ABSTRACT

FEEDING PATTERN IN PEROMYSCUS MANICULATUS:
THE RESPONSE TO TEMPORAL FOOD DEPRIVATION

By

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Temporal food deprivation can be imposed on Peromyscus by unfavorable meteorological conditions, particularly during periods of cold winter weather. The effects of light, temperature, humidity, wind, snow, etc. on the activity of deer mice are reviewed. Mechanisms of energy storage (caches, fat deposition, etc.) and conservation (torpor, nest building, etc.) are then considered. From this review it is hypothesized that P.m. bairdi are temporally opportunistic in their nocturnal feeding and, if deprived, will concentrate their daily intake into those times when access to food is most available.

P.m. bairdi from the laboratory, however, showed little accomodation to a schedule of temporal food deprivation. When permitted only the initial six hours of their 12 hour dark activity period for feeding, five of the six animals died by Day 4. This intolerance to temporal food deprivation prompted an examination of the experimental conditions which affect the accomodation to food deprivation.

Experiment I examined the effect of prior deprivation experience on survivability under a more severe test deprivation (a 15 day period where food was present each day during the initial seven hours

of the 12 hour dark period). It was hypothesized that laboratory Peromyscus, maintained under ad libitum conditions, would show greater mortality than those with prior experience. Such was supported. Furthermore, the experienced mice consumed no more food than the controls.

The hypothesis that greater activity (induced by access to a running wheel) reduces survivability under these conditions of temporal food deprivation was also tested. The results supported this hypothesis, suggesting that the nature of the deprivation experience lies, at least in part, in an inhibition of general activity or movement.

Regardless of experience, P.m. bairdi demonstrated little capacity to adjust their food intake to the seven hours of availability per day. Experiment II was conducted to see if the food intake is influenced by the temporal properties of when food is accessible. Intake is greater and survival enhanced when the food is available during the final six hours of the nocturnal period as opposed to the initial six hours. This result implies a circadian regulation of food consumption. The strictly nocturnal activity of Peromyscus might necessitate an organization where late-night feeding can correct for deficit and prepare the mouse for the upcoming light phase. It is hypothesized that foraging and hoarding are most prominent early in the night and can become increased at that time in response to deprivation.

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DEDICATION

I would like to dedicate this to my fellow graduate students and to Jan Harper who helped make this a most enjoyable experience.

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INTRODUCTION

The natural occurrence of temporal food deprivation in rodents and its consequences to their feeding behavior have not been explored. Food deprivation generally connotes a shortage in quantity or density, which requires increased searching and optimization of effort (energetic efficiency in terms of type and size of food consumed). In contrast to the quantity of food, however, many species experience temporal restrictions on foraging, which may be the more prevalent form of food deprivation. The temporal world of the animal must therefore be accounted for when describing feeding strategies. If unfavorable weather conditions affect the opportunity for foraging in the strictly nocturnal Peromyscus, we would hypothesize that these mice are able to adjust their daily feeding to coincide with the more favorable variations in light intensity, temperature, precipitation, etc. The result would be to enhance thermoregulation by avoiding unnecessary energy and water loss and to maximize concealment from predators while the mouse is out of the nest and active. This dissertation focuses on the question of the capacity of Peromyscus maniculatus bairdi to compensate for daily periods of temporal food deprivation by increasing intake during the times of accessibility.

In this laboratory prairie deer mice, P.m. bairdi, showed little accomodation to a deprivation schedule which allowed for six

continuous hours of access to food per day (Jaeger, unpub. obs.). Adult male mice were maintained in separate cages on a L:D ratio of 12:12 with ad libitum food and water and with access to a running wheel. When permitted only the initial six hours of their dark activity period for feeding, five of the six animals died by the fourth day. This result is particularly surprising when it is considered that under ad libitum laboratory conditions these mice spent on the average a total of only one and one half hours per day feeding, considerably less time than the six hours allowed here. Further, this feeding appeared to be distributed throughout the dark hours and not concentrated in the late night (see Figure 1). Rats, in contrast, can be made to concentrate their daily intake into fixed-periodic meals (Lawrence and Mason, 1955; Tepperman and Tepperman, 1958; Cohn et al., 1962; Baldessari et al., 1971). A maximal adjustment to a single, one-hour meal per day was reported by Dufort (1964).

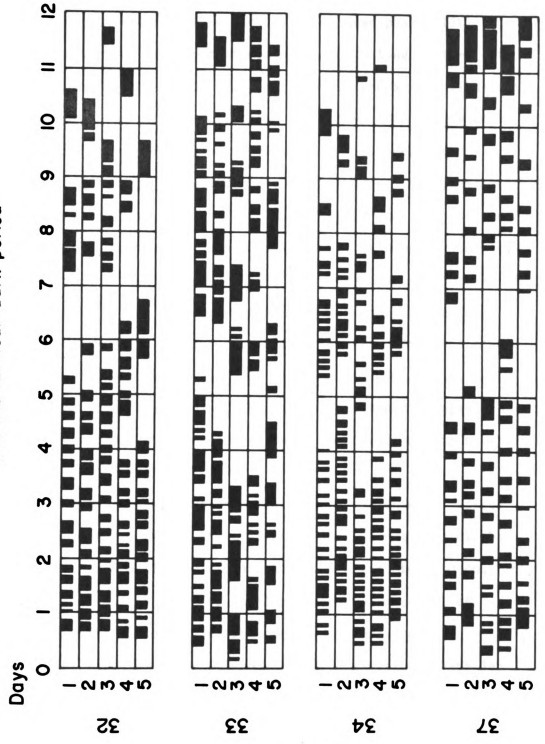
This observation of intolerance to deprivation in these mice suggests the following alternatives:

(1) Either P.m. bairdi have a more or less fixed pattern of daily food intake which cannot be collapsed to fit a reduced period of access, or

(2) These mice can adjust their feeding to accomodate temporal food restriction, but under a set of circumstances different from those of the original observation (i.e., adequate experience, optimal circadian timing, etc.).

The first alternative is likely if P.m. bairdi is not naturally confronted with temporal food deprivation, or if other mechanisms are

Figure 1. The food intake pattern (taken from Esterline Angus recordings) of four P.m. bairdi for five consecutive nights each.


Time (hours)
into the 12-hour dark period
Days
0 1 2 3 4 5 6 7 8 9 10 11 12
1 2 3 4 5
32
33
34
37
Animal Number

available which exclude the need for an adjustable pattern of daily feeding. The literature review will examine these possibilities. Here, the assumption will be defended that fluctuating weather conditions (light, rain, humidity, air temperature, snow, and wind) can and do impose temporal restrictions on the activity of Peromyscus. Next, the mechanisms of food storage (hoarding, fat deposition, coprophagy) and energy conservation (torpor, seasonal acclimatization, nest building, huddling) will be evaluated as alternatives to feeding adjustments. Where possible the limitations of each mechanism will be pointed out as they are understood for Peromyscus. From this, it will be suggested that storage mechanisms fail after prolonged periods of unfavorable weather (i.e., late winter). It is concluded from the literature review that P.m. bairdi must then rely on conserving energy by remaining in a suitable microhabitat and foraging for only limited periods of time, during those weather fluctuations which most favor out-of-the-nest activity.

The experimental portion of this dissertation will address itself to the second of the above alternatives. Conditions of the original observation (lab-reared animals with access to food only during the initial six hours of dark) suggest two variables of potential importance to the feeding biology of Peromyscus:

(a) prior experience with temporal food deprivation, which lab-reared animals would not have had, might enable these mice to respond to restricted temporal access to food by increasing their rates of intake; and/or

(b) an early vs. late night circadian influence on food intake may exist, whereby the greater adjustment to deprivation is made with late-night access to food.

Prior experience and circadian influence will, therefore, be examined for their effects on the survivability, weight loss, and food consumption of P.m. bairdi.

LITERATURE REVIEW

I. Influence of Weather on Activity

Both laboratory and field observations reveal that "elements" of weather influence activity in small mammals. Considered here will be light, rain, humidity, snow, temperature, and wind, as well as their combined long-term effects. The mouse's response to any of these weather factors is based either on its need for concealment from predators or its regulation of energy and water resources.

Activity, as it is used here, is a general term taken to include feeding, exploration, grooming, etc. It is assumed that the animal cannot be feeding or foraging if it is not moving about. In this laboratory the feeding and wheel-running of P.m. bairdi show a close temporal association, such that a bout of feeding is immediately preceded or followed by running. Therefore, throughout this review "activity" will be taken as a measure of feeding. The reader should be cautioned, however, that different measures of activity (i.e., via wheel-running, movement back and forth across a treadle, or a delicately balanced cage which detects subtle disturbances) measure different sets of behaviors and can therefore appear to contradict one another. When this situation occurs, we will question the extent to which the measures include feeding.

A. Light

It has been well established that the daily light-dark cycle acts to entrain the circadian activity of the nocturnal Peromyscus (Johnson, 1926; Behney, 1936; Hatfield, 1940; Stinson, 1952; Falls, 1953; French, 1956; Getz, 1959; Layne, 1971). P. leucopus, for instance, were reported to be 99.5% nocturnal in their wheel-running on lighting regimes which included artificial twilights (Kavanau, 1969).

Seasonal changes in the length of the photoperiod influence the temporal limits of daily activity by extending them over a longer period during winter than during summer nights (Johnson, 1926; Falls, 1953). When the available time for nocturnal activity is very short, as it is during mid-July in the Yukon Territory, activity can occur in as few as five hours per day (Swade and Pittendrigh, 1967). The effect of the dark period duration on the total daily amount of activity is, however, less clear. Activity is not continuous throughout a 12 hour nocturnal period, but rather interspersed with varying periods of "rest" or inactivity (Figure 1). Foraging might be constant during the extremely reduced night of the sub-arctic summer, without differing in total amount from that occurring during long dark periods.

Habitat characteristics can also affect day length. The forest-dwelling species P.m. gracilis remained active longer than did P.m. bairdi on an adjoining beach (Falls, 1953). Similarly, P. floridanus, found in a relatively more open habitat than is P.

gossypinus, showed the greater decline in time spent out of the nest and in movement across a treadle with increased photoperiod (Layne, 1971).

Exceptions occur, however, when activity is greater on a long-day photoperiod (16:8 LD) than on a short-day photoperiod (9:15 LD) (Lynch and Lynch, 1973). In outdoor cages in northwest Canada, P. maniculatus began increasing daytime movement in mid-March with the nocturnal peak of activity becoming bimodal. This trend continued through the spring and by mid-June, when the dark period was only about three hours, activity persisted for six hours after dawn (Stebbins, 1971). The presence of snow in the cages appeared to correlate negatively with the extent of movement across treadles; snow cover and air temperature might together mask an influence of day length.

Beyond light as a Zeitgeber, changes in its intensity within either the light or dark phase of the day can influence outside movement through effects on both vision and concealment. Nocturnal, large-eyed Peromyscus will favor dark but visually perceptible surroundings for "outside" activity. Manipulation of light intensity in the laboratory bears this out. The greatest amount of activity occurs in a range of dim light, between darkness and that equivalent to a full moon, approximately 0.024 ft-c (see Fall's review, 1968). When exposed to a dim-dark light cycle, P. leucopus were active during the dim phase, not the dark (Kavanau, 1968). He noted an optimum range for activity from 0.00018 to 0.015 ft-c.

Illumination from the moon is, therefore, a potential deterent to unconcealed movement. It was found to be the most potent factor

affecting the activity of Peromyscus polionotus leucocephalus on the open beach at Santa Rosa Island, Florida (Blair, 1951). The trapping and tracking records indicated much less movement at light intensities from a half to a full moon than at those when the moon was slight or obscured by clouds. Similar findings have been reported for other species of Peromyscus, particularly those found in more open habitat such as old-field or desert (Gentry and Odum, 1957; Gentry, Golley, and McGinnis, 1966; Falls, 1968; Owings and Lockard, 1971). The forest dwelling P.m. gracilis, on the other hand, appeared to be unaffected by the lunar cycle (Falls, 1968). This lunar inhibition of movement has been reported to reduce greatly trapping success in a population of known density for a period of up to six consecutive days (Caldwell and Connell, 1968). Avoiding visual exposure, therefore, seems to be the important consequence of inactivity at "higher" light intensities. For Peromyscus it appears that those situations with the greatest potential for serious temporal food restriction due to light intensity are (1) extremely short summer nights such as found in the Canadian sub-arctic and (2) a period of successive nights which are clear and moonlit.

B. Rain

The effect of rain on the activity of small mammals is unclear. The accompanying overcast provides concealment, whereas the rain can be a masking noise, making a predator's detection of a mouse by sound more difficult. Direct contact with rain, however, can result in wet pelage and reduced insulation. In general, Peromyscus are more active on nights with a light to moderate rainfall (Burt, 1940; Blair,

1951; Gottschang, 1952, from Martin, 1973; Gentry and Odum, 1957; Hays, 1958; Hirth, 1959; Gentry et al., 1966; Falls, 1968), presumably because rainy nights are also the darkest nights. Heavy rainfall, however, restricts the movement of small mammals (Falls, 1968; O'Farrell, 1974).

C. Humidity

The influence of humidity on deer mouse activity is also difficult to assess; its effects are confounded with cloud cover, air temperature, and wind. Similar to the other weather factors, there likely exists a favored range of humidity, with either extreme being avoided. Field studies do suggest a direct relationship between humidity and activity, except possibly near saturation (Orr, 1959; Falls, 1968; Martin, 1973). Under controlled lighting and temperature in the laboratory, however, the activity of P.m. bairdi decreased as the vapor pressure increased (Stinson, 1952; from Falls, 1968). The high humidity associated with cloud cover and light rain evidently has no adverse influence on movement. If humidity does reduce the opportunity for foraging by Peromyscus, this may be at low vapor pressures, which threaten desiccation. The cactus mouse, P. eremicus, for instance, becomes torpid in response to negative water balance and will spend up to several weeks in humid burrows during the desert summer (MacMillen, 1965).

D. Snow

Snow cover can influence the activity of Peromyscus in a variety of ways. It offers concealment for subsurface movement, but

if densely packed it can also become an obstacle to tunneling. Considerable tunneling and sporadic daytime activity has been reported for P.l. noveboracensis when their cages contained several inches of newly fallen snow (Behney, 1936). The over-all movement of three individually housed P. maniculatus was found to be reduced during the winter in the Northwest Territories (Stebbins, 1971). The animals had to tunnel to find their food or to exercise. The increase in activity in late March coincided with the loss of snow cover over the top of the cage. Deep or densely packed snow could, therefore, have an adverse effect on foraging. Snow, in fact, seems related to seasonal migrations of P. boylei in California (Storer et al., 1944). They observed mice moving back into previously vacated areas after the snow had melted.

In addition, the surface of the snow can provide a contrasting background making the movement of the mice across it very conspicuous. Peromyscus, nevertheless, are active on the snow, as is evidenced by their tracks. O'Farrell (1974) noted P. maniculatus as the only desert rodent he studied that remained active when snow was present. The effect of the snow per se on the extent of surface activity is, however, not well understood. Reduced catches of P.l. noveboracensis were observed in Michigan following heavy snowfalls (Brand, 1955; from Stickel, 1968). This result might have been due to the placement of his traps at regular intervals. Snow can possibly restrict the movement of Peromyscus to protected areas such as brush piles and under logs (Fitch, 1958; Beer, 1961).

Snow as an insulative agent can also be an important influence on small mammal activity. Under the conditions of winter in northern Canada (i.e., low temperatures and deep snow) Peromyscus were reported as almost impossible to trap (Fuller et al., 1969). But with very little snow cover, a temperature of -19°F did not seem to curtail the activity of either P. leucopus or Clethrionomys gapperi, although both populations suffered heavy losses during that period (Beer, 1961). Pruitt (1957) examined subnivean conditions on the taiga near Fairbanks, Alaska. He observed that in late October when the snow reached a critical depth of 15 to 20 cm that a change occurred in the behavior of forest floor mammals. The activity of shrews and red-backed voles switched from the snow surface to below it. Presumably the animals went beneath the snow to take advantage of its insulative properties.

Snow density can modify this insulative effect by altering the thermal conductivity (Fuller et al., 1969). Thawing increases snow density, which lowers subnivean temperatures. A southerly ranging subspecies, P.m. bairdi, can be exposed to wider seasonal extremes and more fluctuation in temperature than one found farther north as is P.m. gracilis (Pruitt, 1959). This is attributed to the permanent winter snow cover on the northern study plots in contrast to intermittent snow cover, thaws, winter rains, and a greater amount of summer insolation (heat from the sun) in the south.

Comprehensively, snow cover appears to reduce or restrict the surface movement of Peromyscus. The subnivean refuge makes the mice less conspicuous to predators and offers shelter from low temperature

and wind. The extent to which mice are active beneath the snow and are able to forage for food is, however, unknown.

E. Temperature

Activity away from the nest not only requires predator evasion, but also thermoregulation. For each homeotherm there exists a region of thermoneutrality in which the metabolism is independent of the ambient temperature. At low temperatures the rate of metabolism is proportional to the temperature differential between the body and the environment. Above this region the metabolism again increases until the lethal temperature is reached. McNab (1963) pointed out that a homeotherm, such as Peromyscus, expends most of its energy for thermoregulation. At lower temperatures increased movement and shivering can compensate for heat losses; for example, oxygen consumption is 480% greater at 10°C than at 31° to 34°C in antelope ground squirrels, Ammospermophilis leucurus (Dawson, 1955). This suggests that outside activity at low temperatures would necessitate more foraging for greater amounts of food. It has been found that P.m. bairdi consume almost 2.5 times the number of calories at 0°C than at 36°C (Dice, 1922). He observed that "most small mammals are able to survive one day or longer without food at ordinary laboratory temperatures, but it is doubtful that any trapped small rodent can exist overnight without food or nest material when the temperature drops much below 10°C." A similar observation has been made by Howard (1951) for both P.m. bairdi and P.l. noveboracensis regarding what he termed "cold weather starvation."

Mammals commonly select a suitable temperature zone when in an environment which is not thermally uniform (Herter, 1934; 1936; Kalabuchov, 1939; Bodenheimer, 1941; all from Stinson and Fisher, 1953). Individual P.m. bairdi distributed themselves between 20°C and 30°C when placed in an eight foot aluminum tube in which a temperature gradient existed ranging from 6°C to 50°C (Stinson and Fisher, 1953). The perception of the thermal zone was apparently through foot contact with the substratum, rather than via the ambient temperature.

Correspondingly, Peromyscus activity seems reduced at hot or cold temperatures (Howard, 1951; Hart, 1953; Falls, 1953; Orr, 1959). For instance, reduced surface movement has been observed in conjunction with low winter temperatures (Stebbins, 1971; O'Farrell, 1974); and the distance of capture of P. leucopus from their trapping centers has been reported to diminish at high temperatures (Haresign, 1964). In a four year study, involving 2,666 rodents, Sidorowicz (1960) found that Clethrionomys glareolus and Apodemus flavicollis were caught most readily at certain optimum temperatures. The greatest nocturnal captures were between 24.1°C and 27.0°C, and were reduced above and below this with the most reduction occurring at minimum temperatures.

F. Wind

Air movements can accentuate the physiological effects of temperature by increasing both evaporative water loss and the extent of cooling. Little attention, however, has been given to wind as an influence on activity. Trapping success of P. maniculatus was recorded at regular distances from a windbreak (Vose and Dunlap, 1968). More mice were found in the area of greatest wind shelter and

snow depth. The subnivean temperatures, however, were not markedly different at any distance, probably because snow cover remained thin, not reaching 15 cm in depth. High wind speeds accompanied by blowing sand were observed to lower rodent activity in the desert (O'Farrell, 1974). It was reasoned that "fine wind-blown sand would be highly uncomfortable and a hindrance to vision; additionally, since many rodents locate seeds by olfaction, high wind speeds would greatly affect this ability negatively." It has also been suggested that the noise associated with wind may make detection of predators more difficult and, as a consequence, inhibit movement (Davis and Golley, 1963).

G. Summary

In summary, unfavorable weather conditions can have a prohibitive effect on the outside movement of Peromyscus. Favorable weather might include light rainfall or cloud cover, moderately high temperature, and high humidity. Alternatively, mice avoid situations which make them conspicuous and/or which make excessive energy or water demands: for example, a clear, cold night. Winter weather, particularly in the more northern latitudes, offers the greatest number of adversive conditions. Low temperature, wind, reduced foliage, clear moonlit nights, a contrasting background of snow, insufficient snow depth for insulation, or densely packed snow can all provide for periods of temporal restriction to foraging.

II. Mechanisms of Food Storage and Energy Conservation

If "exposed" foraging can be temporally restricted by unfavorable weather, can temporal food deprivation result? Must Peromyscus concentrate feeding during the "most favorable" times? The answer to these questions will be "yes," unless they depend upon other strategies, such as food storage or torpor. The role of such alternative mechanisms will now be examined. Those dealing with food storage will be considered first; they include hoarding, body fat deposits, coprophagy, and cannibalism. Other mechanisms exist which function to conserve energy; those to be considered are both physiological (torpor, geographic differences in metabolic rate, and seasonal acclimatization) and behavioral (burrowing, nest building, and huddling).

A. Storage Mechanisms

(1) Deprivation from restricted foraging can be avoided by maintaining sufficient stores of food. The occurrence of hoarding behavior or the resulting food caches have been reported for many species of Peromyscus (Cogshall, 1928; Sumner and Karol, 1929; Criddle, 1950; Linduska, 1950; McCabe and Blanchard, 1950; Howard, 1951; Houtcooper, 1972; Rice and Terman, 1972; Barry, 1974). The caches of P.m. bairdi in outdoor next boxes appeared to be most prominent in October and early November, and were found to contain nonperishable foodstuffs, such as seeds and acorns (Howard, 1949; Howard and Evans, 1961). The largest store occurred in a nest box in which 12 deer mice resided. In less than one month, 1050 cc of weed seeds, 565 acorns, and six deer pellets were cached.

Concerning seasonal food stores, two important questions arise: (1) how long can they last, and (2) how easily can they be replenished? The gathering and maintaining of a food supply capable of sustaining a group of mice through five months of subarctic winter has not been studied. Howard and Evans (1961) did note that much of the stored food, in nest boxes on the George Reserve in southern Michigan, was gone by the end of December, and all of it by March. Their work, however, considered but one year. It is unfortunate that neither they nor Stebbins (1971) give winter information about the amount of food consumed per unit time, the addition of new food to a cache, or the establishment of new caches.

(2) Seasonal food storage in deer mice can also be accomplished physiologically in the form of elevated fat deposits (Hadaway, 1972; Morris, 1975). Hayward (1965a) examined the gross body composition of six geographic races of Peromyscus and found that the average fat content in relation to the fat-free body weight was nearly twice in winter what it was in summer for all races except P. m. sonoriensis where the reverse was true. He attributed the higher winter fat values to the functions of increased tissue insulation and energy reserve. The P. m. sonoriensis, taken from the high altitude desert of Nevada, showed the highest summer fat levels (Bodenheimer, 1952; Wright, 1954). Desert homeotherms, including Peromyscus, tend to store fat for use during the hot, dry summers at a time when food intake is reduced because of reduced water intake (McNab, 1968).

How long can this energy supply from fat last? Is it readily mobilized? Fat reserves of P. polionotus could account for 1.2 to 1.7

days of energy reserves when foraging was limited (Caldwell and Connell, 1968). For a lactating female, however, with three young of five days of age, the estimate was lowered to between 0.7 and 1.2 days. With the stomach contents included, the mice were provisioned for 2.8 days at the basal rate of metabolism. The nursing female had a supply for 1.1 days. It was concluded that "some individuals must at times forage for food under bright moonlight since our estimates of fat and stomach energy reserves would not otherwise permit survival through an extended period of clear weather. However, as the trap data suggest, these forages are most certainly restricted to a short radius from the nest" (Caldwell and Connell, 1968). They also found captures in live traps down approximately 42% from overcast to moonlit nights, even for four to six day periods under clear skies.

(3) Coprophagy, too, might be considered a form of food storage. This refers to the recycling of food through the consumption of feces. The laboratory rat recycles 30 to 50 percent of its total fecal output on a nutritionally adequate diet, and up to 100 per cent on an inadequate diet (Barnes, 1962). When the experimental conditions permitted access to feces, P.m. bairdi endured the removal of all dietary protein for 100 days (Karch, 1974). Coprophagy, however, is generally held as a way to compensate for a particular metabolic deficiency, and is probably of limited value as an energy source.

(4) In addition, each animal itself can be viewed as a potential nutrient store. Both P.l. noveboracensis and P.m. bairdi showed a

tendency toward cannibalism when deprived of food and water at low temperature (Sealander, 1952).

B. Conservation Mechanisms

(1) Many birds and mammals respond to energy stress with intermittent periods of torpor. Here a reduction in body temperature is accompanied by behavioral lethargy and a decrease in energy expenditure. This condition has been observed in many species of Peromyscus under both controlled (Sealander, 1953; Morrison and Ryser, 1959; McNab and Morrison, 1963; MacMillen, 1965; Morhardt and Hudson, 1966; Fink, 1973) and field conditions (Howard, 1951; Mullen, 1971; Stebbins, 1971).

Food availability has the greatest effect on whether or not torpor will occur (Hudson and Bartholomew, 1964; Morhardt and Hudson, 1966). In the laboratory, P. eremicus undergoes a typical cycle of daily torpor when food is limited. Well-fed animals maintain their body temperatures between 33° and 38°C, even when exposed to ambient temperatures as low as 5°C (MacMillen, 1965). Similarly, Morhardt (1970) found five species of Peromyscus to become torpid in response to starvation at ambient temperatures from 0° to 23°C. Torpor was not observed in animals provided with excess food.

It has been reported, however, that Peromyscus will enter torpor in the presence of food (Stebbins, 1971). This "spontaneous" torpor was observed during winter in P. leucopus that had been acclimatized to cold weather the preceding fall (Gaertner et al., 1973).

A torpid animal, by definition, rewarms without the aid of external heat. Species with relatively labile body temperatures have been designated heterotherms. When the phenomenon occurs in Peromyscus it is a daily event taking place during the normal period of inactivity (light phase) and terminating before the time the mouse would usually begin to seek food. For one species the duration of daily torpor was usually less than eight hours and never as long as 12 hours (Morhardt, 1970).

(2) As another physiological adaptation, it has been suggested that species and races of Peromyscus can be characterized by different metabolic rates, each appropriate to a general climatic situation (i.e., desert, alpine, taiga). These adaptations are presumed to be genetically fixed. Desert Peromyscus, as an example, have lower basal metabolic rates and body temperatures than mesic forms, presumably to prevent overheating (McNab and Morrison, 1963). Similar findings have been put forth regarding both desert and alpine mice (Cook and Hannon, 1954; Murie, 1961). Other investigators, however, maintain that the metabolic rates of races they examined, including a desert form, are not different from a predictable, weight-dependent relationship and are, therefore, not adapted to climate (Scholander et al., 1950; Hayward, 1965b).

(3) Seasonal acclimatization is also believed to have a significant effect on the mouse's response to temperature. Cold-acclimatized, winter Peromyscus can withstand lower ambient temperatures than warm-acclimatized, summer individuals (Sealander, 1951; Hart and Heroux, 1953). These mice also show a lower existence

metabolism than the summer-acclimatized mice when compared at the same temperature (Morris, 1975). This is attributed to the greater insulation afforded by longer hair, greater pelage weight, and increased lipid reserves. The fact, however, that no change in the critical temperature (lower limit of the thermoneutral zone) accompanied seasonal acclimatization to cold in Peromyscus suggested to Hart (1957) that insulative changes are insignificant. He also demonstrated that the metabolic rate at any temperature below thermoneutrality is similar in summer and winter mice, with the exception that in winter the low temperature limit for survival is extended by approximately 20°C. This extension, he concluded, was due to an enhanced "capacity" for more intensive and sustained metabolic activity.

Hayward (1965b) pointed out that "this phenomenon of seasonal metabolic acclimatization would not allow continuous exposure to subfreezing temperatures. Its function is likely to permit short periods of intensive energy production associated with occasional exposure to very low winter temperatures. Such exposure may occur when it is necessary for animals to forage for food." This exposure can be metabolically costly. It was calculated that a 20 g Peromyscus eats approximately 1.95 g of food per day at 21° to 23°C (around 5.7 calories), and that it would have to more than quadruple its food intake to meet energy requirements at -15°C (Hayward, 1965b). He concluded "it is safe to say that a mouse in its natural winter environment is forced, in terms of energy balance and long-term weight stasis, to seek a moderate microclimate."

The above mechanisms can be considered physiological controls of metabolic rate. What follows are behavioral controls whereby Peromyscus seek out and/or construct a suitable microhabitat.

(4) The role of snow in providing a microhabitat of relatively constant temperature has been discussed. Burrowing, in general, appears to be a climatic adaptation to reduce the body-to-air temperature gradient. The digging and gnawing movements employed by Peromyscus for burrowing or enlarging cavities in tree stumps have been described (Eisenberg, 1968). Deer mice from widely divergent habitats have been observed to use these excavations (Sumner and Karol, 1929; Hayne, 1936; MacMillen, 1965; Pengelley and Fisher, 1968; Houtcooper, 1972; Davenport, 1974; Jaeger, pers. obs.). Hayward (1965c) attached thermistors to representatives of five geographic races of P. maniculatus and monitored temperatures in the burrows and other shelters they entered. His results indicated that the microhabitat provides an environment of moderate temperature where seasonal extremes are avoided. Winter microhabitat temperatures were never below freezing and were very similar in all habitats despite the considerable differences in gross climates.

(5) Nest building is a means of further modifying the microenvironment. The implications of this behavioral insulation for deer mice have been discussed by King (1963, 1968). It appears that winter acclimatization and a more northern geographic distribution both correlate positively with the extent of nest construction. For P.l. noveboracensis the nest temperature in cold weather has been reported to be as much as 24°C higher than that of the surroundings (Johnson,

1926). Nest temperatures of Peromyscus were also recorded that ranged from 7° to 21°C higher than air temperatures (-30° to -35°C) with a tendency for the gradient to diminish as the thermogenic fatigue of the mouse set in (Sealander, 1952).

Sealander (1951) compared survival times and total percentage of initial weight lost by winter animals having nest protection with data for unprotected winter animals at the same temperature. He found that winter animals thus protected were able to increase their survival to the equivalent of a rise in the temperature of their immediate surroundings of as much as 25°C. Summer animals having nest protection were similarly able to prolong their survival times.

Nests have been observed which contain aggregations of deer mice. Larger aggregations are formed in winter, and these groups occasionally consist of unrelated mice of the same or of different species (Howard, 1949). One of these contained seven P.m. bairdi and three P.l. noveboracensis. Stebbins (1971) counted 28 P. maniculatus in one nest discovered in late March.

(6) This huddling is yet another important mechanism of food conservation and winter survival; its function is to reduce the amount of surface area across which heat is lost. Food consumption per gram of body weight by laboratory mice varies inversely with the number of animals in the group (Prychodko, 1958). As the ambient temperature is lowered there is an increasing divergence in the amount of food consumed by the different groups. The effect of huddling on survival times of P.l. noveboracensis and P.m. bairdi exposed to temperatures of -23°C was investigated by Sealander (1952). In this study, the

mean survival time of each individual in a group of two was nearly double that of individuals exposed singly. Survival time increased in much smaller increments as the group size was increased beyond two. Similarly, the oxygen consumption for a group of albino mice at 8°C was determined to be roughly the same as for a single mouse at 15°C (Mount and Wilmott, 1967).

C. Summary and Conclusion

It is difficult to summarize the combined effects of these mechanisms of energy storage and conservation on the feeding biology of Peromyscus. Nevertheless, in light of the wide range of available alternatives just discussed, it would appear that isolated, short-term restrictions (as might occur with the lunar cycle) would not result in serious food shortage and energy depletion. Moreover, food caches and fat reserves together with coprophagy would likely assure energy for longer periods of restriction, imposed for instance by winter weather. The building of these energy stores, however, coincides with favorable weather and optimal food availability (i.e., in autumn). In a temperate-zone winter (e.g., Michigan), these stores can become depleted by late winter or early spring, at a time of poor food availability when the caches are difficult to replace. This is also a time of continued unfavorable weather, including deteriorating snow conditions, which reduce cover and increase thermal conductivity via thawing. Late winter through early spring can, therefore, be an energetically critical period for deer mice. This is the time of greatest mortality, lowest reproduction, and lowest population levels for many species of Peromyscus (Howard, 1949; McCabe and Blanchard,

1950; Beer, 1961; Brant, 1962; Sadleir, 1965; Fuller et al., 1966; Martin, 1973; Myton, 1974).

The mechanisms of energy conservation become particularly important when food stores are depleted. When the mouse conserves energy while huddled in its nest without stored food, it is temporally food-deprived. It then has two alternative strategies, either to remain sheltered, or to venture out for food, even at a relatively great energy expense. A temporally flexible feeding pattern would determine which alternative the mouse takes.

The question thus remains viable, to what extent are these mice able to adjust their daily feeding to accomodate the more favorable fluctuations in light intensity, low temperature, precipitation, etc? What is the capacity of Peromyscus to compensate for daily periods of temporal food deprivation by increasing intake during the times of accessibility?

EXPERIMENT I--EFFECT OF PRIOR DEPRIVATION EXPERIENCE ON SURVIVABILITY

A. Purpose

There is reason to expect that Peromyscus must compensate for daily periods of temporal food deprivation by increasing their intake when the food is accessible. An initial observation indicated that P.m. bairdi have very little tolerance to six hours of food availability per day. Since these were laboratory-reared mice, they might have been particularly vulnerable because they had no prior experience with food deprivation. The purpose of this experiment is, therefore, to examine the effect of prior experience on the deer mouse's survival under temporal food deprivation. More specifically, does experience with periods of progressively more restricted daily exposure to food enable Peromyscus to survive longer in a later and more severe test deprivation? Gradual experience with progressively greater food deprivation is intended to be analogous to the experience wild mice might incur as fall progresses into winter and the weather becomes more severe.

B. Subjects

For this study 38 male P.m. bairdi were used. They represent the males of 18 litters, from 12 distinct matings. At the initiation

of the experiment these mice averaged 109.4 ± 2.4 days of age (± one standard error), with an average body weight of 15.82 ± 0.28 g.

All animals were the first laboratory generation from parents caught in the vicinity of East Lansing, Michigan. At weaning (21 days of age) the mice were housed with the male littermates in plastic laboratory cages (28.6 x 12.7 x 15.2 cm). They were provided wood shavings and a cotton Nestlet (Anicare). Food (Wayne Mouse Breeder Blox) was provided ad libitum by means of a wire mesh hopper in the top of each cage. Water was also available ad libitum. The laboratory environment was maintained at approximately 21°C under a 15:9 hour light-dark cycle.

C. Experimental Design

The deprivation experience consists of successive blocks of time (approximately 21 days each) during the first of which the food is available for nine hours each day and during the second for eight hours. The "experienced" mice are then compared with controls for their survivability under a test deprivation where food is accessible for only seven hours per day. The experimental design is presented in Table 1, while the types of experience and the test deprivation are illustrated in Figure 2. Initially, both the group to receive the deprivation experience and the controls undergo a baseline period (24 days) where their food is available each day during the 12 hours of dark (see Row 1 of both Table 1 and Figure 2). (Under all experimental conditions a 12:12 hour light-dark cycle prevailed.)

Table 1.--Design for Experiment I.

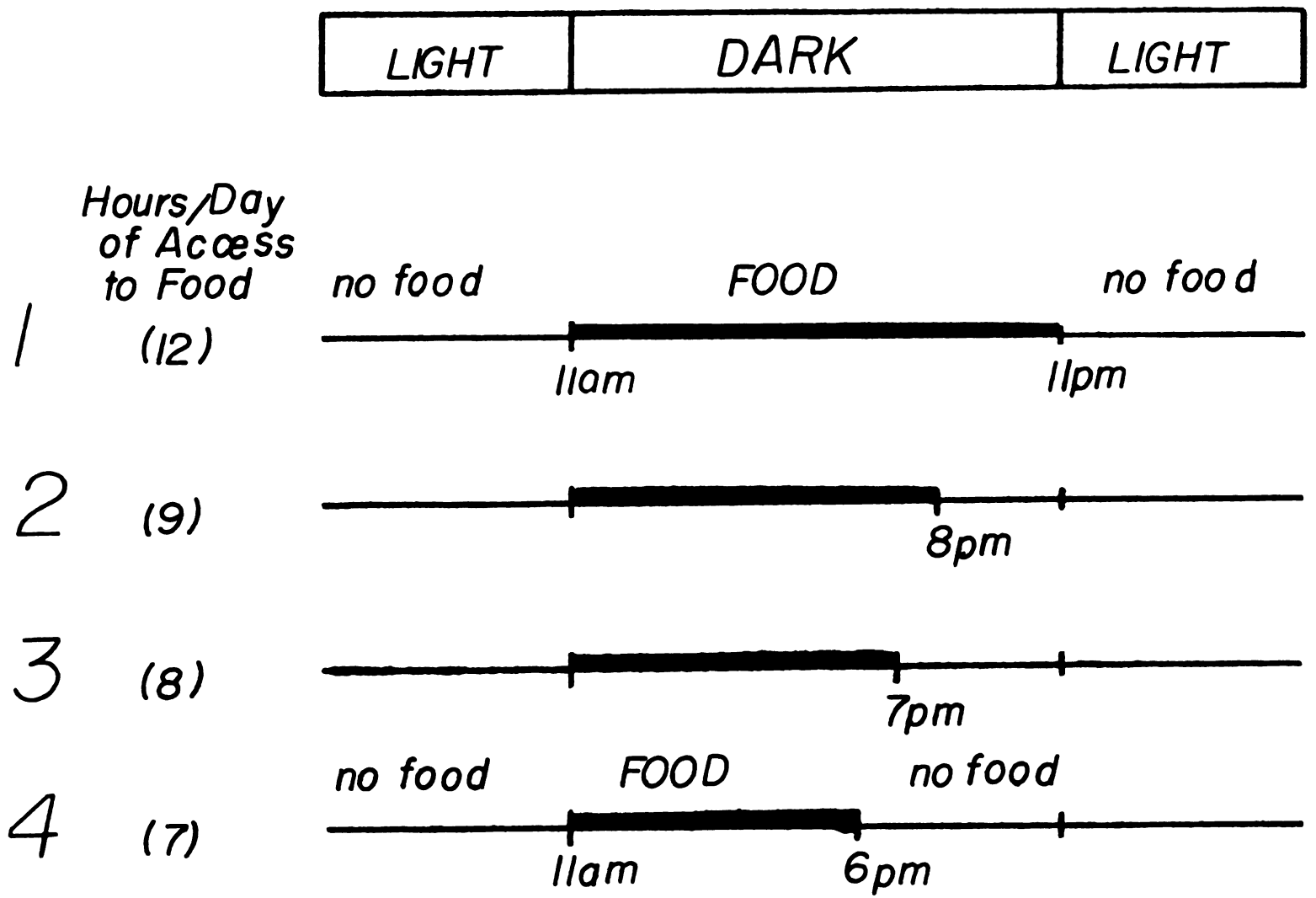
Experimental Timetable		Hours/Day of Access to Food*			
		Control		Experience	
Experimental Organization	Number of Days on Each Regime	Long-Term Control (n = 9)	Short-Term Control (n = 12)**	Immediate Experience (n = 9)	Past Experience (n = 9)***
1. Baseline	24	12		12	12
2. Experience	23	12		12	9
3. Experience	20	12		9	8
4. Experience	20	12	12	8	12
5. Test	15	7	7	7	7

*See Figure 2.

**One animal of this group died on Day 8 of baseline conditioning.

***One animal of this group died on Day 69, three days after returning to 12 hours of access to food per day.

Figure 2. Daily presentation of food for Experiment I.


LIGHT
DARK
LIGHT
Hours/Day of Access to Food
1 (12)
no food
FOOD
no food
11am
11pm
2 (9)
8pm
3 (8)
7pm
4 (7)
no food
FOOD
no food
11am
6pm

The controls remain on this baseline schedule until they are tested by providing them with food only during the initial seven hours of the 12 hours of dark (see Table 1, Row 5, and Figure 2, Row 4).

Prior to this test deprivation, the experienced animals undergo a first exposure (20 to 23 days) where their daily food is present for the initial nine hours of the dark phase (Table 1, Row 2 or 3 and Figure 2, Row 2). This is followed by a second, more restricted, exposure (20 days) where the food availability is reduced to the first eight hours of dark (Table 1, Row 3 or 4 and Figure 2, Row 3).

The experience group is subdivided as follows: (a) those mice who receive the periods of deprivation experience immediately prior to the test deprivation and thereby follow the experimental sequence designated as (12 baseline) - (12) - (9) - (8) - (7 test); and (b) those who receive a past experience with the deprivation and are designated by the sequence (12 baseline) - (9) - (8) - (12) - (7 test). This latter group is intended for the purpose of examining the general applicability of deprivation experience as it is presented here. Will those mice allowed to return to ad libitum conditions (12 hours of access to food) for three weeks (past experience) respond to the test deprivation as do the controls or as do the immediate experience animals?

The control group is also subdivided into (a) controls for the two experience groups (long-term controls) designated (12 baseline) - (12) - (12) - (12) - (7 test); and (b) and a short-term control group intended to replicate the conditions of the original observation; this followed the sequence of (12 baseline) - (7 test).

D. Procedure

At approximately 70 days of age all mice were placed in separate cages where they remained socially isolated until the termination of the experiment. The cages were housed in a test-room with a reverse 12:12 hour light-dark cycle. Daytime lighting was provided by four overhead light bulbs (two 60 watt plus two 7 1/2 watt bulbs). Illumination six inches to the front of the three tiers of cages read 130 fc, 65 fc, and 16 fc top to bottom. At night the two 7 1/2 watt bulbs remained lit providing dim illumination (two fc, one fc, and 0.5 fc, respectively). Daily temperatures varied from 26°C at the end of the 12 hour light period to 23°C at the end of the dark period. Food and water remained available ad libitum. The food was changed to Purina lab pellets because they were less breakable than the breeder chow. The mice were given 40 days to adjust to these conditions.

At the end of this adjustment period the mice were randomly assigned to one of the four experimental groups. The individuals within any one group were, in turn, randomly assigned to a cage position on any one of the three available tiers.

Beginning with the baseline period (12 hours of food availability), food was no longer available ad libitum from the overhead hopper. Instead it was hung from the side of the cage by way of a wire passed through holes drilled in the pellets. This method facilitated the daily presentation and removal of the food, with a minimum of disturbance. Each animal received two food pellets (mean wt. = 12 g) at the beginning of the daily dark period for the allotted

time. The food was removed after each group received the scheduled feeding term.

A clean cage with fresh wood chips and a new Nestlet was provided to all mice on the first day of each new 20 to 24 day period. Other than for the scheduled removal of food, traffic into and out of the test room (for weighing the mice or changing their cages) took place only during the hour preceding lights-off (10:00 to 11:00 A.M.).

E. Analysis

Survival under conditions of the test deprivation is the primary dependent variable of this study. The hypothesis to be tested is that this survival is dependent on the previous deprivation experience. The data are fitted to two-way contingency tables (Sokal and Rohlf, 1969) with chi-square analyses (for Model II designs). Two animals died (one control and one experience) under 12-hour conditions and are not included in these analyses (see Table 1).

Food consumed per day and body weight (taken at approximately four day intervals) were also recorded, to the nearest tenth of a gram. If survival is dependent on experience, it is hypothesized that the experienced animals would consume more food per gram body weight per day during the test deprivation than would the control animals. This is to be tested by a single classification (experience *vs.* control) analysis of variance (Model I) with unequal sample sizes (Sokal and Rohlf, 1969). An *a priori* comparison of means will be applied to the grouped-controls *vs.* the grouped-experience animals. Homogeneity of variance is determined by the Fmax test.

Spillage of food appeared negligible. What did occur was assumed to be constant across groups and was discounted. The accumulation of spilled food across periods was prevented by cage changing.

F. Results

The chi-square analysis shown in Table 2 indicates that the survivability of P.m. bairdi on the test deprivation is, indeed, dependent on the previous experience with food deprivation ($P<0.005$). Here all of the controls ($n = 20$) are compared with all of the experienced mice ($n = 17$). The percentage of mortality among the controls is 50%, considerably higher than the mortality of 5.9% observed among the experienced animals. Furthermore, no difference existed in the initial body weights (taken immediately prior to the test deprivation) of the two groups: controls averaged 17.1 $\pm$ 0.3 (S.E.) g and experienced animals averaged 17.1 $\pm$ 0.6 g. Those mice that died did so at an average of 81.1 $\pm$ 1.7% of their initial body weights.

Results for each of the four groups are summarized in Figure 3. It is noted that four of the nine long-term controls died; one by Day 3, two by Day 4, and four by Day 5 of the test deprivation. For the short-term controls, four of 11 animals were dead by Day 4, five by Day 5, and six by Day 8. One mouse died in the experienced group (under immediate experience); it was dead on Day 7 of the test deprivation. Clearly, no differences in mortality exist within either the control or experience group.

Table 2.--Contingency table (2 x 2) of survivability for experienced vs. control P.m. bairdi on the test deprivation (food available during the first seven hours of the 12 hour dark period for 15 days).

	Experienced		Control		Σ
	Observed	Expected	Observed	Expected	
Died	1	5.1	10	5.9	11
Survived	16	11.9	10	14.1	16
Σ	17		20		37

$X^2 = 8.75$; $X^2_{0.005(1)} = 7.879$; $P<0.005$

In addition, the chi-square analysis presented in Table 3 shows that the survivability of past-experience mice is, in itself, significantly better than that of the long-term controls ($0.05>P>0.025$). The experience, therefore, either immediate or three weeks past, has been effective in reducing mortality.

It was hypothesized that experience would manifest itself in a greater daily food consumption under the test deprivation. Through the stepwise presentation of the deprivation experience P.m. bairdi would learn to increase their rates of intake in response to food availability. To examine this, the food consumed per gram of body weight (that at the initiation of the test deprivation) is compared between groups for Day 3 of the test. Day 3 was selected because it appeared to be a critical time in the animal's response to the deprivation (mode for time of death was Day 4). Results of the analysis of variance are shown in Table 4. No differences exist among

Figure 3. Daily mortality on the test deprivation of Experiment I for P.m. bairdi.

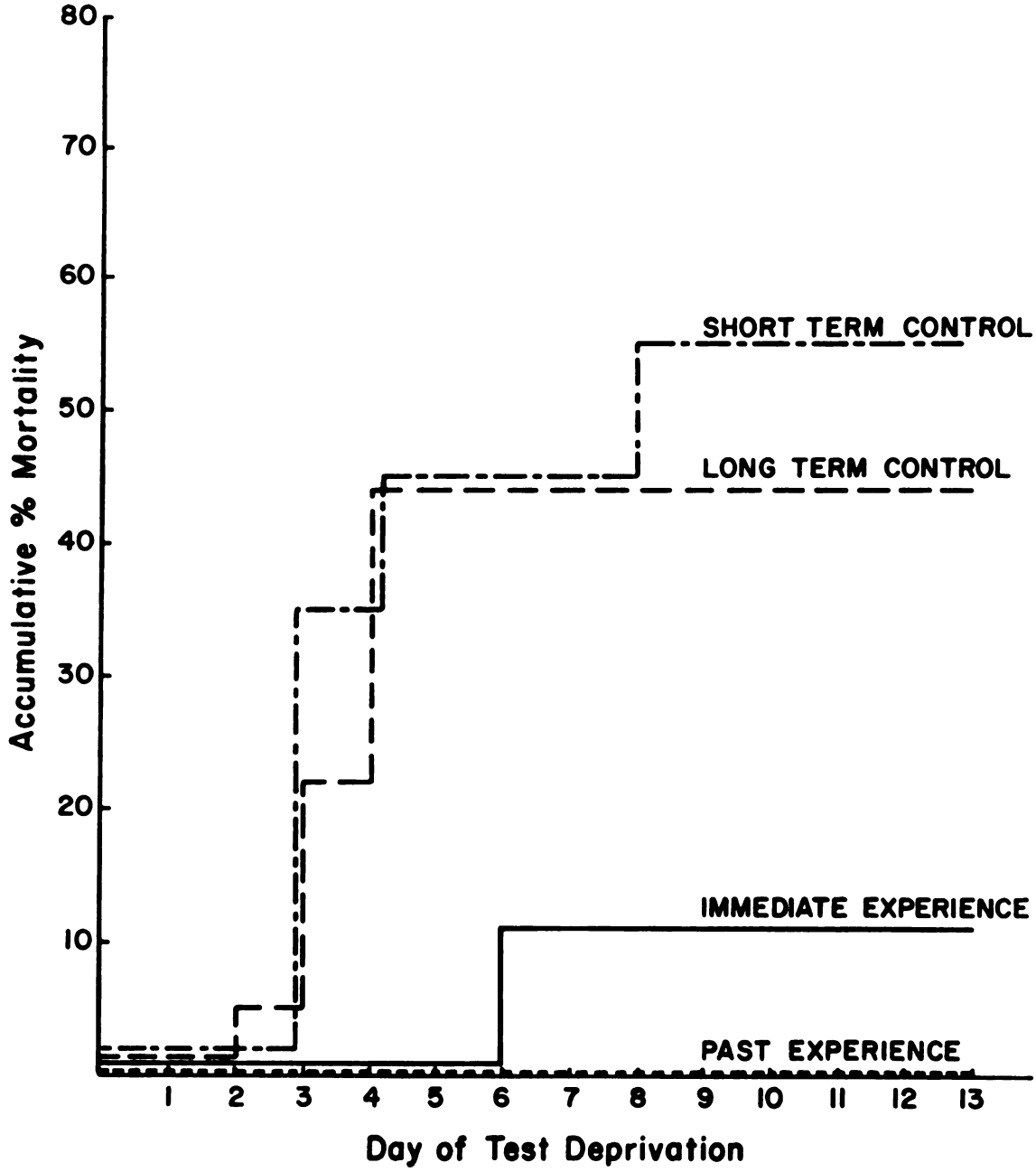

80
70
60
50
40
30
20
10
Accumulative % Mortality
SHORT TERM CONTROL
LONG TERM CONTROL
IMMEDIATE EXPERIENCE
PAST EXPERIENCE
1
2
3
4
5
6
7
8
9
10
11
12
13
Day of Test Deprivation

Table 3.--Contingency table (2 x 2) of survivability for past-experience vs. long-term control P.m. bairdi on the test deprivation.

	Past-Experience		Long-Term Control		Σ
	Observed	Expected	Observed	Expected	
Died	0	1.88	4	2.12	4
Survived	8	6.12	5	6.88	13
Σ	8		9		17

$X^2 = 4.64$; $X^2_{0.05(1)} = 3.841$; $0.05>P>0.025$

Table 4.--Analysis of variance (Model I single classification analysis of variance) for grams consumed per gram body weight in P.m. bairdi on Day 3 of the test deprivation.

Source of Variance	d.f.	SS	MS	F Ratio
Treatments	3	1,299.68	433.23	0.19
Control vs. Experience	(1)	(940.12)	940.12	0.42
Within	33	73,902.05	2,239.46	
Total	36	75,201.73		

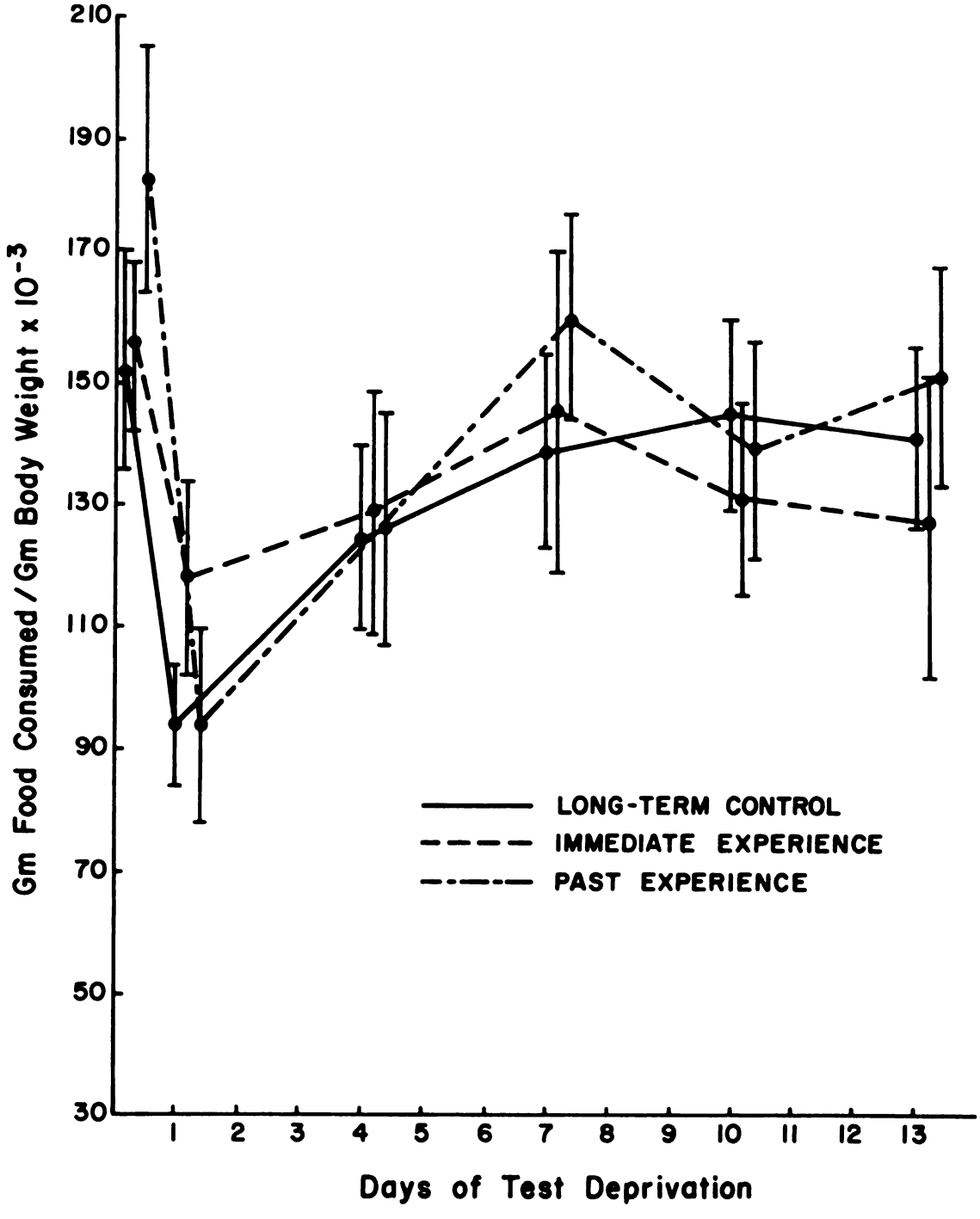
the four groups ($P>0.75$) or between the grouped-controls and the grouped-experience animals ($0.50<P<0.75$). Figure 4 illustrates this similarity throughout the test. The effect of the experience, therefore, is not to facilitate food intake during this specific time of availability.

G. Discussion

Various types of experience have been shown to affect the survival of adult rats and mice on severe food deprivation; these include post-weaning handling (Weininger, 1956); handling in infancy (Levine, 1957; Levine and Otis, 1958; Denenberg and Karas, 1959); early handling and later avoidance-learning (Denenberg and Karas, 1961); early malnutrition and isolation (Levitsky and Barnes, 1972); and infantile handling or faradic-stimulated shock interacting with post-weaning intermittent fasting (Kendrick, 1973). In these instances, however, there appears to be little that is interpretable regarding the nature of the experience(s). The underlying experiential factors are assumed to be related to the animal's "excitability" in response to the deprivation (Lát and Holěcková, 1971). The interplay of emotion or CNS excitement with food deprivation is, however, abstract and difficult to interpret in any consistent pattern.

Here, too, the term experience means little in and of itself. To discuss its significance necessitates an understanding of how it might affect the behavior or physiology of the mouse. What is known is that the effect of this experience might be manifested in either a greater energy input (i.e., food intake or utilization) or in a more conservative energy use (i.e., reduced time or intensity of physical activity), or possibly in both.

Figure 4. Food consumption of P.m. bairdi on the test deprivation of Experiment I.


Gm Food Consumed / Gm Body Weight x 10⁻³
210
190
170
150
130
110
90
70
50
30
1
2
3
4
5
6
7
8
9
10
11
12
13
Days of Test Deprivation
LONG-TERM CONTROL
IMMEDIATE EXPERIENCE
PAST EXPERIENCE

In regard to the first alternative, rats may be trained to ingest their daily food in fixed periodic and force-fed meals (Lawrence and Mason, 1955; Tepperman and Tepperman, 1958; Cohn et al., 1962; Baldessari et al., 1971). About three weeks are required for rats to adjust maximal intake in a single one-hour meal per day (Dufort, 1964). A number of days are also required, after return to ad libitum food, for the daily consumption to drop to pre-deprivation levels (Lawrence and Mason, 1955; Bauer and Stebbins, 1972). The net effect of the deprivation experience in my experiment, however, was not such a build-up or concentration of intake. There was no greater intake during the seven hours of access per day for the experienced than for the control animals (Figure 4). Conceivably the experienced mice could have been more efficiently processing and utilizing the food that they consumed.

Alternatively, the mice could have reduced the energy output. It has often been reported that general activity (via stabilimeter cages, running wheels, open-field movement, or exploration) increases as a result of food deprivation (Campbell et al., 1961; Bolles, 1965; Cornish and Mrosovsky, 1965; Jakubezak, 1973). This increase presumably enhances the probability of the animal making contact with food. Under conditions of temporal food deprivation, however, a high general level of activity might be inappropriate. It has been demonstrated that the activity response to deprivation can be negligible or even be reduced depending on the specific environmental circumstances or on the species tested (Hall, 1956; Strong, 1957; Teghtsoonian and Campbell, 1960; Symons, 1973). Is, then, one effect of the deprivation experience of this experiment to lower the level of

general activity and thereby reduce the daily energy requirement? Bolles (1963), for instance, did find that hungry rats (12 days on a daily deprivation schedule) after approximately one week of deprivation spent more time resting or just standing motionless than did control animals. Does a lower level of activity enhance survival under the test conditions?

Data were collected in conjunction with Experiment I which have a bearing on these questions. (See Appendix A for experimental procedures). Here, one group of P.m. bairdi was given ad libitum access to running wheels during both a baseline period and the test deprivation identical to that of Experiment I; a second group was housed in the previously-described colony-type cages throughout the baseline and test periods. If mice with access to the wheels are more active and expend more energy, then the hypothesis can be made that this greater ambulation will reduce survival under the test deprivation.

The results confirm the hypothesis. Mortality reached 19 of 23 animals (83%) in the Wheel group compared to only six of 23 (26%) for the No-wheel mice. A pooled chi-square analysis (Table 5) shows this difference to be significant ($X^2 = 14.81$, $P<0.005$). Day 4 again showed the greatest daily percent drop in survivors. For those that died (25 out of 46) the average time to do so was at 4.5 ± 0.3 days, with a range from Day 3 (six mice) to Day 11 (one mouse). Food intake per gram of body weight was compared between groups for all animals for Day 2 of the test deprivation. Again there was no difference ($T = 1.11$, $0.4>P>0.2$), supporting the contention that food intake per se was not the critical variable.

Table 5.--Chi-square analyses (Run 1, Run 2, pooled, and homogeneity) of survivability for wheel vs. non-wheel P.m. bairdi on the test deprivation (food available during the first seven hours of the 12 hour dark period for 15 days).

	Wheel		No Wheel				
	Survived	Died	Survived	Died	X^2	d.f.	p
Run 1	4	9	9	4	3.85	1	0.05>p
Run 2	0	10	8	2	13.34	1	0.005>p
Sum of 1 & 2					17.19	2	
Pooled	4	19	17	6	14.81	1	0.005>p
Homogeneity					2.38	1	0.5>p>0.1

Woolf, 1968.

The data suggest, rather, that it is the level of general activity that is important for survival under these conditions. In fact, it was observed that wheel running, as visually monitored through an Esterline-Angus event recorder, intensified in response to the removal of food and often continued well into or through the light period.

Deprivation has been shown to increase activity in running wheels much more than in stationary cages when the two devices are directly compared (Treichler and Hall, 1962; Weasner et al., 1960). This is probably because locomotion on a running wheel produces greater visual, auditory, and kinesthetic stimulation than does locomotion in a stationary cage (Gross, 1968). This running seems to be "self-reinforcing," as rats will bar-press to obtain access to a wheel (Kagun and Berkun, 1954). In addition, the confinement to a small

nest-box, such as those employed here, would encourage use of the adjoining wheel.

This outlet for increased activity (wheel running) has also been observed to have a profound detrimental effect on the survival of food-deprived rats (Weasner et al., 1960; Routtenberg and Kuznesof, 1967). This outcome is presumed to be due to the disparity between energy input (food), which remains static, and energy output (via the running wheel), which greatly increases. The greater this disparity, the higher is the likelihood of mortality. Symons (1973) found that the level of wheel-running for each of four mouse strains correlated negatively with their survival time on the food deprivation. In addition, Routtenberg and Kuznesof (1967) reported that administration of the drug chloropromazine lowered the wheel activity of food-deprived rats and resulted in a significantly reduced mortality.

It should be made clear that these findings only suggest an association between deprivation experience and activity level. Very little is understood concerning the behavioral effects resulting from prolonged or repeated experience with "mild" food deprivation.

The experience may affect activity by altering the animal's perception of the deprivation situation. Considerable evidence indicates that deprivation per se does not increase activity, but rather increases the reactivity to external or novel stimuli; this is manifested as more locomotor activity (Baumeister et al., 1964). This is consistent with the result here that the food removal seemed to stimulate an immediate increase in activity. Fehrer (1956) found that hungry animals left a familiar environment to explore a novel one faster than did satiated ones. Halliday (1968) suggested that food

deprivation increases exploratory activity only until the animal finds that there is no food in the situation; thereafter exploratory behavior decreases with deprivation. No data, however, have been put forward to support this hypothesis.

Experience might also partially extinguish the learned association between eating and movement activities associated with the procurement of food. Richter (1972) first reported that periods of locomotor activity (via the running wheel) are closely associated in time with the feeding bouts of the rat. A similar observation has been made for P.m. bairdi (Jaeger, unpub. obs.). Feeding and wheel-running have, in addition, been shown to be mutually reinforcing, such that an animal will not only increase wheel-running to obtain food but also increase food intake to obtain access to a running wheel (Premack and Premack, 1958). Finger et al. (1960) found a differential reinforcement of activity on mild deprivation depending on the length of the interval between the period of access to a running wheel and the food presentation. Significantly less activity occurred when food availability followed access to the wheel by one hour than when the food was available immediately upon removal from the wheel. These examples, therefore, suggest that the experience might provide sufficient time for the feeding reinforcement to become dissociated from a burst of running activity, and that this results in a diminished running reaction to the food removal. The results of Premack and Premack (1958) support this interpretation. They found that when deprived of a wheel the food intake of rats increased to a maximum on about the third post-wheel deprivation day, and that intake did not return to baseline for about 14 days. It is interesting to note here

that the mode for day of death on the test deprivation was Day 4, similar to the time of their maximum response.

It appears, therefore, that activities associated with foraging might increase or decrease depending on the reinforcement properties of the feeding situation. Experience might, therefore, play a very important role in whether or not an "appropriate" response is made in a deprivation situation. For circumstances of low food density that response might be to increase search activity, while for unfavorable weather, reduced movement (i.e., remaining in a suitable microhabitat) might be the more appropriate. It is also conceivable that foraging for a food, which is evenly scattered but in very low density, can be energetically more costly than the food return. Here again conserving energy output might be the most effective approach, particularly if the deprivation situation is temporary, for example a temporal gap between the maturity or availability of different food sources.

Deprivation experience and energy conservation notwithstanding, inactivity must be complemented with periods of foraging, especially when food stores are unavailable. It is hypothesized that deer mice will concentrate this foraging into periods of restricted access (i.e., due to conditions where exposure to either low temperature or predators must be minimized).

EXPERIMENT II--THE EFFECT OF THE TIME OF PRESENTATION ON FOOD INTAKE: EARLY-NIGHT VS. LATE-NIGHT

Regardless of the deprivation experience, P.m. bairdi demonstrated little capability in adjusting their daily intake to seven hours of food availability. Both control and experience animals ate the same reduced amounts of food per gram of body weight; and both groups lost appreciable weight. This outcome suggests that food intake might be influenced by the temporal properties of the presentation and removal. It will be recalled that, during the test deprivation, food was available early, from the onset of the dark period.

Some evidence shows that feeding can be affected by the circadian timing of food availability (Welch, 1968; Baldessari et al., 1971). Nelson et al. (1973) reported that the survival of young BALB/c mice, after abrupt restriction to a single four hour span of daily food accessibility, depended on the temporal placement of this feeding span in relation to the lighting regime. Those mice allowed access to food during the initial four hours of their twelve hour diurnal period began dying within three days with 50 percent mortality by the fifth day; while mice allowed food in either the initial or final four hours of their nocturnal period began dying on the fifth

or sixth day with 35 percent mortality by Day 13. That there can be a circadian influence on the nocturnal foraging in Peromyscus is suggested by the work of Hirth (1959). He observed a differential reaction to rainfall within the nocturnal period of P.l. noveboracensis, with a tendency for catches to be low if rain fell before midnight and higher if it fell afterward.

A. Purpose

Are P.m. bairdi able to concentrate their daily food intake into a particular time period during the diel cycle in order to compensate for a period of deprivation? Experiment II addresses itself to this question. The specific hypothesis to be tested is that food intake is greater and survival is enhanced when the food is available during the final six hours of the dark period as opposed to the initial six hours. This experiment is further intended as a replication of Experiment I, but with a new experience schedule. Here the effects of both early deprivation and late deprivation experience will be examined under early and late test deprivation conditions.

B. Subjects

Successive runs of this experiment employed a total of 60 male P.m. bairdi. The 26 mice used in the inital run (from 31 October, 1974 to 20 December, 1974) weighed an average of 18.25 $\pm$ 0.36 g and were 118 $\pm$ 2.8 days of age at the beginning of the experiment. These animals represented nine litters from five mated pairs. The second run (from 18 January, 1975 to 5 March, 1975) was experimentally identical to the first; it used 34 deer mice at an average age of 134.8 $\pm$ 3.6 days and an average body weight of 18.00 $\pm$ 0.31. These animals

represented nine more recent litters from the same five mated pairs. The genetic history, rearing conditions, and test room conditions were the same as those described for Experiment I.

C. Experimental Design

The experimental design shown in Table 6 is similar to that of Experiment I. The animals are divided into four equal groups of 15 mice each, forming two control groups and two experience groups. Initially all of the animals undergo a baseline period of ten days where the food is available each day during the 12 hours of dark (Row 1, Table 6). Both control groups remain on this schedule for an additional 25 days (Rows 2-7), after which time they undergo five days of test deprivation (Row 8). At this time the Early-food controls have access to food for the initial six hours of the dark period and are deprived for the final six hours. The Late-food controls, on the other hand, are deprived during the initial six hours of dark and have access to food during the last six hours. Following the test deprivation the survivors of both control groups are given one recovery day of 12 hours of access to food (Row 9). The reverse test deprivation is then imposed for five days (Row 10). Here, the Early-food controls receive early deprivation and late access and vice versa for the Late-food controls.

Following the baseline period, the experience groups undergo 25 days of their respective Early-food or Late-food experience. The Late-food experience begins with ten days where the access to food is in the final nine hours of the dark period (Row 2). This is followed by successive five-day blocks (Rows 4 and 6) allowing first the final

Table 6.--Design for Experiment II.

Experimental Timetable			Hours/Day of Access to Food			
			Control		Experience	
Experimental Organization	Days	Regime	Early Food (n = 15)	Late Food (n = 15)	Early Food (n = 15)*	Late Food (n = 15)*
1. Baseline	10	Baseline	12	12	12	12
2. Experience	10	Experience	12	12	9 Early	9 Late
3. Experience	1	Recovery	12	12	12	12
4. Experience	5	Experience	12	12	8 Early	8 Late
5. Experience	1	Recovery	12	12	12	12
6. Experience	5	Experience	12	12	7 Early	7 Late
7. Experience	3	Recovery	12	12	12	12
8. Test	5	Test	6 Early	6 Late	6 Early	6 Late
9. Test	1	Recovery	12	12	12	12
10. Test	5	Reverse Test	6 Late	6 Early	6 Late	6 Early

*One animals in each group died during the ten-day baseline period.

eight hours and then the final seven hours for access to food. A recovery day with 12 hours of access separates each experience block (Rows 3 and 5), with three such days after the seven hour block (Row 7). The Early-food schedule of experience is the same as above with the exception that the nine, eight, and seven hours blocks refer to the initial hours of food availability per dark period (Rows 2, 4, and 6). The respective test and reverse test deprivations are the same as those described for the controls (Rows 8 and 10). The experimental procedures throughout are the same as those described for Experiment I.

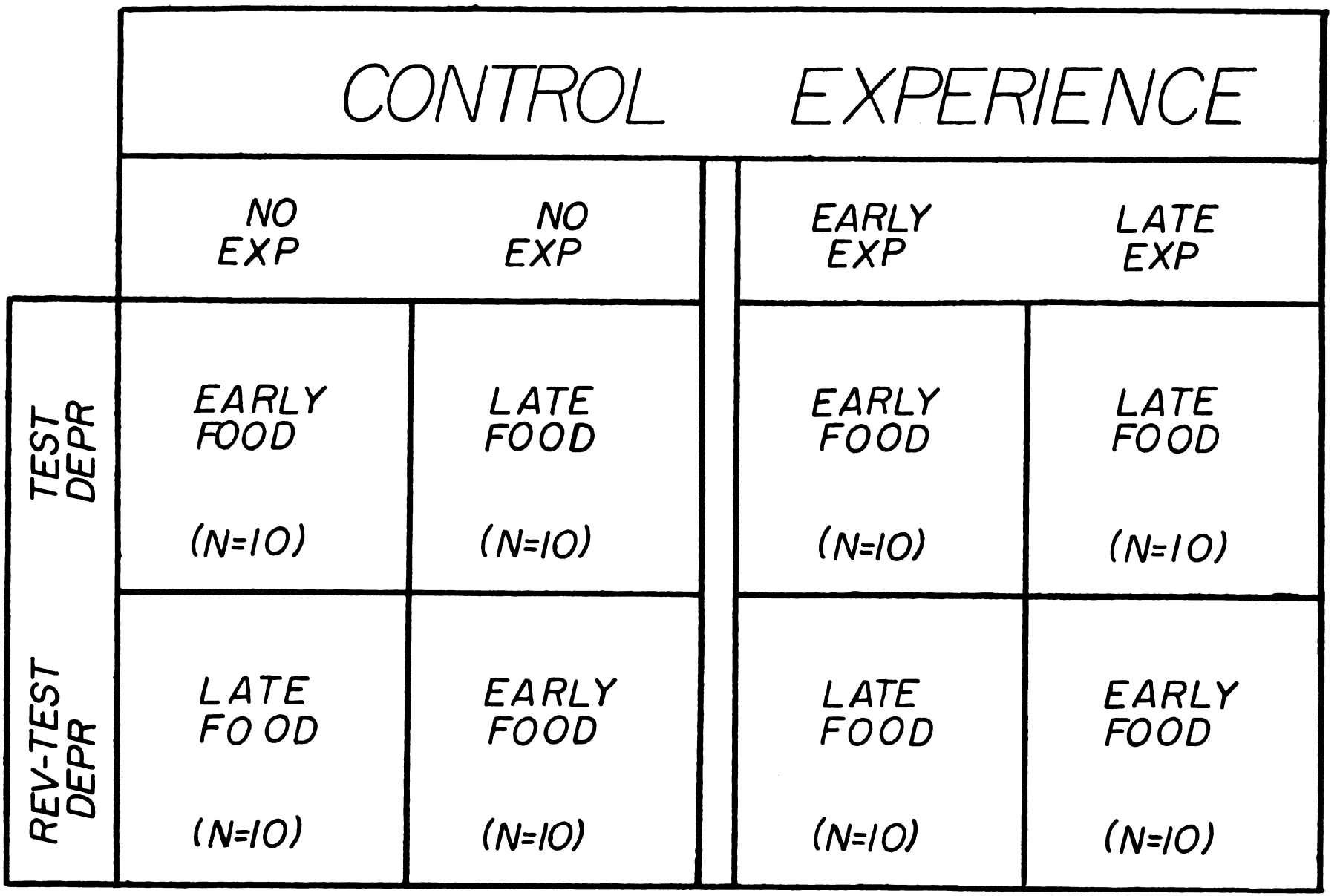
D. Analysis

The dependent variables considered in this experiment are survival, body weight change, and daily food consumption.

Survival *vs.* death is again tested *via* a chi-square (Model II design) analysis of a two-way contingency table. Because the experiment was conducted in two separate, but equal, runs, it is necessary to check the subsamples for homogeneity before legitimately pooling the results. The chi-square values and the degrees of freedom for the two subsamples are added. A probability value (i.e., whether the subsamples were taken from the same population) results from the difference between the total chi-square value and the pooled chi-square value and is distributed with degrees of freedom equal to the difference between those of the total and pooled degrees of freedom (Woolf, 1968).

The data on body weight change and daily food consumption are analyzed using a split-plot, repeat measure design with Latin Squares in the sub-plots. This is illustrated in Figure 5. Here each subject

Figure 5. Split-plot, repeat measure design with Latin squares in the subplots for Experiment II.


CONTROL
EXPERIENCE
NO EXP
NO EXP
EARLY EXP
LATE EXP
TEST DEPR
EARLY FOOD
(N=10)
LATE FOOD
(N=10)
EARLY FOOD
(N=10)
LATE FOOD
(N=10)
REV-TEST DEPR
LATE FOOD
(N=10)
EARLY FOOD
(N=10)
LATE FOOD
(N=10)
EARLY FOOD
(N=10)

receives both the late and early test (or reverse test) deprivation, but with either deprivation experience or no deprivation experience (control group). The main effects of the experience vs. control treatment are said to be completely confounded with other differences among these blocks. This confounding, however, does not affect the interpretability of the treatment effects, only the precision of the estimate. On the other hand, the main effects of early vs. late food presentation and the interaction between the experience and the time of food presentation are free from such confounding and are generally the more powerful tests (Kirk, 1968).

This split-plot design has two error terms. One corresponds to the pooled variation among subjects within the experience vs. the control groups; while the other source is the pooled interaction of the early vs. late test treatment within each block. For the F ratios associated with each error term to follow an F distribution, the sources of variation within each term must be homogeneous. These can be tested by means of the Fmax test (Kirk, 1968).

The repeated measures aspect of this design offers the advantage of controlling subject heterogeneity. Differences among subjects are often such as to obscure the treatment effects. An important limitation to the use of these repeated measures, however, lies in the likelihood of the error components from the reverse test deprivation not being independent from those of the preceding test deprivation. When this is the case, the variance-covariance matrix departs from the required form. The procedures found in Kirk (1968) for testing the equality of covariance matrices are those employed here. When the hypothesis of equality of the variance-covariance

matrices is accepted (the obtained chi-square value is less than the tabled value), independence is assumed.

In addition to information from the above tests, the means of individual elements within the design will be compared. If the interaction between experience vs. no experience and the time of food presentation (early vs. late) is significant, it will be of interest to determine in what way the early vs. late differences are not of the same magnitude for controls as for the experienced mice. It will be of further interest to compare the means of the early-late deprivation test sequence controls with those of the early-late sequence experience mice, as well as the means of the late-early controls with those of the late-early experience animals.

E. Results

The results are organized under three headings: survivability, bodyweight loss, and food consumption. The effects of both treatments (control vs. experience and early vs. late food presentation) will be considered for each of these dependent variables. In addition, each section will open with a summary of the findings as they are interpreted for that particular variable.

1. Survivability

As was hypothesized, there is a circadian effect (within the nocturnal period) on survivability under the present conditions of temporal food deprivation. All of the fatalities of P.m. bairdi under the four conditions resulting from late or early food presentation with or without deprivation experience are presented in Table 7. All of the fatalities of P.m. bairdi (11 dead out of 58 animals) occurred when

Table 7.--Fatalities of P.m. bairdi under the test deprivation and reverse test deprivation conditions.

Group	Test Deprivation (TD)		Reverse Test Deprivation (RTD)	
	Initial Number of Animals	Number of Fatalities	Initial Number of Animals	Number of Fatalities
1. Early food control	15	[5] *	10	0
2. Early food experience	14	[0]	14	0
3. Late food control	15	0	15	[3] *
4. Late food experience	14	0	14	[3]

*Brackets represent the condition where food is available for only the initial six hours of dark; no brackets therefore represent the condition where food is available during the final six hours.

mice were subjected to the early food presentation (initial six hours of the 12 hour dark period). Refer to TD(1), RTD(3), and RTD(4) in Table 7. This result occurred regardless of experience with late food presentation (RTD(3)) or the sequence of testing (early-late or late-early). No mice, however, with early food access experience died on the early food access test (or reverse test) deprivation (TD(2)).

The chi-square analysis (Table 8) indicates that the mortality of P.m. bairdi on the test deprivation depends on the time of the food presentation (pooled chi-square = 0.05; $0.025>p>0.01$). The results from the two runs do appear homogeneous (chi-square = 0.05; $0.9>p>0.5$). During the five days of the early-food test deprivation, five of 29 mice died (17.24%), while not one of the 29 mice subjected to

Table 8.--Chi-square analyses (Run 1, Run 2, pooled, and homogeneity) of survivability for late food test deprivation (food available during the final six hours of the 12 hour dark period for five days), vs. early food test deprivation (food available during the initial six hours), in P.m. bairdi.

	Late Food Test Deprivation		Early Food Test Deprivation				
	Survived	Died	Survived	Died	X^2	d.f.	p
Run 1	13	0	10	3	3.39	1	0.1>p>0>05
Run 2	16	0	14	2	2.13	1	0.5>p>0>1
Sum of 1 & 2					5.52	2	
Pooled	29	0	24	5	5.47	1	0.025>p>0.01
Homogeneity					0.05	1	0.9>p>0.5

Woolf, 1968.

the late-food deprivation test died. Two of the animals were dead by the morning of Day 3, and one each by Days 4, 5, and 6.

Similar findings are presented in Table 9 for early food vs. late food P.m. bairdi on the reverse test deprivation (pooled chi-square = 5.53; 0.025>p>0.01; homogeneity chi-square = 0.45; 0.9>p>0.5). Here six of 29 mice died (20.68%) during five days of the early food reverse test deprivation. Two were dead by Day 3, three by Day 4, and one by the morning of Day 5. Again no mice with access to food during the final six hours of the 12 hour dark period died. Those 11 animals that died in the test or reverse test deprivations did so at an average of 76.92 $\pm$ 1.57 (S.E.) percent of their initial body weights.

The finding of Experiment I, regarding the survival advantage associated with early food experience, was confirmed here. The

Table 9.--Chi-square analyses (Run 1, Run 2, pooled, and homogeneity) of survivability for early food vs. late food P.m. bairdi on the reverse test deprivation.

	Late Food Reverse Test Deprivation		Early Food Reverse Test Deprivation				
	Survived	Died	Survived	Died	X^2	d.f.	p
Run 1	10	0	11	2	1.80	1	0.5>p>0.1
Run 2	14	0	12	4	4.18	1	0.05>p>0.025
Sum of 1 & 2					5.98	2	
Pooled	24	0	23	6	5.53	1	0.025>p>0.01
Homogeneity					0.45	1	0.9>p>0.5

Woolf, 1968.

chi-square analysis (Table 10) indicates that survivability on the early food test deprivation is dependent upon experience with early food deprivation (pooled chi-square = 5.59; 0.025>p>0.01; homogeneity chi-square = 0.11; 0.9>p>0.5). Here five of the fifteen control mice died (33.33%) while all of the early food experience animals survived the five days of the test deprivation.

The effect of the late food experience on survivability is less clear, although it appears to be minimal. Under the reverse test deprivation, with early food, the survivability of late food experience mice (Table 7, RTD(4)) does not differ significantly from that of the early food experience animals on the early food test deprivation (Table 7, TD(2)) (pooled chi-square = 3.36; 0.1>p>0.05; homogeneity chi-square = 0.02; 0.9>p>0.5). These data are presented in Table 11.

Table 10.--Chi-square analyses (Run 1, Run 2, pooled, and homogeneity) of survivability of early food experience vs. early food control P.m. bairdi on the early food test deprivation.

	Early Food Experience		Early Food Control				
	Survived	Died	Survived	Died	X^2	d.f.	p
Run 1	6	0	4	3	3.41	1	0.1>p>0.05
Run 2	8	0	6	2	2.29	1	0.5>p>0.1
Sum of 1 & 2					5.70	2	
Pooled	14	0	10	5	5.59	1	0.025>p>0.01
Homogeneity					0.11	1	0.9>p>0.5

Woolf, 1968.

Table 11.--Chi-square analyses (Run 1, Run 2, pooled, and homogeneity) of survivability for early food experience vs. late food experience P.m. bairdi on the early food test deprivation and the early food reverse test deprivation, respectively.

	Early Food Experience		Late Food Experience				
	Survived	Died	Survived	Died	X^2	d.f.	p
Run 1	6	0	5	1	1.09	1	0.5>p>0.1
Run 2	8	0	6	2	2.29	1	0.5>p>0.1
Sum of 1 & 2					3.38	2	
Pooled	14	0	11	3	3.36	1	0.1>p>0.05
Homogeneity					0.02	1	0.9>p>0.5

Woolf, 1968.

The trend, however, suggests that the early experience mice are more successful under these conditions. In this case three of the late experience animals died while, again, there was no mortality among the early experience mice.

2. Body Weight Loss

The results here confirm the early vs. late effect shown on survivability; significantly more weight was lost under early food availability. There is, however, no effect of experience on body weight loss. The early food experience mice, therefore, lose weight to the same degree as do the controls or the late food experience mice when on the early food deprivation. In addition, there appears to be no interaction between experience and the time of food presentation. These results do not support the hypothesis that experience affects a reduction in activity during deprivation.

The analysis of variance for body weight loss for experience vs. control P.m. bairdi is presented in Table 12. This is based on the difference between the initial weight measured at the onset of both the test and reverse test deprivations and the weight after three days (taken on the morning of Day 4) of early or late test or reverse test deprivations. The analysis is based on a sample size of 80 (40 mice in each of two test conditions). The nature of this design (repeat measures) dictates that the sample size be the same for each of the four groups (combination of early vs. late with experience vs. control), and that those animals considered in the reverse test be the same as those in the test deprivation (see Figure 5). Because five of the 15 early food controls died during the test deprivation (Table 7,

Table 12.--Analysis of variance table for body weight loss (grams) for experience vs. control P.m. bairdi after three days of early vs. late test (or reverse test) deprivation.

Source	SS	d.f.	MS	F
1. Between subjects	22.3705	39		
2. Experience vs. control	0.3919	1	0.3919	0.6391
3. Subjects within groups	23.3036	38	0.6132	
4. Within subjects	83.8950	40		
5. Test vs. reverse test deprivation	0.1619	1	0.1619	0.2752
6. (2) x (5)	0.6130	1	0.6130	1.0423
7. Early vs. late	60.5519	1	60.5519	102.9619*
8. (2) x (7)	0.0607	1	0.0607	0.1032
9. Error	21.1725	36	0.5881	
10. Total	106.2555	79		

*$p<0.001$.

Row 1), it was necessary to select randomly ten animals from each of the remaining three groups for this analysis.

Table 12 indicates that early vs. late test (or reverse test) conditions had significantly different effects on body weight loss ($F = 102.9619$; $p<0.001$). Mice with access to food during the initial six hours of the dark period lost an average of 1.84 ± 0.10 (S.E.) g compared with an average loss of 0.10 ± 0.10 g for those with access during the final six hours.

Those Peromyscus with previous deprivation experience (early or late) lost an average of 0.90 ± 0.17 g while the controls dropped 1.01 ± 0.17 g. This difference is not significant ($F = 0.6391$; $0.50> p>0.25$). The effects of early and late experience are compared separately in Table 13. Neither type of experience differs from its control for either the test or reverse test deprivation or for the two tests taken in sequence. As was suggested from Experiment I, early food experience does not manifest itself through reduced weight loss.

Figure 6 illustrates these effects of time of food presentation, experience, and the degree of interaction between them ($F = 0.1032$; $p>0.50$).

It should also be noted that no difference is found between the test and reverse test deprivations ($F = 0.2752$; $p>0.5$ (Table 12(5))), nor does this variable appear to interact with the experience vs. control factor ($F = 1.0423$; $p>0.25$ (Table 12(6))).

Results of the Fmax tests, for homogeneity of variance within error terms, are shown in Table 14. Homogeneity is accepted for both. In addition, the hypothesis of the equality of the experience vs.

Table 13.--Comparison of mean body weight loss in grams for experience vs. control P.m. bairdi after three days of early vs. late test (or reverse test) deprivation.

	Control		Experience	
Test Deprivation ($\bar{Y} \pm$ S.E.)	Early food (1) -1.52 ± 0.17	Late food (3) -0.29 ± 0.26	Early food (5) -1.59 ± 0.24	Late food (7) -0.29 ± 0.24
Reverse Test Deprivation ($\bar{Y} \pm$ S.E.)	Late food (2) -0.10 ± 0.14	Early food (4) -2.24 ± 0.31	Late food (6) +0.29 ± 0.10	Early food (8) -2.00 ± 0.22

	Comparison of Means	F
Late food experience	(3) x (7)	1.000
	(4) x (8)	0.4978
Early food experience	(1) x (5)	0.0423
	(2) x (6)	0.2800
Late vs. early sequence	(3)(4) x (7)(8)	0.2495
Early vs. late sequence	(1)(2) x (5)(6)	0.4429

F (0.05) 1,38 = 4.08

Figure 6. Body weight loss (in grams) for experience (early or late) vs. control P.m. bairdi from Day 0 to Day 3 of early vs. late test (or reverse test) deprivation.

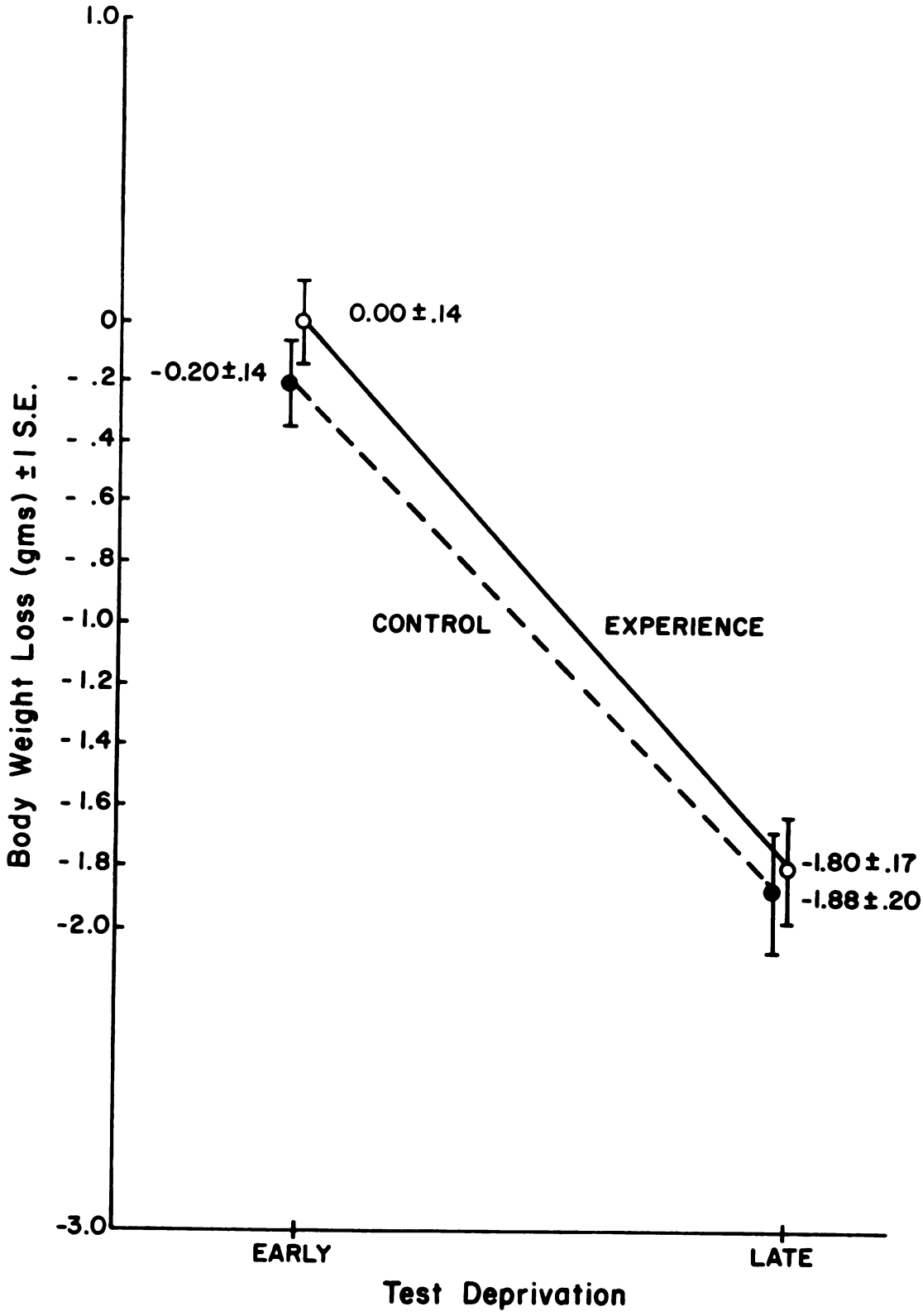

1.0
0
- .2
- .4
- .6
- .8
- 1.0
- 1.2
- 1.4
- 1.6
- 1.8
-2.0
-3.0
Body Weight Loss (gms) ± 1 S.E.
0.00 ± .14
-0.20±.14
CONTROL
EXPERIENCE
-1.80 ± .17
-1.88 ± .20
EARLY
LATE
Test Deprivation

Table 14.--Fmax tests for homogeneity of variance within error terms of body weight change analysis.

a. Partition of subjects within groups sum of squares (no. 3, Table 12)

Source	SS	d.f.	MS	Fmax
Subjects within groups	23.3036	38		
Within control group	11.4938	19	0.6490	1.0442
Within experience group	11.8098	19	0.6215	

Fmax (0.05) 2,20 = 2.46

b. Partition of early vs. late subjects within groups sum of squares (no. 9, Table 11)

Source	SS	d.f.	MS	Fmax
Early vs. late subjects within groups	21.1725	36		
Within early group	13.4480	18	0.7471	1.7409
Within late group	7.7245	18	0.4291	

Fmax (0.05) 2,20 = 2.46

control variance-covariance matrices is tenable (chi-square = 0.9552; $p>0.5$, with three degrees of freedom).

3. Food Consumption

These results are consistent with those found for body weight loss. That is, on the late food regime significantly more is consumed than with early food availability. Here the total five day food consumption, for the test or reverse test deprivation, is the dependent variable. Again, there appears to be no effect of either prior experience or an interaction between experience and the time of presentation. This re-confirms the finding that experience is not being manifested in an increased food consumption.

Furthermore, evidence indicates that this late food advantage is due to an adjusted, or concentrated, six-hour uptake which excedes that for the same period under ad libitum conditions. It is noted that a greater adjustment is made during the first day on late food than over the five days on early food.

The analysis of variance for the total amount of food consumed during the five day test or reverse test deprivation periods is found in Table 15. Here the early vs. late test (or reverse test) conditions had significantly different effects on the total food intake ($F = 100.9693$; $p<0.001$). The animals with immediate access to food consumed an average of 9.13 ± 0.47 (S.E.) g in five days compared to 12.24 ± 0.67 g for the mice with the food available during the final six hours.

Previous deprivation experience (early or late) again effected no significant difference ($F = 0.9146$; $p>0.25$ (Table 15(9))). The

Table 15.--Analysis of variance table for total food consumed (grams) for experience vs. control P.m. bairdi for 5 days of early vs. late test (or reverse test) deprivation.

Source	SS	d.f.	MS	F
1. Between subjects	1,034.3349	39		
2. Experience vs. control	24.3101	1	24.3101	0.9146
3. Subjects within groups	1,010.0248	38	26.5796	
4. Within subjects	268.7250	40		
5. Test vs. reverse test deprivation	3.0811	1	3.0811	1.6004
6. (2) x (5)	0.0102	1	0.0102	0.0052
7. Early vs. late	194.3761	1	194.3761	100.9693*
8. (2) x (7)	1.9532	1	1.9532	1.0145
9. Error	69.3044	36	1.9251	
10. Total	1.303.0599	79		

*$p<0.001$.

experienced animals did, however, consume more food than did the controls: 11.24 ± 0.58 (S.E.) g and 10.13 ± 0.66 g respectively. Table 16 breaks experience into its early and late components and compares each with its control for either the test or reverse test situation and for these two situations combined. No significant differences appear, however.

Further, there is no interaction between the experience with deprivation and the early vs. late test or reverse test conditions ($F = 1.0145$; $p>0.25$ (Table 15(8))). The relationship is shown graphically in Figure 7.

Both error terms test homogeneous (Table 17). In addition, the variance-covariance matrices (experience vs. control) are accepted as equal (chi-square = 6.7063; $0.1>p>0.05$).

Having established the importance of the time of food availability within the nocturnal activity period, it is of interest to know whether the late food mice increase their six-hour food intake over the baseline amount for the same period, or whether they normally consume the greater percentage of their 12-hour ad libitum intake during the final six hours. When the amount of food consumed on Day 1 of the early food test or reverse test deprivation is taken as a percentage of that consumed the previous ad libitum day, the result is an estimate of the percentage of total intake consumed during the initial six hours of ad libitum day (one with access to food during the entire 12 hours of dark). In this experiment that percentage was 49.41 ± 1.96 (S.E.)%. (This and subsequent percentages are all derived from the same 47 survivors.) It follows, then, that 50.59 percent of the total intake occurred during the final six hours. Now, the amount of

Table 16.--Comparison of mean total food consumption in grams for experience vs. control P.m. bairdi for five days of early vs. late test (or reverse test) deprivation.

	Control		Experience	
Test Deprivation ($\bar{Y} \pm$ S.E.)	Early food (1) 7.92 ± 0.87	Late food (3) 11.94 ± 1.68	Early food (5) 10.27 ± 0.78	Late food (7) 11.84 ± 0.96
Reverse Test Deprivation ($\bar{Y} \pm$ S.E.)	Late food (2) 11.14 ± 1.42	Early food (4) 9.55 ± 1.12	Late food (6) 14.07 ± 1.35	Early food (8) 8.78 ± 1.05

	Comparison of Means	F
Late food experience	(3) x (7)	0.0019
	(4) x (8)	0.1115
Early food experience	(1) x (5)	1.0389
	(2) x (6)	1.6149
Late vs. early sequence	(3)(4) x (7)(8)	0.0696
Early vs. late sequence	(1)(2) x (5)(6)	2.6221

F (0.05) 1,38 = 4.08

Figure 7. Total food consumed (in grams) for experience (early or late) vs. control P.m. bairdi during five days of early vs. late test (or reverse test) deprivation.

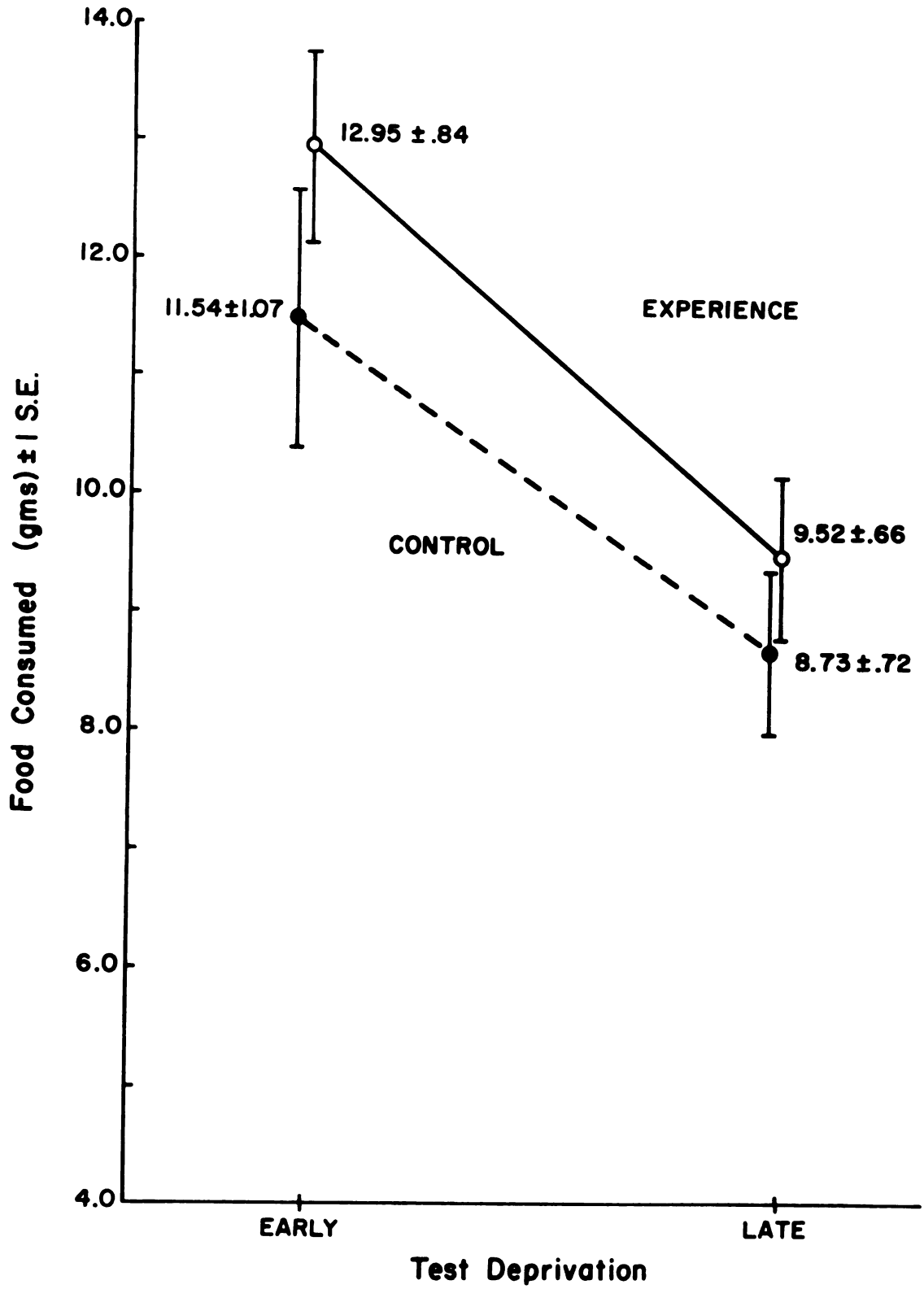

14.0
12.0
10.0
8.0
6.0
4.0
Food Consumed (gms) ± 1 S.E.
12.95 ± .84
11.54±1.07
EXPERIENCE
CONTROL
9.52 ± .66
8.73 ± .72
EARLY
LATE
Test Deprivation

Table 17.--Fmax tests for homogeneity of variance within error terms of 5-day totals of food consumed (grams).

a. Partition of subjects within groups sum of squares (no. 3, Table 15)

Source	SS	d.f.	MS	Fmax
Subjects within groups	1010.0248	38		
Within control group	595.5288	19	31.3436	1.4367
Within experience group	414.4960	19	21.8155	

Fmax (0.05) 2,20 = 2.46

b. Partition of early vs. late subjects within groups sum of squares (no. 9, Table 14)

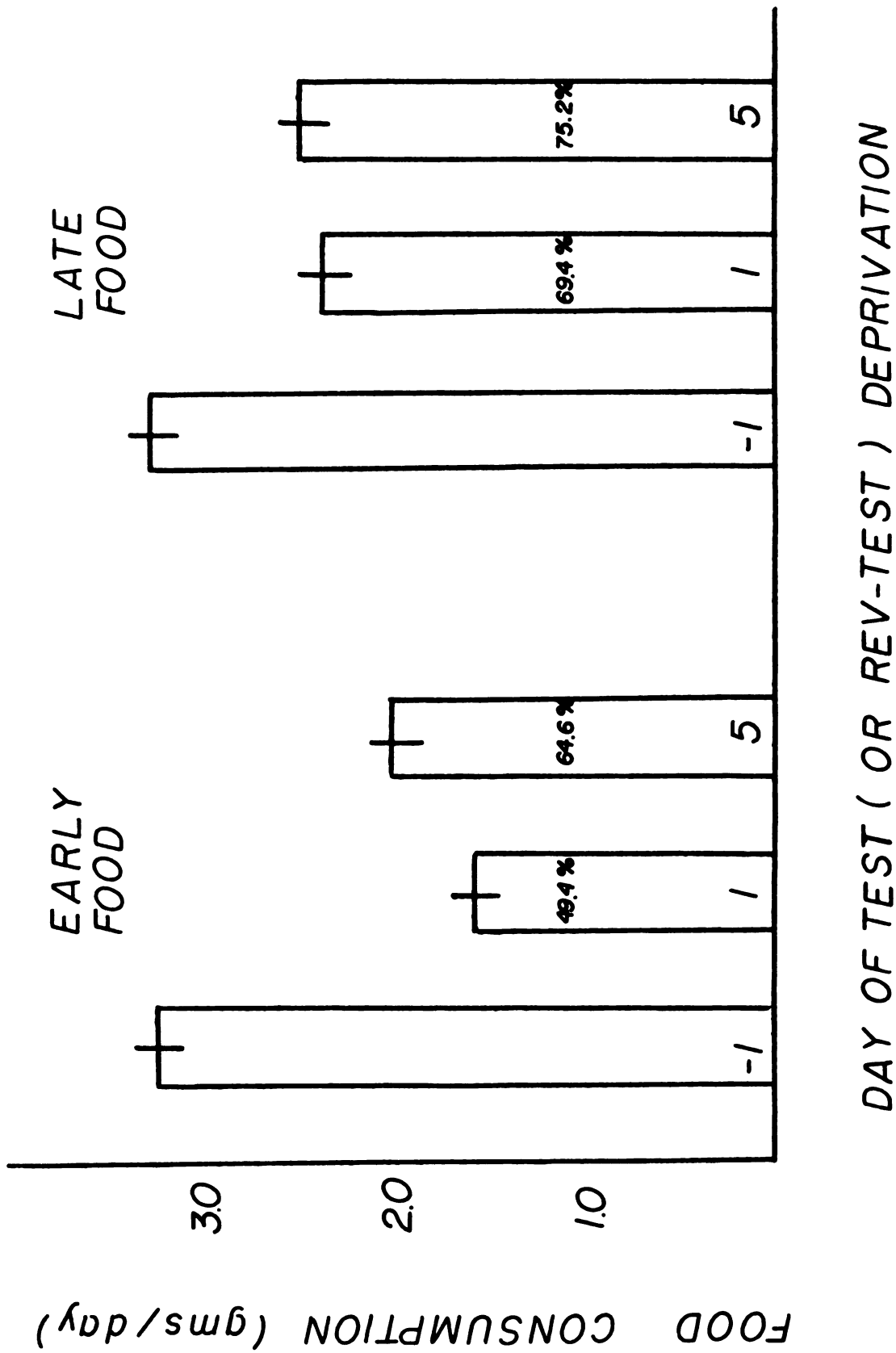
Source	SS	d.f.	MS	Fmax
Early vs. late subjects within groups	69.3044	36		
Within early group	45.3047	18	2.5169	1.8877
Within late group	23.9997	18	1.3333	

Fmax (0.05) 2,20 = 2.46

food consumed on Day 1 of the late food test or reverse test deprivation is found to be 69.43 ± 2.07% of that consumed the previous *ad libitum* day. The late food mice ate an average of 2.27 ± 0.13 g on Day 1 of the test or reverse test deprivation compared with 1.55 ± 0.08 g for the early food animals. This implies that the late food animals did increase food intake per unit time.

Of further interest is whether the daily food intake of deprived mice increases through the course of the deprivation period. The difference in food intake between Day 1 and Day 5 is an average increase of 0.43 ± 0.06 (S.E.) g for the early food mice and 0.14 ± 0.06 g for the late food mice. These differences are illustrated in Figure 8. On Day 5 the early food mice ate 64.45 ± 2.77% (1.98 ± 0.09 g) of the Day 0 *ad libitum* intake of 3.23 ± 0.17 g; this is an increase over the 49.41 ± 1.96% (1.55 ± 0.08 g) observed on Day 1. The late food animals increased their Day 5 intake (2.41 ± 0.12 g) slightly to 75.21 ± 2.9% of their baseline intake (3.28 ± 0.16 g). It appears, therefore, that *P.m. bairdi* can make a greater accommodation in one day with late food (access for the final six hours of dark) than through five days with early food (access for the initial six hours). Such is the case within both the test deprivation ($T = 1.752$, $p<0.05$, one-tailed) and the reverse test deprivation ($T = 1.834$, $p<0.05$, one-tailed). These values are less than they might be because only the survivors were considered; those animals that died did so during the late deprivation.

Figure 8. Food consumption (in grams) during Day 1 and Day 5 of the test (or reverse test) deprivation for late vs. early deprived P.m. bairdi.


FOOD CONSUMPTION (gms/day)
3.0
2.0
1.0
EARLY FOOD
LATE FOOD
-1
1
5
-1
1
5
49.4%
64.6%
69.4%
75.2%
DAY OF TEST (OR REV-TEST) DEPRIVATION

F. Discussion

These results show that P.m. bairdi can indeed compensate temporal food deprivation by increasing their intake per unit of time but only when food is available in the late food presentation. The experiment however did not explore the limits of this capacity. Can Peromyscus for example adjust their daily intake to a single one-hour meal per day as Dufort (1964) reported for the rat? This concentration of feeding into fewer but larger bouts can have important implications for over-wintering mice. "Meal-eating," in contrast to a more diffuse "nibbling" pattern, when food consumption per day is kept constant in each, can bring about increased lipid metabolism and fat deposition (Cohn and Joseph, 1960; Hollifield and Parson, 1962; Fábry and Braun, 1967; Leveille, 1967) together with increased gastric hypertrophy which results in greater absorptive efficiency of the gut (Holečková and Fábry, 1959). In addition, questions arise regarding the possible temporal interdependency of feeding with other activities. How are these activities affected by an extreme feeding pattern? What are the ecological consequences? These ramifications of temporal food deprivation have not been explored.

That Peromyscus will compensate temporal food deprivation is not surprising in itself. What is of particular interest, however, is that this capability is under circadian restraints beyond those imposed by the light-dark cycle. This appears to limit the opportunity for compensation via increased food intake. Consider, also, that early morning, when the compensation seems to be greatest, is often the coldest and therefore the most unfavorable time of the day for food

procurement. How is this paradoxical "late-night" effect on feeding to be explained?

The term feeding has, throughout this dissertation, implied that both foraging and food consumption occur simultaneously. This is to say that the food is consumed when it is located; and this might often be the case, particularly with live, mobile prey such as insects or lumbricids. It remains very likely, however, that other foods such as seeds, fungi, herbaceous plants, or associated plant parts, are transported back to a concealed cache to be eaten at a later time. Might, therefore, Peromyscus be more opportunistic as to when they will gather and store food than as to when they will consume it? Does Experiment II imply an early-night tendency to forage for and hoard food, with some consumption, and a late-night tendency to depend on a cache to make up any deficit in food intake? This question can be tested in a manner similar to that employed here, but including the opportunity for, and a measure of, food hoarding. The daily activity records of P.m. bairdi support such a temporal organization of feeding (Jaeger, unpub. obs.). Under ad libitum conditions, the feeding bouts of longest duration were often observed late in the nocturnal period, at a time when wheel-running was greatly reduced. (See Figure 1, particularly Numbers 32 and 37.)

A circadian regulation of food consumption is suggested by the result that P.m. bairdi could not correct their daily intake over a five-day period of early-night access and late-night deprivation, but could readily do so in a single day when these six-hour periods of deprivation and access were reversed. This result may, in part, provide a clue to the understanding of the regulation of food intake

for the strongly nocturnal Peromyscus. A great deal of effort has focused on this problem in the laboratory rat (see the review by LeMagnen, 1971). These studies have used the underlying assumption that food intake is ultimately regulated at the level of the individual meal, whose size is determined in part by both that meal which preceded it and that which will follow. Daily consumption, then, is a consequence of the regulation of individual meals. This can be appreciated when it is considered that rats eat a more or less constant number of discrete meals per day, and that these meals are spaced throughout both the day and night (LeMagnen and Tallon, 1966). The present evidence for Peromyscus, however, points to a daily regulation of food intake where late-night feeding can make up for a deficit incurred during the early-night period. The relatively strict nocturnal existence of Peromyscus offers an added dimension to the problem; that is, the nocturnal intake must be adjusted to account for the diurnal half of the day when food is not normally consumed. In light of this, the making up of the nightly deficit prior to the onset of the day is understandable. It assures a nutrient supply until feeding is again resumed the following night.

It has been reported however that P. maniculatus are frequently caught with their stomachs filled to less than one-third of their capacity (Harling and Sadleir, 1974). However, only two mice of their sample were captured seven or more hours after sunset (suggesting reduced foraging after this time), and one of those had a full stomach. The fact that actively foraging deer mice had relatively empty stomachs supports the hypothesis that daily intake might be regulated in the late night at a food cache.

The nocturnal organization of feeding that has been proposed here also offers an explanation for the seasonal formation of caches and the conservative use of them. It may be that Peromyscus hoard storable food throughout the year in a manner described above; that is, foraging, consuming, and hoarding during the early-night and feeding from the cache prior to the onset of day, during the late-night. If food is not plentiful, if it is not in a storable form, or if meteorological conditions are unfavorable, then daily caches do not accumulate. If, however, the above factors are favorable, as might be expected in the autumn, then caches become conspicuous, giving the appearance that hoarding takes place only at this specific time. Along the same line of reasoning, a conservative approach to the use of the cache would result if foraging and hoarding were ongoing behaviors. The cache, then, becomes depleted only when foraging success drops, as might occur in winter. This is opposed to the mouse depending exclusively on an available cache until it disappears and then having to resort solely to foraging, possibly at an inopportune time.

We have discussed the functional ramifications of this late vs. early night adjustment in food intake. Can we now account for this phenomenon in terms of an underlying control mechanism? What physiological process(es) allow P.m. bairdi to concentrate intake readily if food is present "late"? The answer to this question lies, in part, in an understanding of the conditions which initiate and maintain feeding. It has been mentioned previously that food intake and locomotor activity (i.e., in a running wheel) are very closely associated in time. This is very apparent in the rat where the relatively few (eight to ten), but discrete, daily bouts of feeding

are preceded by bouts of physical activity (Wyrwika, 1967). One consequence of this activity would be an increase in metabolic rate. Does this elevated metabolic state, with its resulting energy consumption, affect food intake such that the greater the metabolic rate the more food consumed per unit time? This is to hypothesize that for maximal feeding, activity must precede the feeding period. Now for the early-food P.m. bairdi the food is presented at the point of transition from light to dark where activity, followed by metabolic rate, are only beginning to build and gather momentum. The late-food mice, on the other hand, receive food after a six hour period of activity where we would expect the metabolic rate to be higher and the daily energy deficit to be greater.

Not only does the level of activity differ for the periods preceding early vs. late food availability but it differs in the reverse for the periods which follow. Early food is succeeded by a period of activity whereas late food is followed by rest. It is known that inactivity subsequent to feeding will facilitate or promote energy storage (fat deposition, etc.) (Nisbett, 1972). Rats that are returned to food availability from deprivation will eat large meals which are followed by relatively long periods of rest (Finger, 1951; Evans, 1971). This was also observed in Peromyscus (Jaeger, unpub. obs.). This "recovery response" agrees with the hypothesis that for maximum energy storage, feeding has to be followed by inactivity. If this applies in the present situation, the late-food mice would have greater energy reserves per gram of food consumed than would early-food mice. This could be an important advantage in dealing with 18 hours of deprivation per day.

GENERAL DISCUSSION

In his review on feeding strategies Schoener (1971) passed over a consideration of "optimal foraging period" except to state that, "No formal theory yet covers optimal placement of feeding periods over the activity cycle. Obviously basic components are metabolic costs of activity under different climatic conditions and time distributions of climatic factors, food, and predator abundance. A host of observations indicate that climate will be overwhelmingly important in models of optimal feeding period."

The results presented here suggest two features important in understanding the feeding biology of P.m. bairdi:

(1) that there exists a temporal organization of nocturnal feeding behavior; and

(2) that previous experience with temporal food deprivation cannot effect an increased consumption during periods of restricted access to food, but that this experience may result in a reduced locomotor response to the deprivation and thereby play a role in energy conservation.

These features will now be considered in terms of a general feeding strategy.

In the temporal organization suggested here, feeding behavior is reduced to three components: Foraging (locating), hoarding

(gathering), and consumption. Under ad libitum laboratory conditions these behaviors are probably distributed throughout the nocturnal period with only a tendency for the late-night bouts of food intake to be of longer duration than the early-night bouts. When stressed with temporal food deprivation, these mice will adjust by concentrating food intake on the late-night but not in the early-night. It is hypothesized that foraging and hoarding are most prominent early in the night and can become increased at that time in response to deprivation. What might such an arrangement mean in terms of feeding strategy?

As has been previously suggested, the "nocturnalism" of Peromyscus may be an important determinant of its short-term feeding pattern. One can speculate that food storage in the stomach (or in caches) must be at the daily maximum just prior to the onset of the light or inactive period (where presumably little or no foraging occurs). The temporal organization of feeding put forth here could assure this. If the stomach is gradually filled once, or even twice, during the nocturnal period, a late-night feeding could correct for any deficit leaving the animal "full" for the upcoming inactive period. In addition the early-night foraging and hoarding would assure that a food supply is available for this late-night feeding.

This pattern differs from that in which the animal forages for and eats a series of discrete meals, each of which loads the stomach (such as was described for the rat). In a meal-type pattern, the day-night transition might occur between meals, when there exists the likelihood of an empty or partially filled stomach. Also, foraging from meal to meal might leave an animal with no late-night food, if

the weather is unfavorable at that time. Either situation enhances the possibility of a P.m. bairdi facing the light period with less than a full stomach.

Moreover, the nocturnal organization described here is, in a sense, loose; as such it can provide a margin of error which allows for unfavorable weather, time-consuming social interactions, etc. Models of feeding strategy are too often inflexible in this regard. They place animals on a very strict time budget. This circadian organization, however, relegates the various aspects of feeding to relatively wide time slots (i.e., early or late). The early-night proclivity to foraging and hoarding, regardless of the not-yet-full status of the stomach, will ensure these activities whenever no conflict exists with the weather or social situation. The food store which results will then allow for the late-night feeding.

As was pointed out earlier, feeding in Peromyscus appears to be temporally associated with other activities. This being the case, the temporal organization of feeding would have important consequences for these other behaviors. For instance, synchronized early-night foraging might facilitate social contact, and, by so doing, increase the time spent "in contact" or reduce the time spent in pursuit of it. Organization, therefore, on the circadian level might lead to greater temporal efficiency than that on a smaller scale (i.e., meal to meal). Again, this can be of particular importance to the strongly nocturnal Peromyscus.

Experience with temporal food deprivation did not affect this organization of feeding. It appears, rather, that experience may play a role in the mouse's recognition of temporal food deprivation or

unfavorable weather such that it seeks a more suitable microenvironment (i.e., becomes less active). Experience, very likely, influences the effectiveness of other of the mechanisms of food storage and energy conservation.

FUTURE EXPERIMENTS

An important outcome of the interpretations put forth in this dissertation is the generation of ideas for further experimentation. Those that are of particular interest to me will now be outlined; these are (1) organization of feeding, (2) food storage, and (3) experience with feeding.

1. Organization of Feeding

The main impetus of the work presented here is toward testing the hypothesis that feeding behaviors are organized within the nocturnal period such that foraging and hoarding are predominant early while food consumption can be concentrated late. This can be tested in a manner similar to that employed in Experiment II. Here we will also require measures of hoarding and foraging. These can be made by presenting discrete food pellets which can be transported from the bin in which they are offered back through a tunnel (equipped with treadles) to the plastic cage housing the mouse (via Barry, 1974). The food bin and tunnel form a unit that can be attached to and removed from the home cage. Hoarding is simply measured as the number of pellets found in the home cage and foraging by the number of treadle crossings in the tunnel. It is, therefore, hypothesized that the early-food mice will show more foraging and hoarding than the late-food

mice, but again that the late-food animals will consume the greater amount of food. All hoarded food is removed following the six hours of availability and the amount of food consumed during that period is recorded.

It is also of interest to test the hypothesis that food gradually accumulates in the animal throughout the nocturnal period and that the stomach is filled just prior to the onset of daylight. This can be examined by sacrificing P.m. bairdi (on ad libitum food) at regular intervals throughtout the night and measuring their stomach contents. In addition, is the bi-modal running activity characteristic of longer nights reflected in a bi-modal stomach filling?

2. Food Storage

In regard to food caches the following questions have been generated:

(a) Is food hoarded by P.m. bairdi throughout the year, but found in accumulated caches only during the times of abundance (i.e., autumn)?

(b) Do food caches become exhausted by late winter or early spring?

(c) Are P.m. bairdi able to replenish their food stores during the winter?

These and related questions can be approached through the use of outdoor nest boxes (via Howard, 1949; Stebbins, 1971) which allow stored food to be examined, weighed, and marked for turnover by the investigator. If, for example, food is continuously hoarded we would expect to find, with the addition of excess "supplemental food," accumulated caches at those times when they are not usually found (i.e., during summer).

3. Experience with Feeding

Only one basic regime of deprivation experience was considered here. Another might be more effective; for instance, one where the deprivation is more severe but presented intermittently or for fewer days. In addition, the possible effect of experience with temporal food deprivation on reduced locomotor activity has yet to be resolved. Furthermore, food hoarding and foraging under conditions of a test deprivation might be much more responsive to the appropriate experience than was food intake. These alternatives also merit further investigation.

APPENDIX

THE EFFECT OF ACCESS TO A RUNNING WHEEL ON SURVIVABILITY

APPENDIX

THE EFFECT OF ACCESS TO A RUNNING WHEEL ON SURVIVABILITY

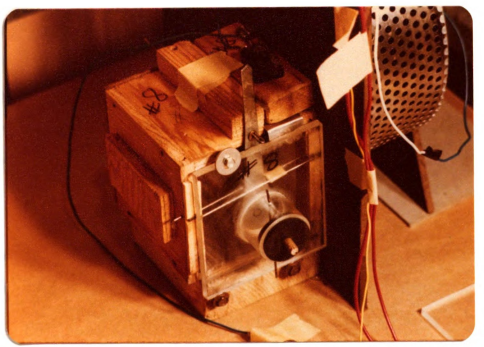
This appendix contains a description of the experimental procedures which were referred to in the discussion of Experiment I. The purpose of this experiment was to examine the effect of general activity on the survival of P.m. bairdi subjected to temporal food deprivation.

In the experiment 46 male P.m. bairdi were considered. These animals were of similar age, body weight, and genetic history as those described in Experiment I.

Colony and test room conditions were also as before with the exception that now a second test room was employed as well. This housed ten nest boxes with their attached running wheels (five on each of two tiers). Above each tier were two 60 watt and two 7 1/2 watt light bulbs. Again the 7 1/2 watt bulbs remained lit during the 12 hours of dark. The door separating the test rooms was kept open throughout the experiment to facilitate ventilation and to insure like conditions of temperature and humidity. This two-room unit was relatively soundproof with respect to activity in the adjacent colony room.

The running wheel apparatus is pictured in Figure A. The wheel itself is eight inches in diameter with a three inch wide running

Figure A.--Running wheel apparatus with adjoining nest-box.



surface of perforated sheet metal. The wheel rotates around a bicycle hub fixed to the side of the nest box. This plywood box has a floor area 3 1/4 inches by 4 inches and is 3 1/4 inches high. Ad libitum access to water is available through a 100 ml graduated cylinder whose spout enters the back side of the nest box. The Purina food pellets are presented at the front in a removable plexiglas face-plate. The pellets are lodged in a 1 1/4 inch diameter plexiglas cylinder fixed horizontally into the center of the face-plate. Access to the food requires the animal to move a pendular aluminum door to one side of the aperture of the cylinder. To remove the food for deprivation, the entire unit is dislodged and replaced by a flat plexiglas face-plate. Two pellets are presented per day, as in Experiment I.

The procedures involved with the rearing and with the adjustment to the test conditions (12:12 hour light-dark cycle, social isolation, and the switch to Purina food pellets) were the same as those previously employed.

This experiment was conducted in two separate runs. In the first, 13 animals were randomly selected from Experiment I (animals tested without running wheels) and compared with an equal number of mice which had been tested concurrently in running wheels. Previous deprivation experience, although varied within a group, was matched across groups. The experimental timetable, including the test deprivation (food available for the initial seven hours of the 12 hour dark period), was, therefore, that described in Table 1.

Run 2 was made immediately following Run 1. It consisted of ten no-wheel mice and ten wheel mice. Again the deprivation experience

was matched across groups. The test deprivation was the same one used in Run 1.

Survival vs. mortality is tested for independence from wheel vs. no wheel via the chi-square analysis of a 2 x 2 contingency table. Wheeled animals from both runs are pooled (n = 23) as are the no-wheel animals (n = 23). Homogeneity between runs is analyzed to satisfy the legitimacy of this procedure (Woolf, 1968). The results are presented in the discussion portion of Experiment I.

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