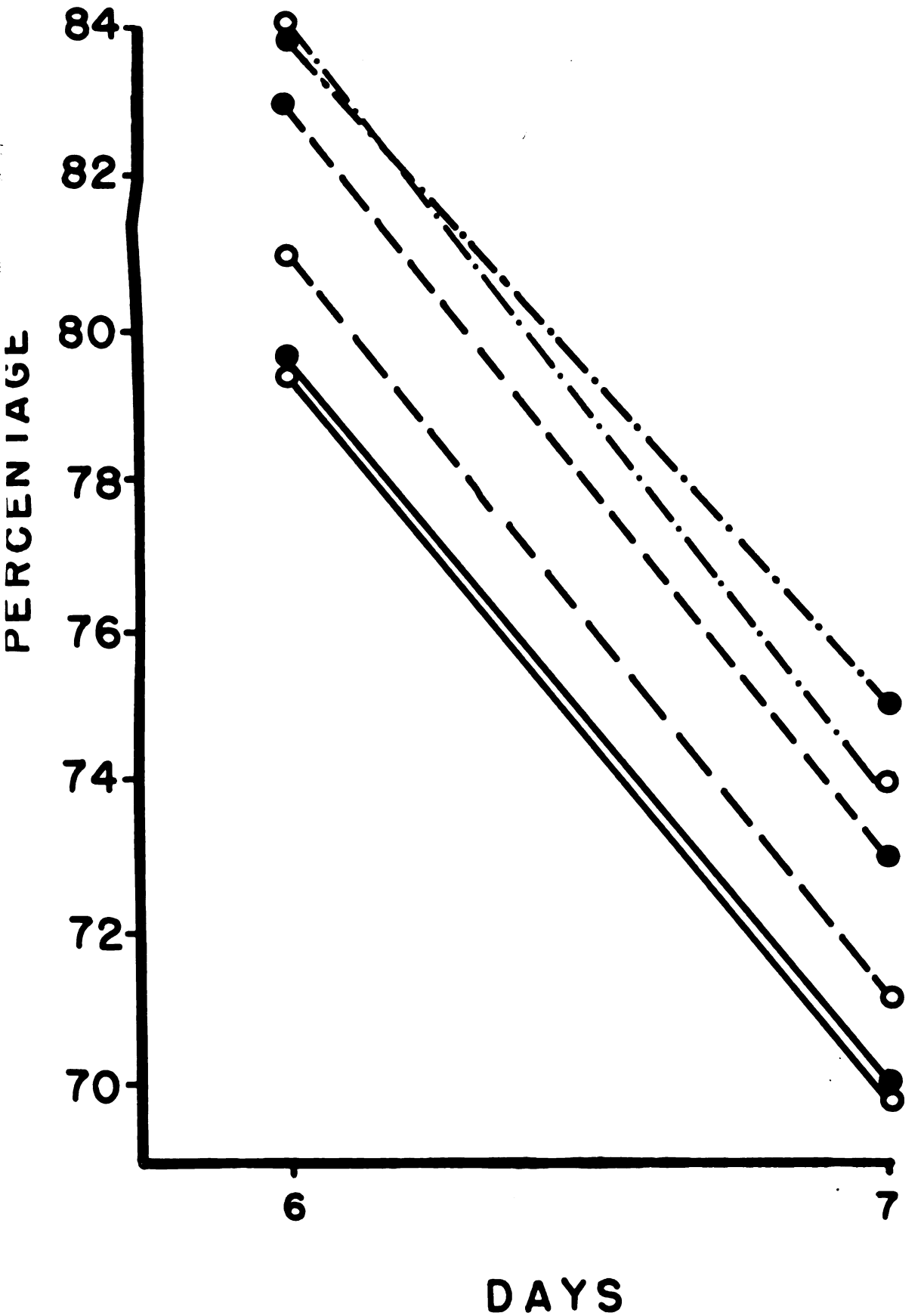


Figure 13. Food consumption for the two days following total water deprivation expressed as the mean percent of the pre-deprivation level. (Open circle = semi-domestic strain; solid circle = wild strain; solid line = natural mother; broken line = outdoor enclosure; dash-dot line = control group.)

FIGURE 13

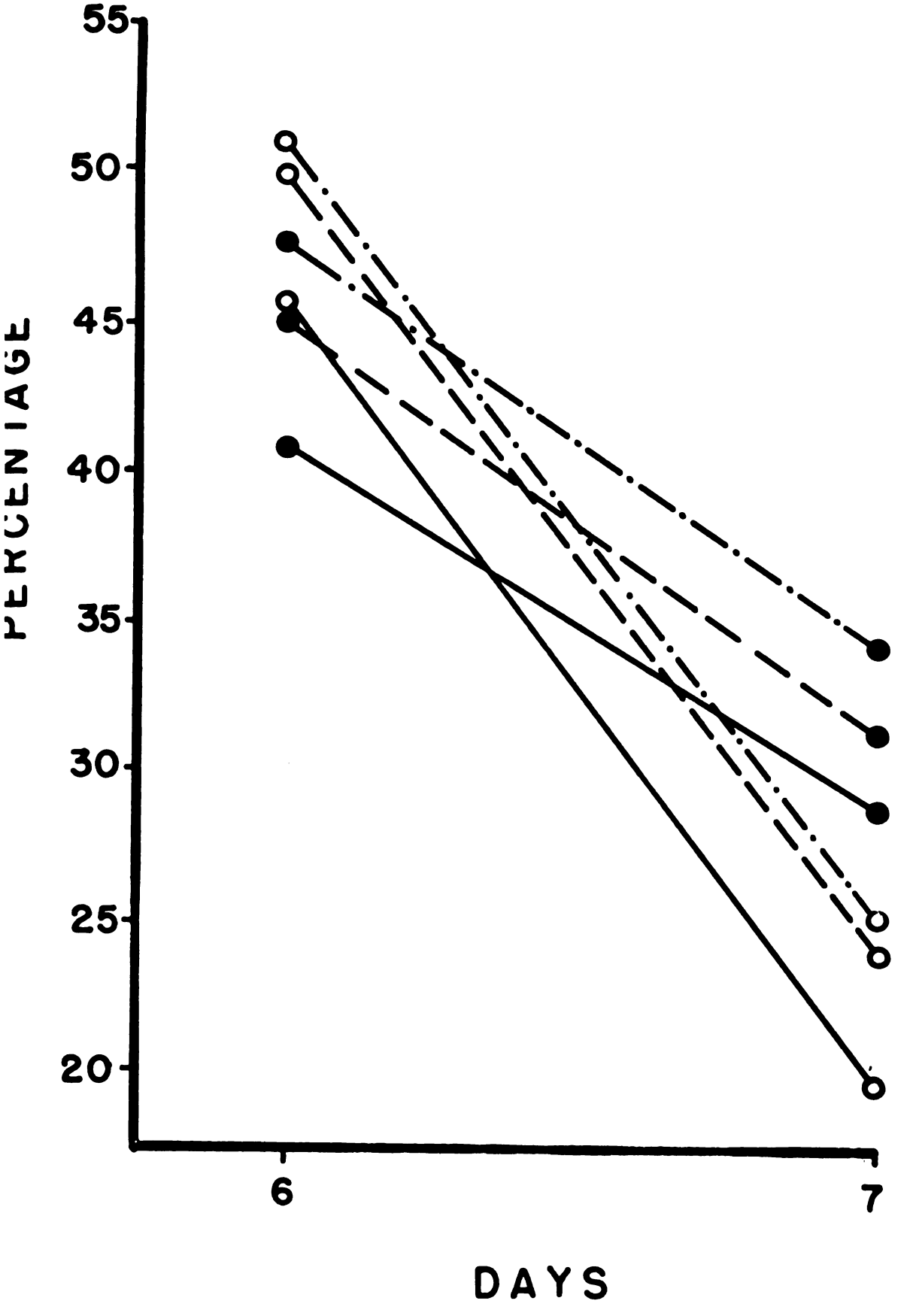


Figure 14. Mean activity units for the day (5) prior to total water deprivation and the two days (6 & 7) following. (Open circle = semi-domestic strain; solid circle = wild strain; solid line = natural mother; broken line = outdoor enclosure group.)

FIGURE 14

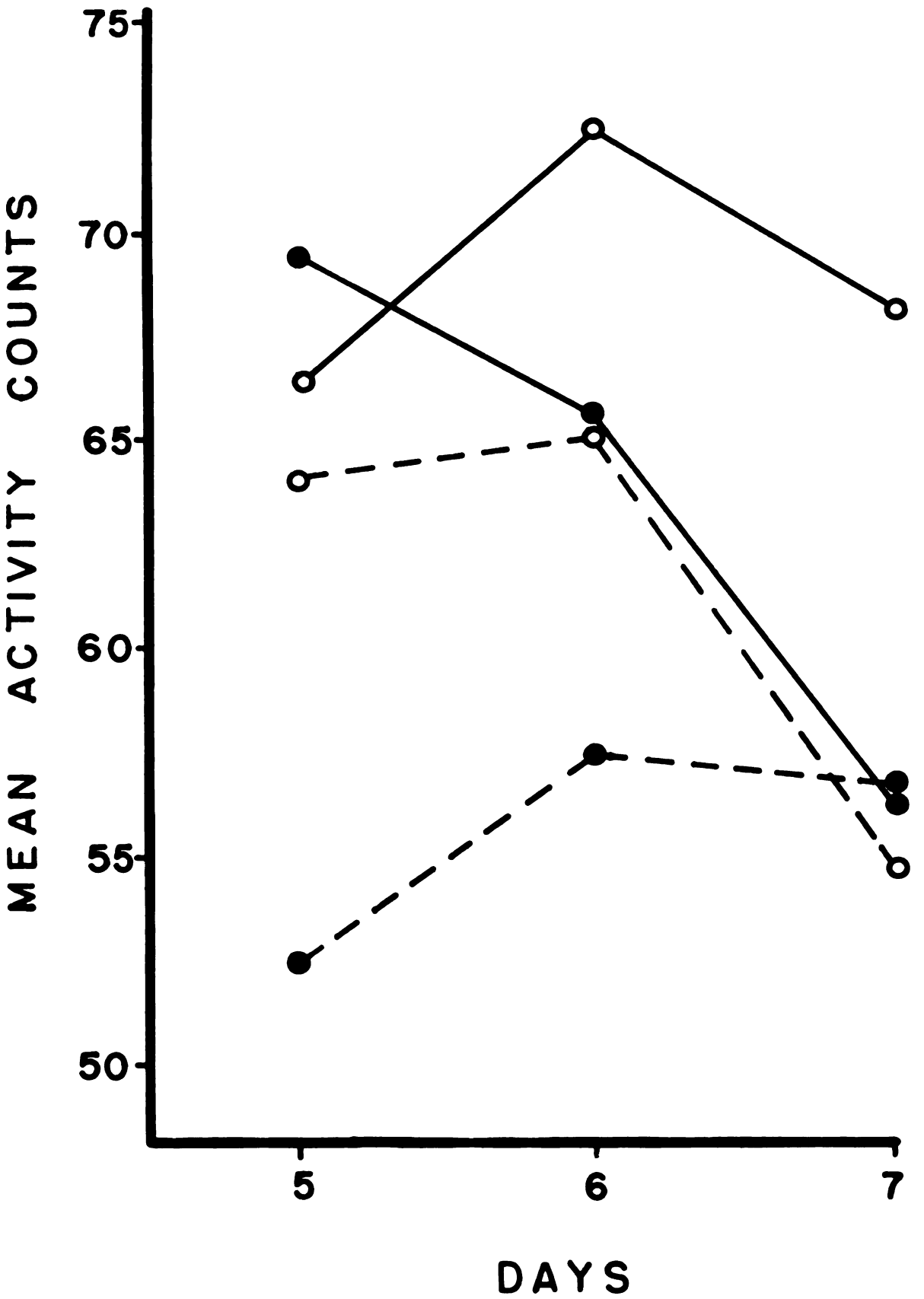


Table 25. Results of the statistical analysis of the rate of body weight loss due to total water deprivation.

1. First day following deprivation

Factor	Sum Sq.	d.f.	Mean Sq.V.	F	Prob.
Strain	15.91	1/114	15.91	1.59	N.S.
Treatment	424.14	2/114	212.07	21.21	.001
Strain x Treat.	20.28	2/114	10.14	.47	N.S.
Error	1142.34	114	10.02		

2. Second day following deprivation (includes first day's loss).

Factor	Sum Sq.	d.f.	Mean Sq.V.	F	Prob.
Strain	46.13	1/114	46.13	3.55	N.S.
Treatment	453.98	2/114	226.99	17.46	.001
Strain x Treat.	12.10	2/114	6.05	.47	N.S.
Error	1481.62	114	13.00		

strains did not differ. The multiple range test applied to these data pointed out that the mice reared by their natural mothers and placed in the activity wheels lost weight significantly faster ($P<.01$) than the control animals (same effect for both strains) while the outdoor enclosure mice occupied an intermediate position.

Table 26. Results of the statistical analysis of the decrease in food consumption due to total water deprivation.

Factor	Sum Sq.	d.f.	Mean Sq.V.	F	Prob.
Strain	154.72	1/228	154.72	1.00	N.S.
Days	21848.51	1/228	21848.51	141.89	.001
Treatment	1392.43	2/228	696.21	4.52	.025
Strain x Days	2014.34	1/228	2014.34	13.08	.005
Strain x Treat.	73.06	2/228	36.53	.24	N.S.
Days x Treat.	4.54	2/228	2.27	.01	N.S.
Strain x Days x Treatment	33.91	2/228	16.96	.11	N.S.
Error	35108.22	228	153.98		

Food consumption during water deprivation was analyzed similarly except that the factor days were included in the analysis. In this comparison the mean food consumption per gram body weight for the three days prior to deprivation was taken as the 100% level and, as in the case of body weight, deprivation levels were expressed as a percentage of these values. Again, the strains did not differ.

Table 27. Results of the statistical analysis of wheel-running activity on test day 5 and the two days following total water deprivation.

Factor	Sum Sq.	d.f.	Mean Sq.V.	F	Prob.
Strain	1040.1	1/132	1040.1	2.46	N.S.
Days	847.6	2/132	423.8	1.00	N.S.
Treatment	2264.2	1/132	2264.2	5.35	.025
Strain x Days	75.0	2/132	37.5	.09	N.S.
Strain x Treatment	9.50	1/132	9.5	.02	N.S.
Days x Treatment	79.40	2/132	39.7	.09	N.S.
Strain x Days x Treatment	1212.3	2/132	606.2	1.43	N.S.
Error	55877.9	132	423.3		

However, significant effects for days ($P<.001$), treatments ($P<.025$) and the strain-day interaction ($P<.005$) were obtained. As expected, food consumption decreased with days. Again, the natural mothered mice experienced the fastest drop, although this drop was significantly faster only between the domestic natural mothered group and the wild control group. The significant interaction between strains and days pointed out that whereas the wild strain

tended to show a faster initial drop in food consumption (not significant) on the second day of deprivation, food consumption was lowest in the semi-domestic strain ($P<.01$ - Multiple Range).

Contrary to the rather typical response of the white rat (see Literature Review) the mice employed in the present study (control groups not included) showed no change in wheel-running activity in response to total water deprivation. Again, some data of certain groups were randomly discarded to achieve an equal subsample N of 12 per treatment group. Since no consistent change in activity was observed due to deprivation, the actual raw data, rather than percent changes, were used in this analysis. The only significant factor obtained (see Table 27) was that of treatment ($P<.025$). As seen in Figure 14, the mice given early experience in the outdoor enclosure were less active than those reared in the laboratory. This is probably indicative of the decreased general activity of this group found previously.

Survival time in days is presented in Figure 15. Table 28 gives the mean survival time in days for the three treatment groups involved. The results of the statistical analysis, involving strains and treatments,

Figure 15. Mean survival time in days following total water deprivation (C = control; NM = natural mother; OP = outdoor enclosure group).

FIGURE 15

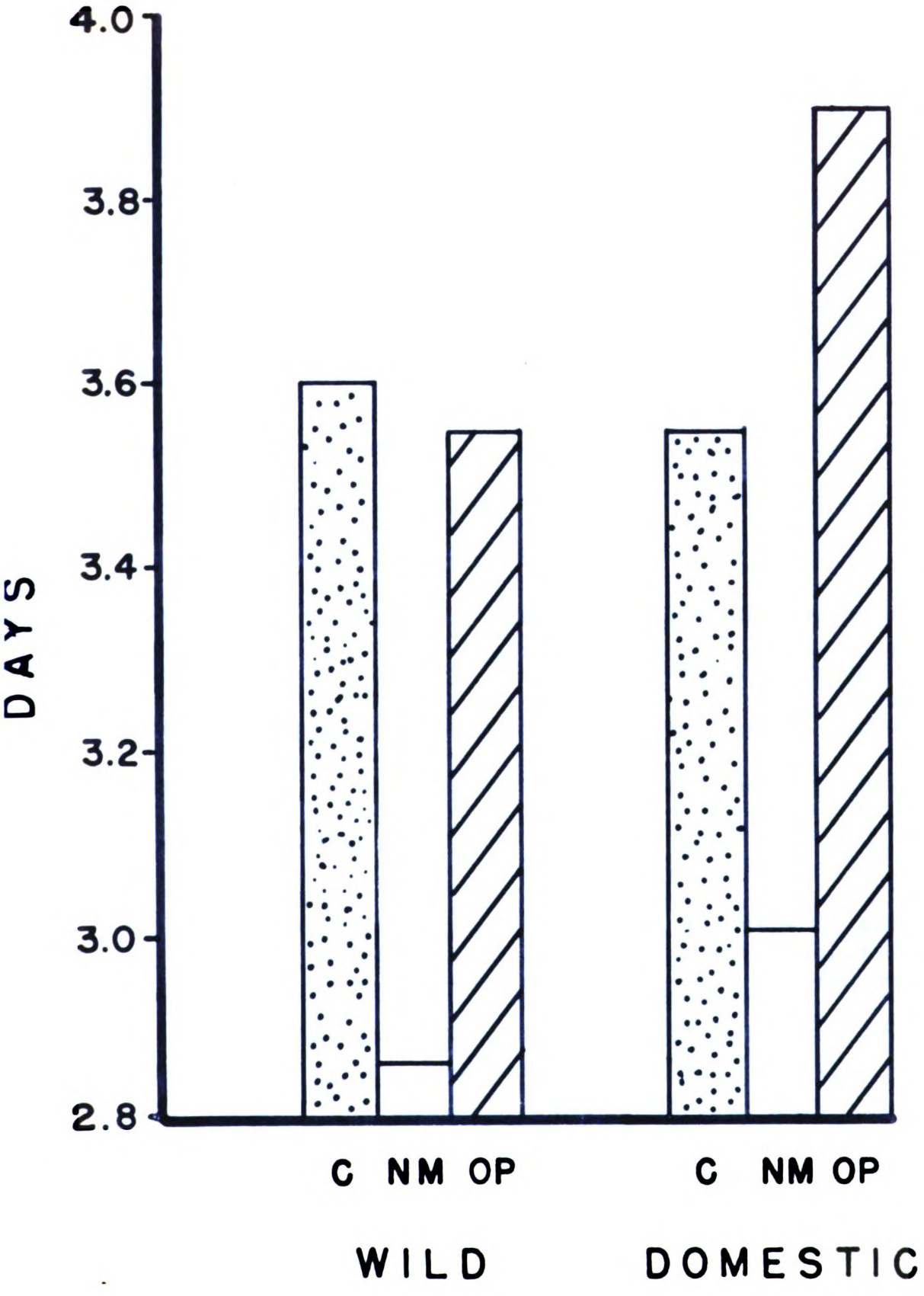


Table 28. Mean survival time in days following total water deprivation (C = control; NM = natural mother; OP = outdoor enclosure group).

	Treatment		
	C	NM	OP
Wild	3.6	2.8	3.6
Semi-Domestic	3.6	3.0	3.9

are given in Table 29. Log scores rather than raw data were used to attain homogeneity of variance. Again, no strain differences were found although a significant treatment effect ($P<.001$) was obtained. This was due to a shorter survival time of the natural mothered group, a result not surprising considering that this group showed the fastest drop in food consumption and body weight following water deprivation.

Table 29. Results of the statistical analysis of survival time in days following total water deprivation.

Factor	Sum Sq.	d.f.	Mean Sq.V.	F	Prob.
Strain	.68	1/114	.68	.46	N.S.
Treatments	146.40	2/114	73.20	49.13	.001
Strain x Treat.	.70	2/114	.35	.23	N.S.
Error	170.03	114	1.49		

DISCUSSION

The behavioral responses of wild and semi-domestic strains of deermice to a novel open-field stimulus are summarized in Table 30. All strain differences indicated are statistically significant.

Table 30. Summarization of the results obtained in the open-field test.

Subjects	Latency to Enter O.F.	
	Slow	Fast
Wild Genotype		
Laboratory-Reared		
Natural Mother	x	
Within Fostered	x	
Cross Fostered	x	
Enclosure-Reared		
Natural Mother	x	
Semi-Domestic Genotype		
Laboratory-Reared		
Natural Mother		x
Within Fostered		x
Cross Fostered		x
Enclosure-Reared		
Natural Mother	x	

The following conclusions can be drawn from these results. First, due to 20-25 generations of laboratory breeding, a semi-domestic strain has diverged (genetically) from a strain representing its wild ancestors to the point that it displays significantly less caution in approaching or investigating a novel stimulus. Secondly, whereas the behavior of the wild strain is relatively "fixed" (remains the same whether reared in the laboratory or in nature) the behavior of the semi-domestic strain is relatively "unfixed" (can be modified by experience). The semi-domestic strain must have experience in the natural environment of the species in order to display the typical "wild type" response to unfamiliar stimuli in its environment. Third, the experience of fostering semi-domestic young on wild-caught females and vice versa had no effect on the behavior of the offspring of either strain.

The "neophobia" of wild animals to novel stimuli is difficult to extinguish (Chitty and Shorten, 1946; Thompson, 1948; Richter, 1953; Menzel, 1964). After 48 hours habituation to the open-field, the wild subjects showed no significant decrease in the "latency to enter" scores. On the other hand, a significant decrease in latency scores following the habituation period was

observed for the semi-domestic mice. On the initial reaction to the least weasel, the scores of the semi-domestic subjects were reversed. The wild subjects also experienced an increase in latency scores to the weasel, an increase that was almost seven times greater than that experienced by the semi-domestic animals. If the mice were responding specifically to the weasel, these results suggested that natural selection operates directly on those responses which enable animals to avoid specific detrimental stimuli in their native habitat. Night-flying moths respond specifically, to the high frequency sounds emitted by bats which hunt them (Roeder, 1963). Escape responses in the sea anemone; Stomphia, (Sund, 1948) are known to be elicited by specific chemical stimuli from predatory starfish. Models resembling hawks will elicit escape responses from several bird species (Tinbergen,1951) while the bobwhite quail exhibits distinct escape responses to a live red-tailed hawk rather than its model (Martin and Melvin, 1964).

In the open-field test, the animals were free to choose whether or not to approach the novel stimulus. The second test was designed to answer the question, "how do the strains differ in their reactions to novel stimuli when suddenly placed in an unfamiliar environment with no opportunity for escape?" This study was expanded to answer the question, "how do the strains differ in their reaction to total water deprivation?" The results of these tests can be summarized as follows. First, activity did not vary differentially with the strains over days in response to

either the novel environment or total water deprivation. Activity was significantly higher for both strains during the first 24 hours in the wheels than thereafter. This may have been the result of an initially high exploratory drive and/or it may represent initial attempts to escape from the novel living quarters. Secondly, body weight did not change in either strain prior to deprivation. In response to water deprivation, the strains showed no differential rate of weight loss. Thirdly, food consumption was significantly lower in the wild strain during the first 48 hours in the new environment than thereafter, while the amount of food consumed by the semi-domestic strain did not change over days (prior to water deprivation). This "neophobic" response of the wild subjects to their new environment was confirmed by observing that the wild controls, when moved to different cages with familiar cues, showed a significant increase rather than decrease) in food consumption. Both strains exhibited a drop in food consumption in response to water deprivation but the difference between strains was not significant until the second day of deprivation when the semi-domestics consumed significantly less food.

As in the open-field test, the type of maternal care produced no significant effect upon activity, initial body weight or food consumption.

Early experience in the natural environment (as opposed to the laboratory) seems to have a depressing effect on activity in the laboratory. This was shown by Price (1963) in a simple tilt-box test for activity, whereby

wild-caught prairie deermice were significantly less active than either their own offspring (born and reared in the laboratory) or a semi-domestic stock. In the present test, wheel running activity was found to be depressed in mice given early experience in nature, regardless of the strain. The decreased activity of these subjects could serve as a possible explanation for the following observed phenomena: (1) the higher "latency to enter" scores for the enclosure-reared semi-domestic animals employed in the open-field tests, (2) the somewhat higher body weight of these animals, (3) the lower level of food consumption when housed in activity wheels (less food needed to maintain physiological homeostasis than a highly active mouse), (4) the slower decrease in body weight and food consumption under conditions of total water deprivation and (5) the longer survival time during this deprivation.

Rather than think of activity, per se, as a causal explanation for these phenomena, it is possible that decreased activity in this case, is merely a side effect of a general increase in emotionality or sensitivity to changes in its environment. This could be engendered, on one account, by the complete change in environment when these animals were brought into the laboratory for purposes of testing. The change from an environment in which nearly complete freedom of movement was possible to one where movement over only 55 square inches was possible stands in sharp contrast to the constancy of the laboratory environment experienced by animals born and reared therein. The change from

a situation where conspecifics could be avoided to one where a conspecific was always present, could likewise, have significant consequences, not to mention those associated with a sudden loss of climatic fluctuations. Such changes are bound to have important consequences on the behaviors of the animals involved. Postulation of increased reactivity to unfamiliar stimuli in these animals seems especially appropriate considering that decreased ambulation has often been used as a correlate of heightened emotionality in the standard open-field test used commonly in studies on the rat (Hall, 1936; Weininger, 1956: Broadhurst, 1958; Denenberg 1962). On the other hand, an animal living in a constantly changing environment might be more resistant to environmental change and show a decreased sensitivity to novel stimuli. Levine, Alpert and Lewis (1958) have shown that rats handled early in life showed a much earlier maturation of the adrenocortical response to stress. Levine postulated that the laboratory environment provides insufficient opportunity for proper stimulation of the animal's hormonal system. This hypothesis is further substantiated by the superior development of the adrenal glands of wild Norway rats as compared to their domestic counterparts (Richter, 1959). Whereas this postulated hypersensitivity of unstimulated animals to unfamiliar environmental stimuli could account for the inferior resistance of the natural-mothered groups to total water deprivation, the lack of an initial depressed food consumption in response to being

placed in the activity wheels indicates a relative insensitivity to novel stimuli. A hormonally controlled response however, would serve well to explain the sex difference obtained among the enclosure reared semi-domestic animals in reaction to the open-field. Although this difference was found to be non-significant in the statistical analysis, larger samples might well establish this difference as significant.

Since food consumption most adequately displayed the strain differential "neophobic" response to an unfamiliar environment, the results of the first 24 hour test period are summarized diagrammatically in Table 31. All differences indicated are statistically significant. Although the food consumption of the enclosure-reared semi-domestics was significantly lower than that of the laboratory-reared groups it is questionable if this actually represents "wild type" behavior in that food consumption did not rise with days as it did with the genotypically wild animals, but rather stayed at a constant low level.

It was first thought that the decreased food consumption of this semi-domestic group was made possible by a reduction in activity. This probably is not the case, however, since the wild enclosure-reared subjects

displayed the same activity phenomenon but still showed the initial depression of food consumption. Accepting the depressed food consumption of the semi-domestic enclosure-reared animals as representing "wild type" behavior, a comparison of Tables 30 and 31 reveals that the conclusions

Table 31. Initial food consumption in response to being placed in a strange environment with no opportunity for escape.

Subjects	Food Consumption	
	High	Low
Wild Genotype		
Laboratory-Reared		
Natural Mother		x
Within Fostered		x
Cross Fostered		x
Enclosure-Reared		
Natural Mother		x
Semi-Domestic Genotype		
Laboratory-Reared		
Natural Mother	x	
Within Fostered	x	
Cross Fostered	x	
Enclosure-Reared		
Natural Mother		x

warranted by the results of these two tests are essentially the same and, therefore, will not be repeated. In both cases the genetically wild deermice displayed a definite "neophobic" reaction to novelty in their environment, a behavior which was not altered by early rearing experience (in the laboratory versus the natural environment). On the other hand, the response of the semi-domestic animals to unfamiliar stimuli was minimal and involved behavior which was modifiable by the type of early experience received.

These same conclusions were reached by Wecker (1963) who studied the role of early experience in the habitat selection in prairie deermice. In this study he showed that a wild stock of mice correctly chose the field environment whether reared in nature or in the laboratory. A semi-domestic stock (related to the one used in the present study) about 15-20 generations removed from the wild, failed to choose the field habitat unless given early experience in the natural field environment. In seeking a genetic explanation for this loss of the innate capacity for habitat selection, Wecker (op. cit.) proposed the "Baldwin Effect" (Baldwin, 1896) to explain the genetic acquisition of habitat selection in this species. One explanation for the "Baldwin Effect" merely states

(Simpson, 1953) that random mutations, which genetically determine responses previously acquired in each generation, will be selected for and in enough time will be represented by the entire population. In the writer's mind this is merely stating the mechanism by which "natural selection" works. Therefore, Wecker's explanation of the loss of a "predetermined" habitat selection response in the semi-domestic stock by a "reverse Baldwin Effect," merely postulates the relaxation of natural selection. Such relaxation undoubtedly occurs in captivity and could, in part, account for the loss of the genetic predisposition of this response in a mere 20-25 generations.

Another interpretation of the "Baldwin Effect" that recognizes the importance of genetic systems in the "acquisition" of behavior is one advanced by Schmalhausen (1949). In this interpretation he postulates that selection operates on the ability to acquire characters and not on specific genetical characters, themselves. An acquired character necessarily occurs within a genetically-determined reaction range, with natural selection determining the breath or narrowness of this range of reactivity. If a broad reaction range is selected for, many adaptive responses are possible. If the range is narrow few

alternatives are possible. Thus, the evolution of the genetic predetermination of a response, such as habitat selection, can occur by a progressive reduction in the number of possible alternatives available in the behavioral repertoire of the species. A response formerly dependent on a combination of genetic and environmental factors may become genetically fixed. The possible responses to novel stimuli, for example, may be pre-determined by the range of species' reactivity to these factors. If a high degree of reactivity to novel stimuli is favorable for survival in nature, the range of responses to unfamiliar stimuli may be narrowed by selection so that high reactivity becomes genetically predetermined. If the reactivity range becomes broader by a relaxation or reversal of natural selection, the degree of reactivity to novel stimuli may depend, in part, on responses acquired or modified by the environment. Thus, this mechanism exists as a possible explanation for the loss in reactivity of the semi-domestic strain to unfamiliar stimuli in its environment and the modifiability of this behavior tempered by the environment in which the individuals of this strain are reared.

A somewhat similar mechanism called "Genetic

Assimilation" has been proposed by Waddington (1961). This theory states that in response to environmental change, the genetic systems making possible an adaptive response will become subject to selective forces, thus, increasing the incidence of the response with time. As Mayr (1963) points out the use of the term "genetic assimilation" for this phenomenon is unfortunate since the hereditary materials are present in the population from the start. Mayr proposes the term "threshold selection" to describe this phenomenon in that, according to the scheme proposed by Waddington and his co-workers, environmental change merely lowers the response threshold below that of phenotypic expression so that, now, natural selection is free to work on the genes governing the response by increasing or decreasing their frequency in the gene pool of the population. Thus, the environmental change merely "reveals which individuals in the population already carry polygenes or modifiers of the desired phenotype."

Genetic assimilation may be summarized as a four-step phenomenon involving: (1) a change in the environment; (2) subsequent lowering of the threshold for a specific adaptive response; (3) discharge of this response by those individuals already possessing the capacity to

respond; and (4) the influence of natural selection, favoring those individuals which emit the adaptive response in the right situation. The lowering of reactivity to novel stimuli during domestication can result from this sequence of events in reverse. The transition from nature to the laboratory, where reactivity to unfamiliar stimuli is no longer important for survival, causes a cessation of natural selection on the behaviors determining the degree of reactivity. The relaxation of natural selection allows competing responses to develop so that the response threshold to novel stimuli is raised. The capacity to respond adaptively in novel situations will lie dormant until a sufficient change occurs in the environment to cause the response to be reinstated. The "wild type" responses of these deermice to novel factors in their environment have been lost during domestication by the elevation of the response threshold. Early rearing experience in a semi-natural outdoor enclosure so lowers the threshold that "wild type" responses to novel stimuli are elicited.

Both of the proposed explanations are based on the assumption that a relaxation or a reversal of natural selection occurs in regard to reactivity to novel stimuli when a population of animals is taken from the wild and

placed in captivity. Whether the reduction in reactivity observed is due to a broadening of the reaction range or a shifting of the response threshold, the fastest alterations in behavior during domestication will involve responses where "reverse selection" is involved. As stated in the introduction, a high reactivity to novel stimuli might be highly advantageous in nature while the same behavior could be disadvantageous in captivity. Hence, selective forces may be reversed in regard to certain behaviors during the transition from nature to the laboratory.

Since the reproductive potential of animals under psychological stress is severely reduced (see Literature Review) one can assume that the least reactive individuals of a wild-caught population in captivity will leave the bulk of the offspring. If low reactivity to environmental change is positively correlated with reproductive success in captivity, one can positively assert that "reverse selection" favoring this behavior does occur during domestication. Correlation studies of the behavior of wild-caught individuals with subsequent reproductive performance would test this relationship. Although this was not done,

the reproductive performance of some 50 wild-caught females was compared with the performance of 75 semi-domestic females (Price, 196_). It was found that only 60.0 percent of the wild-caught females had given birth in the laboratory by four months following pairing as opposed to 90.7 percent of the semi-domestic females (X^2 = 14.90; d.f. = 1; P<.005). If the non-breeding wild group represents the highly reactive individuals of the population, then, in this first generation in captivity, severe selection for non-reactive behavior will have occurred. By the process of reverse selection, rapid changes in behavior will occur among populations involved in the process of domestication.

SUMMARY

A stock of prairie deermice, 17 years and approximately 20-25 generations removed from the wild, was compared with a genotypically wild population for their reactivity to several selected novel situations. It was postulated that a loss in reactivity to unfamiliar stimuli had accompanied the domestication process as a result of genetic modifications caused by a change in selection pressures in the laboratory. A total of 360 subjects, including the semi-domestic stock and offspring of a representative sampling of wild-caught animals was used for this comparison. The first test measured the tendency to approach an unfamiliar arena (open-field) and a natural predator (least weasel), before and after habituation. It was hypothesized that when compared with wild subjects the semi-domestic mice would exhibit: (1) shorter latencies to enter the open-field and greater activity therein; (2) similar latencies and activity following adequate opportunity for habituation to the open field;

and (3) shorter latencies and greater activity in response to a natural predator caged in the open field.

The second test measured the effect of being placed in an unfamiliar living environment (activity wheel) on body weight, food consumption and activity. This latter test was expanded to study the effect of a severe physiological stress, total water deprivation, on the body weight, food consumption, activity and survival time of the two strains. It was postulated that (1) being placed in the novel environment would inhibit the feeding behavior of the wild subjects and not affect the food consumption of the semi-domestic mice; (2) the suppressed feeding of the wild strain would result in a loss in body weight; and (3) differences in wheel-running activity would not explain the initial drop in food consumption by the wild mice.

Furthermore it was postulated that in response to total water deprivation the wild genotype subjects would show: (1) a slower rate of body weight loss; and (2) a slower decrease in food consumption than the semi-domestic strain. An increase in wheel-running activity was predicted for both strains. Lastly, it was hypothesized that the wild subjects would outlive the semi-domestics.

To determine the relative roles of genetic and environmental factors in the behavior tested, young neonates were fostered on mothers of the opposite strain (maternal influence) and young weanlings were reared in a semi-natural outdoor enclosure in contrast to the laboratory (place of rearing influence). The hypotheses tested were that: (1) fostered animals would display the behavior of the maternal strain, and (2) the place of rearing (laboratory versus outdoor enclosure) would not influence the reactivity level to novel stimuli.

The results indicated that when compared with wild subjects the semi-domestic strain showed: (1) significantly shorter latencies in approaching and investigating the open field; (2) habituation to the open-field whereas the wild strain did not; and (3) shorter latencies in approaching and investigating the predator.

The second test revealed that: (1) food consumption of the wild strain decreased when placed in unfamiliar living quarters whereas the consumption level of the semi-domestic subjects did not change; (2) neither strain changed in body weight; (3) the strains did not exhibit differential activity in the novel environment; (4) both strains had the same rate of body weight loss, food

consumption and survival time in response to total water deprivation; and (5) water deprivation had no initial accelerating effect on wheel-running activity. Enclosure-reared subjects and a control group for handling and isolation showed greater tolerance to water deprivation than mice reared in the laboratory by their own mothers.

Fostering had no major effects. Whereas the behavior of the wild subjects was not affected by the place of rearing, the behavior of the semi-domestic mice given experience in the outdoor enclosure became similar to that of the wild strain. It was concluded that the behavior of the wild mice was relatively "fixed" but the behavior of the semi-domestic subjects could be modified by experience.

The factors contributing to the decreased reactivity of the semi-domestic strain to novel situations were discussed. It was proposed that this change in behavior has resulted from: (1) a relaxation of natural selection (present in nature), (2) natural selection in the laboratory caused by decreased reproduction among highly reactive animals and, (3) unconscious artificial selection by man. The genetic changes resulting from these selection phenomena may have favored an upward

shift in the response threshold for reactivity to novel stimuli. Its modifiability following semi-domestication may be due to a broadening of the range of environmental influence (decreased genetic control).

LITERATURE CITED

Adolph, E. F. 1947. Urges to eat and drink in rats. Amer. Jour. Physiology, 151: 110-125.

Baldwin, J. M. 1896. A new factor in evolution. Amer. Nat. 30:441-451, 536-553.

Barnett, S. A. 1956. Behavior components in the feeding of wild and laboratory rats. Behaviour 9: 24-43.

Barnett, S. A. 1958. Experiments on "neophobia" in wild and laboratory rats. Brit. Jour. Psych. 49: 195-201.

Barnett, S. A. 1963. The Rat: A Study in Behavior. Aldine Publ. Co., Chicago.

Beck, R. C. 1964. "Some effects of restricted water intake on consumatory behavior of the rat," in Thirst, ed. by M. J. Wayner, MacMillan, New York. pp. 305-316.

Bindra, D. and Thompson, W. 1953. An evaluation of defecation and urination as measures of fearfulness. Jor. Comp. Physiol. Psych., 46 (1): 43-45.

Bing, F. C. and Mendel, L. B. 1931. The relationship between food and water intakes in mice. Amer. Jour. Physiol. 98: 169-179.

Broadhurst, P. L. 1958. Determinants of emotionality in the rat: strain differences. Jour. Comp. Physiol. Psych. 51: 55-59.

Broadhurst, P. L. 1960. Experiments in psychogenetics: applications of biometrical genetics to the inheritance of behavior. In Experiments in Personality Vol. I. Psychogenetics and Psychopharmacology. ed. by H. J. Eysenck. pp. 1-102. Routledge & Kegan Paul, London.

Broadhurst, P. L. 1961. Analysis of maternal effects in the inheritance of behaviour. Animal Behavior 9: 129-141.

Brobeck, J. R. 1945. Effects of variations in activity, food intake and environmental temperature on weight gain in the albino rat. Amer. Jour. Physiol. 143: 1-5.

Brody, E. G. 1942. The genetic basis of spontaneous activity in the albino rat. Comp. Psychol. Monogr. 17 (5): 1-24.

Campbell, B. 1964. Theory and research on the effects of water deprivation on random activity in the rat. In Thirst, ed. by M. J. Wayner. pp. 317-334. MacMillan, New York.

Campbell, B. and Cicala, G. 1962. Studies of water deprivation in rats as a function of age. Jour. Comp. Physiol. Psych., 55 (5): 763-768.

Chevillard. 1935. Cited in Chew, Robert M. 1951. The water exchanges of some small mammals. Ecol. Monographs 21 (3): 215-225.

Chew, R. M. 1951. The water exchanges of some small mammals. Ecol. Monographs 21 (3): 215-225.

Chew, R. M. 1961. Water metabolism of desert-inhabiting vertebrates. Biol. Revs. 36: 1-31.

Chew, R. M. and Hinegardner, R. 1957. Effects of chronic insufficiency of drinking water in white mice. Jour. Mamm. 38 (3): 361-373.

Chitty, D. 1954. Control of Rats and Mice (ed. two Vol.) Clarendon Press, Oxford.

Chitty, D. and Shorten, M. 1946. Techniques for the study of the Norway rat. Jour. Mamm. 27: 63-79.

Christian, J. J. and Davis, D. E. 1964. Endocrines, behavior and population. Science 146 (3651): 1550-1560.

Coburn, C. A. 1922. Heredity of wildness and savageness in mice. Behavior Monographs. 4 (5): 1-71.

Darwin, C. 1875. The Variation of Animals and Plants Under Domestication. Vol. 1., John Murray, London.

Denenberg, V. H. 1962. The effects of early experience. Chap. 6. In: The Behavior of Domestic Animals, ed. E.S.E. Hafez pp. 109-138. Williams & Wilkins, Baltimore.

Denenberg, V., Carlson, P. and Stephans, M. 1962. Effects of infantile shock upon emotionality at weaning. Jour. Comp. Physiol. Psych. 55 (5): 819-20.

Denenberg, V., Ottinger, D. and Stephans, M. 1962. Effects of maternal factors upon growth and behavior of rats. Child Development 33: 65-71.

Denenberg, V. and Whimbey, A. 1963. Behavior of adult rats is modified by the experiences their mothers had as infants. Science 142 (3596): 1192-1193.

Eleftheriou, B., Bronson, F. and Zarrow, M. 1962. Interaction of olfactory and other environmental stimuli on implantation in the deermouse. Science 137 (3532): 764.

Farris, E. and Yaekel, E. 1945. Emotional behavior of grey Norway and Wistar albino rats. Jour. Comp. Psych. 38: 109-118.

Foster, D. D. 1959. Differences in behavior and temperament between two races of the deermouse. Jour. Mamm. 40 (4): 496-513.

Fredericson, E. 1952. Reciprocal fostering of two inbred mouse strains and its effects on the modification of inherited aggressive behavior. Amer. Psychol. 7: 241-242. (Abstract)

French, R. L. 1956. Eating, drinking and activity patterns in Peromyscus sonoriensis. Jour. Mamm. 37: 74-79.

Ginsburg, B. and Allee, W. C. 1942. Some effects of conditioning on social dominance and subordination in inbred strains of mice. Physiol. Zool. 15: 485-506.

Griesel, R. D. 1964. The activity of rats reared by active and inactive foster mothers. Psychologia Africana 10 (3): 189-196.

Hale, E. B. 1962. Domestication and the evolution of behaviour. In The Behavior of Domestic Animals (Chapter 2)., ed. by E.S.E. Hafez pp. 21-53. Bailliere, Tindall & Cox, London.

Hall, C. 1934. Emotional behavior in the rat: I. Defecation and urination as measures of individual differences in emotionality. J. Comp. Psych. 18: 385-403.

Hall, C. 1936. Emotional behavior in the rat. III. The relationship between emotionality and ambulatory behavior. J. Comp. Psych. 22: 345-352.

Hall, C. 1951. The genetics of behavior. In Handbook of Experimental Psychology. ed. by S. S. Stevens. pp. 304-329. Wiley, New York.

Harris, V. T. 1952. An experimental study of habitat selection by prairie and forest races of the deermouse, Peromyscus maniculatus. Contr. Lab. Vert. Biology, Univ. of Mich., #56, pp. 1-56.

Hediger, H. 1954. Are wild animals in captivity really wild? Scientific American 190 (5): 76-80.

Howard, W. E. 1949. Dispersal, amount of inbreeding and longevity in a local population of prairie deer-mice on the George Reserve in southern Michigan. Contr. Lab. Vert. Biology, Univ. of Mich. #43, pp. 1-50.

Hunt, H. F. and Otis, L. S. 1953. Conditioned and unconditioned emotional defecation in the rat. Jour. Comp. Physiol. Psych. 46: 378-382.

Jenkins, D. 1961. Population control in protected partridges (Perdix perdix). Jour. of Animal Ecology 30 (2): 235-255.

Joslin, J., Fletcher, H. and Emlen, J. 1964. A comparison of the responses to snakes of lab- and wild-reared Rhesus monkeys. Animal Behaviour 12 (2&3): 348-352.

Keeler, C. and King, H. 1942. Multiple effects of coat color genes in the Norway rat with special reference to temperament and domestication. Jour. Comp. Psych. 34: 241-250.

King, H. D. 1939. Life processes in grey Norway rats during fourteen years in captivity. Amer. Anatomical Memoirs #17.

Kleitman, N. 1927. The effect of starvation on the daily consumption of water by the dog. Amer. Jour. Physiol. 81:336-340.

Leopold, A. S. 1944. The nature of heritable wildness in turkeys. Condor 46: 133-197.

Lepkovsky, S., Lyman, R., Fleming, D., Nagumo, M., and Dimick, M. 1957. Gastrointestinal regulation of water and its effect on food intake and rate of digestion. Amer. Jour. Physiol. 188: 327-331.

Lerner, I. M. 1958. The Genetic Basis of Selection. Wiley, New York.

Levine, S. 1957. Infantile experience and consummatory behavior in adulthood. Jour. Comp. Physiol. Psych. 50: 609-612.

Levine, S. and Broadhurst, P. L. 1963. Genetic and ontogenetic determinants of adult behavior in the rat. Jour. Comp. Physiol. Psych. 56: 423-428.

Levine, S., Slpert, M. and Lewis, G. 1958. Differential maturation of an adrenal response to cold stress in rats manipulated in infancy. Jour. Comp. Physiol. Psych. 51: 774-777.

Lindeborg, R. G. 1952. Water requirements of certain rodents from xeric and mesic habitats. Contr. Lab. Vert. Biology, Univ. of Mich. #58, pp. 1-31.

Lindholm, B. W. 1962. Critical periods and the effects of early shock on later emotional behavior in the white rat. Jour. Comp. Physiol. Psych. 55: 597-599.

Martin, R. C. and Melvin, K. B. 1964. Fear responses of bobwhite quail (Colinus virginianus) to a model and a live red-tailed hawk (Buteo jamaiceinsis). Psych. Forschung 27: 323-336.

Mayr, E. 1963. Animal Species and Evolution, Harvard Univ. Press, Cambridge.

Menzel, E. 1964. Responsiveness to object-movement in young chimpanzees. Behavior 24: 147-160.

Muntzing, A. 1959. Darwin's views on variation under domestication. American Scientist. 47: 314-325.

O'Kelly, L. 1963. The psychophysiology of motivation. In Annual Review of Psychology Vol. 14, ed. by P. R. Farnsworth, pp. 57-92., Annual Reviews, Inc., Palo Alto.

Ottinger, C. R., Denenberg, V. H., and Stephens, M. W. 1963. Maternal emotionality, multiple mothering, and emotionality in maturity. Jour. Comp. Physiol. Psych. 56: 313-317.

Owen, S. 1963. The effect on avoidance response extinction in rats of CS continuation and emotional constitution. Jour. Genetical Psych. 103: 147-151.

Phillips, R. E. and Tienhoven, A. V. 1960. Endocrine factors involved in the failure of pin-tail ducks Anas acuta to reproduce in captivity. Journal of Endocrinology 21: 253-261.

Premack, D. and Premack, A. 1963. Increased eating in rats deprived of running. Jour. Exp. Anal. Behav. 6 (2): 209-212.

Price, E. 1963. Morphological, physiological and behavioral changes in the prairie deermouse, Peromyscus maniculatus bairdii, during the process of domestication. Unpublished Master's Thesis, Michigan State Univ.

Price, E. 196_. The effect of reproductive performance on the domestication of the prairie deermouse, Peromyscus maniculatus bairdii (Subm. for publ.).

Price, E. and King, J. 1967. Domestication and adaptation. Chap. 3 in Adaptations of Domestic Animals ed. E.S.E. Hafez. Lea & Febiger, Philadelphia (to be publ.-Sept.).

Ressler, R. 1962. Parental handling in two strains of mice reared by foster parents. Science. 137: 129-130.

Ressler, R. 1963. Genotype-correlated parental influences in two strains of mice. Jour. Comp. Physiol. Psych. 56 (5): 882-886.

Richter, C. P. 1953. Experimentally produced behavior reactions to food poisoning in wild and domesticated rats. Ann. N. Y. Acad. Sci. 56: 225-39.

Richter, C. P. 1954. The effects of domestication and selection on the behavior of the Norway rat. Jour. Nat. Cancer Inst. 15: 727-738.

Richter, C. P. 1959. Rats, man and the welfare state. The American Psychologist. 14 (1): 18-27.

Richter, C. P. and Rice, K. 1954. Comparison of the effects produced by fasting on gross bodily activity of wild and domestic Norway rats. Amer. Jour. Physiology 179: 305-308.

Robinson, R. 1965. The Genetics of the Norway Rat. Oxford, Pergamon.

Roeder, K. 1963. Nerve Cells and Insect Behavior, Harvard Univ. Press, Cambridge.

Rundquist, E. A. 1933. The inheritance of spontaneous activity in rats. Jour. Comp. Physiol. Psych. 16: 415-438.

Schmalhausen, I. I. 1949. Factors of Evolution: the Theory of Stabilizing Selection. Blakiston, Philadelphia.

Schmidt-Nielson, K. and Schmidt-Nielson, B. 1952. Water metabolism of desert mammals. Physiol. Rev. 32: 135-166.

Schneirla, T. C. 1965. Aspects of stimulation and organization in approach/withdrawal processes underlying vertebrate behavioral development. In Advances in the Study of Behavior, Vol I., ed. Lehrman, D., Hinde, R. and Shaw, E. pp. 1-74, Academic Press, New York.

Simpson, G. G. 1953. The Baldwin effect. Evolution 7:110-117.

Southwick, C. H. 1955. Regulatory mechanisms of house mouse populations: social behavior affecting litter survival. Ecology 36: 627-634.

Spear, N. and Hill, W. 1962. Methodological note: Excessive weight loss in rats living in activity wheels. Psych. Rep. 11 (2): 437-438.

Spence, J. T. and Maher, B. A. 1962. Handling and noxious stimulation of the albino rat: II. Effects on subsequent performance in a learning situation. Jour. Comp. Physiol. Psych. 55: 252-255.

Spurway, H. 1955. The causes of domestication: an attempt to integrate some ideas of Konrad Lorenz with evolution theory. Jour. of Genetics. 53: 323-362.

Stevenson, J. A. F. and Rixon, R. H. 1957. Environmental temperature and deprivation of food and water on the spontaneous activity of rats. Yale Jour. Biol. and Med. 29: 575-584.

Stone, C. P. 1932. Wildness and savageness in rats of different strains. In Studies in the Dynamics of Behavior. ed. by K. S. Lashley, Univ. of Chicago Press, Chicago.

Strominger, J. L. 1947. The relation between food and water intake in normal rats and rats with hypothalamic hyperphagia. Yale Jour. Biol. & Med. 19: 279-288.

Sund, P. N. 1958. A study of the muscular activity and swimming behavior of the sea anemone, Stomphia coccinea. Quart. J. Micr. Sci., 99, 401-420.

Thompson, H. V. 1948. Studies of the behavior of the common brown rat (Rattus norvegicus) Bull. Anim. Behavior 6: 26-40.

Thompson, H. V. 1953. Experimental live-trapping of rats with observations on their behavior. Brit. Jour. Anim. Behav. 1: 96-111.

Thompson, W. 1957. Influence of prenatal maternal anxiety on emotionality in young rats. Science. 125: 698-699.

Tinbergen, N. 1951. The Study of Instinct. Oxford Univ. Press, London.

Tobach, E. and Schneirla, T. 1962. Eliminative responses in mice and rats and the problem of "emotionality." In Roots of Behavior ed. by E. L. Bliss. pages 211-229. Harper & Bros., New York.

Treichler, F. R. and Hall, J. F. 1962. The relationship between deprivation weight loss and several measures of activity. Jour. Comp. Physiol. Psych. 55 (3): 346-349.

Tryon, R. C. 1942. Individual differences. In Comparative Psychology ed. by F. A. Moss. Prentice-Hall, New York.

Waddington, C. H. 1961. Genetic assimilation. Advances in Genetics 10:257-293.

Wald, G. and Jackson, B. 1944. Activity and nutritional deprivation. Proc. Nat. Acad. Sci. 30: 255-263.

Wecker, S. 1963. The role of early experience in habitat selection by the prairie deermouse, Peromyscus maniculatus bairdii. Ecological Monographs 33: 307-325.

Weininger, O. 1956. The effects of early experience on behavior and growth characteristics. JCPP 49 (1): 1-9.

Welker, W. I. 1957. "Free" versus "Forced" exploration of a novel situation by rats. Psych. Reports Monogr. Suppl. #2.

Welker, W. I. 1959. Escape, exploratory, and food-seeking responses of rats in a novel situation. Jour. Comp. Physiol. Psych. 52 (1): 106-111.

Welker, W. I. and King, W. A. 1962. Effects of stimulus novelty on gnawing and eating by rats. Jour. Comp. Physiol. Psych. 55 (5): 838-842.

Wiegert, R. and Mayenschein, J. 1966. Distribution and trap response of a small wild population of cotton rats (Sigmodon h. hispidus). Jour. Mamm. 47: 118-120.

Yerkes, R. M. 1913. The heredity of savageness and wildness in rats. Jour. of Animal Behavior. 3: 286-296.

Young, H., Neess, J. and Emlen, J. 1952. Heterogeneity of trap response in a population of house mice. Jour. Wildlife Management 16: 169-180.

Zeuner, F. E. 1963. A History of Domesticated Animals. London, Hutchinson.