THE EFFECT OF PHOTOPERIOD AND TEMPERATURE ON FOOD HOARDING IN DEERMICE (PEROMYSCUS)

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ABSTRACT

THE EFFECT OF PHOTOPERIOD AND TEMPERATURE ON FOOD HOARDING IN DEERMICE (*PEROMYSCUS*)

By

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In northern latitudes, food hoarding has been interpreted as one means of providing for seasonal fluctuations in the availability of food. The relative scarcity of food during the winter months in these latitudes would pose a special problem to a non-hibernating or non-migratory animal in the absence of stored food. Many rodents, including deermice (*Peromyscus*), solve this problem by storing food in the form of body fat or free (unconverted) items of food in or near their nest. It was hypothesized that a short photoperiod and/or low temperature were the environmental stimuli for deermice to hoard during the fall in the northern latitudes. Previous published reports indicated that flying squirrels (*Glaucomys volans*) responded to experimentally shortened photoperiods by intensively hoarding their food. Studies on the laboratory rat also suggested that low temperatures may induce hoarding in at least some species of rodents.

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Five taxa of deermice including P. leucopus noveboracensis, P. l. castaneus, P. maniculatus bairdi, P. m. blandus, and P. eremicus eremicus were tested in the laboratory for the amount of food hoarded in seven consecutive days under various combinations of test temperature (7°C and 27°C) and photoperiod (9L:15D or 15L:9D). Hoarding was operationally defined as the number of pellets carried from a food bin at the end of a 43cm.-long alley attached to the animal's home cage in a 24 hour period. All mice prior to testing were acclimated for 4 weeks either to 7°C or 27°C, with half of the mice tested at the same temperature to which they had been acclimated and half to the opposite temperature. Mice were kept under a constant photoperiod, either a "short day" (9L:15D) or a "long day" one (15L:9D), for both the acclimation period and testing. All mice were laboratory reared and, except for P. l. castaneus, were the first generation from wild caught parents.

The results indicated that the two northern subspecies, P. l. noveboracensis and P. m. bairdi, hoarded significantly more under the low temperature and short photoperiod than they did under the high temperature and long day photoperiod. A similar response to these environmental variables in the wild would lead to a higher level of hoarding in the fall of the year than in the summer. It was also found that photoperiod and temperature were not of equal influence on both P. l. noveboracensis and P. m. bairdi. Test temperature had more of an effect than photoperiod on

the hoarding of *P. l. noveboracensis*, while in *P. m. bairdi* the opposite was true.

Comparisons of the mean hoarding scores of *P. l. noveboracensis* with *P. l. castaneus*, and *P. m. bairdi* with *P. m. blandus* revealed that in both cases the northern subspecies hoarded significantly more than the southern one under the cold test temperature. Under the warm test temperature there was no significant difference in their scores. These findings indicate a selection for hoarding in northern subspecies of deermice living in environments where a scarcity of food is associated with seasonally low temperatures.

Test temperature also had a significant effect on the hoarding of *P. m. blandus*, which hoarded more under 27°C than under 7°C. The increase in hoarding under the warm temperature by this subspecies may have been due either to an inhibition of activity under the cold temperature or to the possibility that warm temperatures in its environment (i.e., southwestern deserts) indicate a summer shortage of food. The high level of hoarding observed for *P. e. eremicus*, in contrast to the other groups studied, was interpreted as perhaps related to the occurrence of summer torpor in this desert species and its reliance on stored food while restricted to burrows during extremes in temperature.

In all groups studied, except possibly *P. m. bairdi*, there was no evidence found to support a model of food hoarding in deermice based on long term nutritional needs or deficits (i.e., losses in body weight) as has recently been proposed for laboratory rats. In *P. m. bairdi* there was only a small correlation between weight change and hoarding scores. In all other groups this correlation was non-significant.

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INTRODUCTION

Hoarding has been defined by McCleary and Morgan (1946) as the "acquisition of property to an extent that exceeds the needs of the moment or the immediate future." Hoarded items are typically "cached" or hidden away where they can be used during times of scarcity (Hamilton, 1939). In northern latitudes, the hoarding of food has been interpreted as one means of providing for seasonal fluctuations in the availability of food. The relative scarcity of food during the winter months in these latitudes would pose a special problem to a non-hibernating or non-migratory animal in the absence of stored food. Many rodents, including deermice (*Peromyscus*), solve this problem by storing food in the form of body fat or free (unconverted) items of food in or near their nest. At other times of the year, a wider variety of food, including insects, fungi, tree buds, and some fruits can be obtained. Many of these food items, however, are unsuitable for storage in caches because they cannot be readily transported or stored without spoiling.

This dissertation examines two environmental cues, temperature and photoperiod, that may influence food hoarding in five taxa of deermice. Deermice were selected because (1) they will hoard food both in the wild and in the laboratory, (2) they can easily be raised under standardized laboratory conditions to control for learning, and (3) they have undergone considerable speciation in a broad geographic section on the North American Continent with most species demonstrating geographic variation and having numerous recognizable subspecies. Deermice are found in practically every sort of available habitat including deserts, grasslands, chaparral, mixed deciduous forests, conifer forests, and even in the tropical rain forests. Caching of food is common in all species of deermice that have been studied, and the items assembled vary depending upon the species and the seasonal availability of food (Eisenberg, 1968). Their food is all very similar and includes grains, seeds, fruits, insects, and largely the mast crops of trees and shrubs (Baker, 1968). Seeds and nuts are commonly stored, although a variety of other items have been found in food caches including the remains of grasshoppers, beetles, and other insects, deer pellets, fox scats, leaves, flower parts, and even lichens (Howard & Evans, 1961). The caches are frequently very large and may contain several pounds of material (Criddle, 1950).

The wide-spread geographical distribution of deermice suggests that their food storage may vary with climate and photoperiod. Food storage by deermice in the northern latitudes appears seasonal in its occurrence, with the greatest amount of activity in the fall months of the year (Burt, 1946; McCabe & Blanchard, 1950; Criddle, 1950; Howard & Evans, 1961). Other seasonal behaviors such as reproduction, hibernation, and migration are influenced by both photoperiod and temperature. Recent information suggested that perhaps hoarding was likewise under the influence of these environmental cues. Muul (1968) found that flying squirrels (*Glaucomys volans*) responded to a shortened photoperiod by intensively hoarding the ripening mast crops. According to Muul this capability allows a precise timing of food storage to the season of the year coinciding with the greatest abundance of food suitable for hoarding. Laboratory studies on food hoarding in the laboratory rat also suggested that perhaps the colder daily temperatures of autumn might similarly increase the intensity of hoarding in at least some rodent species (McCleary & Morgan, 1946).

If food storage in deermice is under the influence of both temperature and day length, the response of any particular species ought to be predictable from a knowledge of their habitat and latitudinal origin. A comparative study of several subspecies along a latitudinal gradient should reveal differences that can be explained on the basis of differential selection for certain behavioral adaptations appropriate in each environment (King, 1968). One would not expect that food storage by deermice from the tropics would vary to any appreciable extent with photoperiod. The seasonal differences in day length increase with latitude, and mice from latitudes close to the equator would experience little change in their day length throughout the year. On the other hand, mice from northern latitudes (i.e., above 35° North Latitude) could use photoperiod as a highly reliable cue to seasonal fluctuations in their food supply. As the photoperiod at each latitude has essentially been constant throughout the evolutionary history of the genus *Peromyscus*, there would have been adequate time to have evolved the capability of responding to the appropriate changes in day length. Climate, however, has been less constant with the relatively recent retreat of the glaciers in what is now the northern range of both *P. maniculatus* and *P. leucopus*. As climate also varies with elevation, this cue might generally be considered less reliable than photoperiod. Nevertheless, climatic factors such as temperature and rainfall may have been sufficiently predictable in the low-elevation habitats of the southern latitudes (i.e., deserts) for some races or species to have evolved a capability of using these factors as cues to the availability of food.

Recent experimental work on the hoarding behavior of laboratory rats has tended to emphasize a physiologic mechanism for food storage. Herberg and Blundell (1970) have proposed a hypothalamic model for hoarding whereby the behavior is motivated by long-term nutritional deficits reflected by losses in body weight or a reduction in fat reserves. The observation that laboratory rats increase their hoarding after food deprivation and under cold temperatures would tend to support their model. Electrical stimulation of the lateral hypothalamic "feeding center" was also found to initiate hoarding in both naïve and satiated rats (Blundell & Herberg, 1973). However, there is little evidence to suggest that such a mechanism may explain hoarding in deermice and other rodents. Most wild species of rodents hoard when food is abundant and in the northern latitudes may even be gaining weight in preparation for winter. The body weights of wild *P. leucopus noveboracensis* apparently do increase during autumn and early winter (Sealander, 1951), which would coincide with their maximal hoarding activity. The weight changes of deermice in my own study were examined under all experimental conditions to see if a correlation did exist between the level of hoarding and weight loss. Since body weight is known to vary with such factors as diet, breeding condition, and age, special procedures were used to control for these variables.

In summary the following three general hypotheses were examined in this investigation:

1. Photoperiod and/or temperature affect the amount of food stored by deermice.
2. Their effect will vary within a single deermouse species depending upon the latitudinal and climatic origin of the subspecies being studied.

Subspecies from the northern latitudes (i.e., above 35° North Latitude) and not those from southern latitudes will hoard more under conditions simulating winter (i.e., 9L:15D photoperiod and 7°C) than under conditions simulating summer (i.e., 15L:9D photoperiod and 27°C).

3. The hoarding of food by deermice is not related to changes in their body weight.

LITERATURE REVIEW

The literature on food storage by mammals can generally be divided into two major categories: experimental and field observations. Experimental studies on food storage have typically been done in the laboratory or with caged animals. In general, the goal of these studies has been to elucidate the mechanisms (both endogenous and exogenous) of the food storage response with the subjects being laboratory rats (Rattus norvegicus), mice (Mus musculus), or hamsters (Mesocricetus auratus). More recently Morris (1962), Ewer (1965, 1967), Muul (1968), and Lockner (1972) have provided additional information from laboratory studies on wild caught animals that have been called "natural hoarders." Some of these studies suffered from the use of very few animals or animals of one sex. The second major category of studies includes a miscellany of published reports on the occurrence of food storage in animals in the wild. Many of these observations were made by the early naturalists around the turn of this century on the mammals of North America. These reports provide information on which species store what kinds of food as well as the possible function of food storage in the animal's own habitat. Many of these early explanations of food storage were speculative, although the results of more recent laboratory studies have occasionally been given similar "naturalistic" interpretations (for example, see Thorpe, 1963).

In the review which follows I have separated the literature on food storage into roughly the two categories just described. First, I will survey the occurrence of this behavior in the various mammalian orders, with special emphasis on the food "hoarding" of rodents. The unique characteristics of rodent food hoarding will be examined, and the possible mechanisms for its evolution will be discussed. Second, I will attempt to provide a complete and critical review of the experimental work done on hoarding behavior in the laboratory.

Phylogeny

A survey of the Class Mammalia immediately reveals that certain of the orders characteristically show no food storage behavior and for obvious reasons. Orders with an entirely aquatic mode of existence (i.e., Cetacea, Sirenia, Pinnipedia) or a truly aerial one (Chiroptera) typically make no attempt either to cache or accumulate food beyond what is of immediate use. Among aquatic mammals, the absence of a permanent home or place in which to store food as well as the type of food itself probably rule out this behavior as a possible adaptation in their environment. Only easily preserved food is suitable for storage and the diet of some species of bats may be solely of insects, fish, or fruit, which cannot be readily stored.

The seemingly inconsistent pattern of food storage in the remaining terrestrial orders of mammals is a little more difficult to explain. The absence of food storage among the ungulates (Perissodactyla and Artiodactyla) and elephants (Proboscidea), could be due to their nomadic existence and the widespread dispersion of their readily spoilable food. Similarly, the absence of the storage habit among non-human primates can probably be attributed to both their type of food (often soft, fleshy fruits) and their lack of a permanent "homesite." A relatively concentrated source of preservable food and a permanent homesite, den or place to store it, appear to be essential conditions of the storage response. The ability to manipulate items of food is also important and may account for the absence of this habit in some mammaliam orders.

Food storage is relatively common among carnivores in all latitudes even though one would expect their food to spoil rapidly. Apparently the problem of food spoilage can often be successfully circumvented through a variety of novel behaviors practiced by those animals which normally store their food. An animal's propensity to eat spoiled food with impunity may also be of some influence on whether it will store its food or not. Characteristically, carnivores will cache surplus and partially eaten prey in small pits or cover the cache with soil, ground litter, or even snow in the northern latitudes. This burial or covering response may actually be an attempt to preserve the food and not simply to conceal or "hide" it, as has frequently been the interpretation. Among North American carnivores, food caching has been reported in the red fox (*Vulpes fulva*; Murie, 1936; Scott, 1943), common badger (*Taxidea taxus*; Snead & Hendrickson, 1942), black bear (*Ursus americanus*; Seton, 1926), wolf (*Canis lupus*; Seton, 1926), mink (*Mustela vison*; Seton, 1926), and both the shorttail and longtail weasel (*Mustela erminea* and *M. frenata*; Seton, 1926).

The absence of food storage in all but a few species of insectivores appears to be related to their diet and feeding behavior. Insectivores are among the smallest mammals and they normally have high basal metabolic rates (Morrison, Ryser, & Dawe, 1959). As a consequence, they require large numbers of insects and other invertebrates and feed almost constantly. It is not surprising, then, that among the few species in which food storage has been reported, it appears to be highly developed. The habit of short tailed shrews (*Blarina brevicauda*) storing live snails in their runways is apparently quite common (Shull, 1907; Hamilton, 1930; Ingram, 1942). In fact, Ingram (1942) found that their runways often have two distinct chambers, one being a "culture" chamber where live snails are kept and one a "discard" chamber where eaten snail shells are placed. Ingram pierced the shells of snails in the culture chamber and found that after 24 hours some of them had been eaten and, as predicted, had been placed in the discard chamber. The European mole (Talpa) also stores earthworms in its runways (Degerbol, 1927). Apparently the moles either decapitate or "paralyze" the worms by biting them in the head before storing them. There have been no reports of American moles storing food, prompting Hamilton (1939) to ask why Blarina would practice storage when food ought to be available all year round in its habitat. Clearly more information on the generality of this habit among insectivores would be instructive and might equal a phenomenon as interesting as the classical ant and aphid relationship in insects.

The habit of food storage is probably best developed in the order Rodentia and is frequently referred to as "hoarding." The dictionary definition of a "hoard" is "an accumulation of something for preservation or for future use" (American College Dictionary, Random House, 1963). The key word is "accumulation," which is of food in this case and which probably best distinguishes this form of storage from those described for the other orders of mammals. The general tendency for rodents to be either seed eaters or herbivores, suggests that their food is more suitable for long term storage than would be soft, fleshy fruits or animal matter. It appears that the grass-eating rodents generally do not store food, while the seed-eaters do. The collection, transportation, and preparation of hoard are all highly developed in many rodents and will be discussed below.

Collection and Transportation

The sequence of behaviors involving the collection and transportation of food items to be cached varies with both the species and the type of food. Tree squirrels will normally cut a large quantity of nuts from the top of mast trees before returning to the ground for their collection (Allen, 1943; Muul, 1968). Usually all twigs, stems, and leaves are removed from the nuts before they are cached. Some squirrels will also discard any nuts which are worm-infested (Mailliard, 1931). Many rodents collect seeds from the ground after they have fallen from trees, shrubs, and other plants. Some species, in particular the kangaroo rats (*Dipodomys*) and pocket mice (*Perognathus*), have the ability to glean small seeds from loose soil at phenomenal rates. Burns (1958) reported that kangaroo rats could place small millet-size seeds in their pouches at an average rate of one seed every 0.2 second. The forepaws in kangaroo rats are extremely important in the collection process and are used to rake and sift small seeds from the loose sand. Both the actual harvesting of the food and the sequence of behaviors involving the caching of it usually involve some use of the front limbs in rodents (Morris, 1962; Eibl-Ebesfeldt, 1963; Ewer, 1965, 1967).

Collected food items are normally carried either in the teeth or in special cheek pouches. These pouches may be either external and fur lined as in the heteromyids (i.e., pocket mice, kangaroo rats) and geomyids (i.e., pocket gophers); or internal and membranous as in some sciurids (i.e., chipmunks, ground squirrels) and a few cricetids (i.e., deermice, hamsters). The evolution of these special pouches suggests that there has been a strong selection pressure for food hoarding in some species.

Preparation of the Hoard

The prevention of food spoilage has given rise to many novel behaviors among the rodents that store food. Western pine squirrels (*Tamiasciurus*) normally cache pine cones in moist debris or logs and sometimes even in pools of water (Shaw, 1936). Shaw observed that this unique behavior prevents the cones from drying out and that he was able to keep cones for over two years if they were kept continually under water. The habit of red squirrels (*Tamiasciurus hudsonicus*) storing mushrooms in trees to dry is apparently also quite common (see Hatt, 1929). Mushrooms and other fungi are placed in the branches of trees where they will dry and may later be transported to dry cavities for winter storage (Buller, 1920; Hardy, 1949). Klugh (1927) has proposed that the red squirrel stores "hard" and "soft" objects differently. He observed that hard things such as seeds and nuts were either buried or stored centrally, while soft things such as fungi, fruit, or pieces of meat were placed individually in the branches of trees. Klugh noted that this squirrel normally does not bury or put into piles things which could either mold or decay readily.

After the winter rains in the semi-arid regions of California, the giant kangaroo rat (*Dipodomys ingens*) stores the still green seeds of pepper grass (*Lepidium nitidium*) and filarie (*Oenothera*) in small pits above its burrows (Shaw, 1934). The seeds dry in these pits before their removal to the underground burrows. Shaw dyed the seeds in some of the pits with mercurochrome and replaced others with kernels of rice, and discovered that the contents of these pits were usually transferred into the burrow by early June. It has also been reported that the pika (*Ochotona princeps*), the only lagomorph known to store food and which inhabits the talus slopes of western mountains, frequently constructs sizeable "haypiles" which cure in the sun before being removed to the shelter of large rocks (Dalquest, 1948). However, this curing behavior is now of some question (see Barash, 1973). A similar food-curing behavior has also been reported in the mountain beaver (*Aplodontia rufa*), a colonial rodent found in the moist, forested areas at high elevations in the Pacific Northwest (Grinnell & Storer, 1924). Piles of "hay" consisting of narrow-leaved lupine (*Lupinus logipes*), which had been cut green and then piled supposedly for curing, were observed along a stream in October of the year. Grinnel and Storer noted, however, that these piles could have been nesting material. As this plant was not the mountain beaver's predominant food, this latter interpretation is probably the more correct one.

Nature of the Hoard

Food hoarding in rodents is often referred to as either a "larder" or a "scatter" type depending upon the nature of the hoard (Morris, 1962). A larder hoarder transports food back to the security of its home nest, den, or burrow for storage. In contrast, a scatter hoarder stores food not in its nest but rather in the general vicinity of its homesite and not all in the same place. Attempts to correlate these two types of hoarding with a taxonomic classification have, however, failed for the most part. Morris (1962) had proposed that larder hoarding was typical of the myomorphs, while at least one hystricomorph, the green acouchi (*Myoprocta pratti*), was a scatter hoarder. Within the sciuromorphs, there appears to be no consistent pattern to the occurrence of either type of hoarding. The African ground squirrel (*Xerus erythropus*) is a scatter hoarder, although it lives in a burrow and might be expected to be a larder hoarder (Ewer, 1965). Ewer proposed that scatter hoarding in this species may be a vestige from their ancestral mode of arboreal life, as their pattern of food burying is almost exactly like that described for the European red squirrel (Sciurus vulgaris) by Eibl-Eibesfeldt (1963). Scatter hoarding does seem to be typical of most North American tree squirrels including fox squirrels (Sciurus niger; Allen, 1943), gray squirrels (S. carolinensis; Brown & Yeager, 1945), and flying squirrels (Glaucomys volans; Muul, 1968). However, the pine squirrel (Tamiasciurus) may be either a larder or scatter hoarder depending upon the type of food (Klugh, 1927). Small conifer seeds are an important dietary item to Tamiasciurus and there is very little competition for this food with other rodents. Neverthless, the pine squirrel stores the complete pine cones in the center of its territory, which enables it to defend its food supply from conspecifics (Smith, 1968). The level of hunger in some species will also influence whether the food will be larder or scatter hoarded. In a laboratory study of hoarding by chipmunks (Eutamias ruficaudus), it was observed that the animals cached more food outside their nests when they were satiated than when deprived (Lockner, 1972). Other sciuromorphs such as the prairie dog (Cynomys) apparently never store food (Scheffer, 1947; Tileston & Lechleitner, 1966).

Seasonality

Food storage has classically been interpreted as an adaptation to the seasonal fluctuations in the animal's food supply, with the assumption that the animal is capable of "anticipating" or "foreseeing" an imminent shortage to come and a need to store food (see Hamilton, 1939). In northern latitudes, food supplies show a pronounced seasonality in abundance that is directly related to changes in both temperature and photoperiod. Most rodents at these latitudes do in fact store food in the fall of the year and use it during the following winter. Muul (1968) found that flying squirrels are capable of using the change in photoperiod as a highly reliable cue to begin intensive storage of the mast crops during the fall of the year. He proposed that this prevented both premature harvesting of unripe nuts as well as the "wasting" of energy searching for food at times of the year when it would either not be present or unsuitable for storage.

Although food hoarding by deermice in northern latitudes apparently occurs at all times of the year, it is most intense during the fall (Criddle, 1950; Burt, 1946). In a study carried out in a 300 acre area of grassland in southern Michigan, it was observed that the prairie deermice (P. m. bairdi) began hoarding in artificial nest boxes about the middle of October while only a few seeds were found in the boxes during the summer months (Howard & Evans, 1961). Seed storage was maximal in this study during November and, surprisingly, most of the items were gone by late December and all by March. However, when some prairie deermice were kept in an outdoor enclosure, they hoarded large quantities of food at all times of the year when it was consistently plentiful (Howard & Evans, 1961). A slightly different finding and one more consistent with the field evidence, was reported by McCabe and Blanchard (1950) for two species of deermice in California. They found that when *P. truei* were held in large outdoor cages, the greatest amount of hoarding occurred during the season of the year associated with the "time of the first rain and cool fall weather" (McCabe & Blanchard, 1950, p. 22). Similarly, caged *P. californicus* tended to hoard more in "late fall" but only sporatically at other times. As food was apparently continually available in the McCade and Blanchard study, this would seem to suggest a seasonality in the intensity of food hoarding by some species of deermice that is unrelated to the mere abundance of their food.

In the southern latitudes seasonal changes in vegetation and food supplies tend to be less striking, although this will vary depending upon the elevation of a particular area and its closeness to large bodies of water. In desert areas food supplies are closely synchronized with the seasonal pattern of precipitation. In these regions, brief periods of rain are normally followed by longer periods of drought. After the rains, large numbers of small annual plants germinate, grow, and then flower, leaving an abundance of seeds that will remain dormant in the soil until the next rains. Rodents inhabiting these arid regions, in particular the heteromyids and probably also deermice, store most of their food after these rains so that it will be available during the subsequent dry periods. In contrast, the tropical southern regions show no regular seasonal changes in vegetation (Richards, 1973). Flowering can occur at any time of the year and tends to vary with each particular plant species. Food hoarding has been reported in several tropical rodents under artificial conditions, including the green acouchi (*Myoprocta pratti*; Morris, 1962), the African ground squirrel (*Xerus erythropus*; Ewer, 1965), and the African giant rat (*Cricetomys gambianus*; Ewer, 1967), but nothing is known about the occurrence of this behavior in the wild. Since a variety of food ought to be available at all times of the year in the tropical habitats, there is little reason to assume that food hoarding would show any pronounced seasonal pattern.

Evolution

In environments where food supplies undergo seasonal fluctuations, the storage of food during times of abundance would have obvious adaptive advantage. Presumably those animals which store food would survive better during subsequent periods of food scarcity. These animals should be selected for and would supposedly contribute more to the next generation's gene pool than individuals that did not store food.

Even if food supplies did not undergo seasonal fluctuations, food storage may impose an adaptive advantage for other reasons. An animal which can store food will naturally have to venture forth from the safety of its home less frequently than one that has no food reserves. If each of these foraging trips exposes the animal to predation, then it follows that the fewer the excursions the less likely the animal might be caught. This may be a somewhat tenuous argument, however, considering that all animals which store food must during some particular period or season spend a great deal more time collecting food than ones that do not store. One possible explanation is that the threat of predation during the time when food is most actively stored is in fact less than it is when the food is scarce. An abundance of available food for storing corresponds in most habitats with a particularly dense vegetative cover providing protection to small mammals that forage within it. Also, in the northern latitudes, food storage among rodents is most frequently done in the fall for use during the winter. Presumably animals searching for food on the snow covered ground of winter would be more heavily preyed upon because of the lack of natural cover than they would be in the fall.

Another possible explanation for food storage is that its adaptive value is measured directly in the survival of offspring which might utilize food caches near the nest. As in the argument given above, juvenile animals could avoid predation if they obtained their first solid food from stores in the nest or burrow. This could be the case in desert-inhabiting species where food storage is greatest after winter rains and during or just before the reproductive season. In northern latitudes, however, food storage does not appear to be related to the reproductive season, and food is probably not stored for the young.

The storage of food may also have adaptive value from a bioenergetic standpoint. Obviously the time, and hence the energy, required to collect and store food when it is abundant is much less than the amount needed when food is scarce. Another fortuitous aspect of food storage is that the items assembled are usually high in caloric content. Seeds and nuts are commonly stored, and these contain high concentrations of energy, especially in regards to carbohydrates (Davis & Golley, 1963). Animals living in the colder climates normally undergo high metabolic demands during the winter season. In the absence of hibernation or seasonal dormancy, stored food would meet this demand without necessitating additional expenditures of energy to search for it. Some small rodents which do hibernate even store food in their burrows prior to entry into hibernation (Lyman, 1954). Apparently the food is used during those periods when the animal awakes and also in the spring.

All of the above arguments for the evolution of hoarding have centered around the thesis that food storage frequently shows a seasonal pattern in frequenty. However, several theories have been proposed in an attempt to explain the initial motivation of the hoarding response. The proposal that larder hoarding may have evolved as a consequence of an animal's desire to eat in some secure place (Morris, 1962; Ewer, 1965) would seem to be supported by earlier findings that laboratory rats apparently hoard to areas of maximum security (Bindra, 1948c). The observation that submissive wild rats in outdoor enclosures show more larder hoarding than dominant animals (Calhoun, 1963), also suggests that the original motivation in some species might have been for security and protection.

Morris (1962) has proposed that under special circumstances scatter hoarding may have developed out of larder hoarding. He suggested that in the green acouchi, a South American hystricomorph, scatter hoarding may have evolved concurrently with the species' propensity to become more mobile and to shun a fixed home site. An animal which is relatively mobile could seek refuge at any temporary site within its home range if it had a scattered food supply cached nearby (Morris, 1962). Ewer (1965) has also offered the explanation that scatter hoarding in a species like the African ground squirrel may have evolved as a result of "food envy" or the practice of satiated animals attempting to hide food from members of their own species. This latter interpretation is very appealing in light of the finding by Lockner (1972) that chipmunks will show more scatter hoarding when satiated than when deprived. One must consider, however, that the nature of the food probably always has had an important bearing on whether it was larder or scatter hoarded, as already pointed out for pine squirrels.

There are several additional advantages unique to scatter hoarding that would also act to aid its selection. Ewer (1965) offered the novel explanation that storing food away from the nest forces the animal to search for it every time the animal is hungry and assures that stored items are not consumed prior to a real shortage of food. If these scattered hoards are not eaten, the seeds will eventually germinate, providing future generations with a new source of food. Undefended scattered hoards can also be utilized by all members of the same species, regardless of which individuals made the cache.

The discussion of the evolution of hoarding up to now has centered around the explanation that this seasonal sort of behavior is apparently "adaptive." Like most evolutionary explanations of behavior there is a paucity of good experimental evidence either to support or refute such ideas. Adaptiveness can be defined as anything that increases the animal's ability to survive and leave fertile offspring. The proposal that food storage by deermice in northern latitudes leads to higher survival has never actually been tested, although several observations have been made that might be construed as evidence for this. Howard (1949) has reported that cold temperatures together with shortages of food probably contribute to winter mortality of deermice in Michigan. He observed prairie deermice (*P. m. bairdi*) dead in next boxes after cold waves in March which had apparently died from starvation. In contrast, *P. l. noveboracensis* when placed outdoors without protection from wind or snow during February and March could survive if given ample food (Howard, 1949). Under laboratory conditions, *P. m. bairdi* seems to be able to tolerate cold better than *P. l. noveboracensis* (Sealander, 1951), which would indicate they both can survive if given sufficient food. The presence of daily torpor in both species probably also leads to higher survival and the prolongation of food stores (Howard, 1951).

An obvious experimental approach to studying whether food storage is critical to these animals, would be the removal of the food stores from some individuals but allowing others to retain and accumulate their food. The field situation described by Howard and Evans (1961), in which nest boxes were placed in a 300 acre area of habitat, would be ideal for such an experiment. If the boxes were left out long enough, the deermice would eventually get accustomed to using the boxes, especially if other species were symstematically excluded from them by the experimenter. Two identical test areas could be set up where in one area the mice would be allowed to accumulate food in the boxes, but in the other area the food would be periodically removed (preferably as often as possible). Survival and reproduction on the two areas could then be measured and compared. A higher survival and reproductive rate on the area with food stores would be good evidence for the "adaptiveness" of this trait.

Experimental Studies

Since Wolfe's pioneer work in 1939 entitled "An exploratory study of food-storing in rats" published in the *Journal of Comparative Psychology*, numerous investigators have attempted to answer the question of what are the critical variables affecting hoarding behavior. Ross, Smith, and Woessner (1955) in their review of the hoarding literature, arbitrarily classified all of the variables into two groups: organismic and situational factors. In the review below, I have used an outline of topics similar to theirs and have retained their use of the words "organismic" to describe all of the possible endogenous motivating factors of hoarding, and "situational" to include all of the environmental factors. The two groups will not always be mutually exclusive.

Organismic Factors

Deprivation.--Studies on the effects of food deprivation on hoarding have led to some contradictory results depending on the species. Morgan *et al*. (1943) found that Lashly brown rats deprived of food for periods of 12, 24, 36, and 48 hours showed higher hoarding scores as compared to scores during satiation. Although their results were ambiguous due to a poor experimental design, they concluded that an accumulation of a physiological deficit was necessary to produce hoarding because deprived rats took several days before they began to hoard. They believed hoarding was an "all or none" behavior as the hoarding scores were essentially the same for all four experimental groups (12, 24, 36, and 48 hour deprivations). They also found that there was some competition between the tendency to eat and hoard. Hoarding scores were higher when measured in the second half hour of the test situation than when measured in the first half hour, which was spent in eating. Females also hoarded more than the males and hoarded sooner during deprivation than males. Stellar and Morgan (1943) verified these results in another study in which they compared the hoarding of rats kept on an 18-day deprivation schedule (given food for only 1 hour daily) with ones kept on a satiation schedule (unlimited food). In the subsequent 7 days of hoarding trials under deprivation conditions for both groups, the deprived rats showed high levels of hoarding almost immediately, whereas those that had been satiated took several days before their scores reached maximal levels. They concluded "that the effects of a deprivation cycle accumulate over a period of days until they reach some critical level of deficit which instigates hoarding . . . (and) . . . the amount of hoarding does not vary quantitatively with the amount of deprivation but rather appears at its maximal amount when deficits in the body accumulated through deprivation reach a 'threshold' level" (p. 53). This theory is commonly referred to as the "deficit hypothesis" of hoarding. Smith and Ross (1950a) found essentially the same results with Wistar rats on a 35-day deprivation schedule during which rats were given one-half hour each day to eat food weighing 1/8 of their body weight and then were tested for 1/2 hour. Once hoarding began in the second week of the schedule it did not drop off significantly for the rest of the 35 days.

The results of experiments on food hoarding in the golden hamster agree with those found for rats. Smith and Ross (1950b) reported that hamsters hoarded significantly more food pellets during a deprivation schedule of only 1 pellet a day as compared to satiation of 3 pellets daily. Lockner (1972) also reported that in the chipmunk (*Eutamias ruficaudus*) deprivation enhances both the amount of food hoarded and the speed at which it is hoarded.

However, not all of the studies have supported the deficit hypothesis. Bindra (1948b) demonstrated that deprivation was not a necessary condition to elicit hoarding when he found that rats would hoard saccharin-treated mash placed in bottle caps even when non-deprived. Bindra altered the experimental situation by using closed alleys, and his conclusions are therefore not directly comparable to those of Morgan *et al.* (1943). Ross and Smith (1953) also reported that the deficit hypothesis failed to explain hoarding in laboratory mice. Using C3H strain mice they found that deprivation tended to have an inhibitory effect on hoarding. They used three experimental regimes of 15 days each in which satiation was alternated with deprivation and found that the hoarding scores were highest when satiation was the initial condition. In an attempt to resolve these conflicting results the adequacy of the laboratory diets was investigated, and these studies are discussed in the next section.

Dietary and energetic deficiencies.--Wolfe (1939) was the first to study the importance of a nutritional deficiency on hoarding behavior. He found that when the rats' normal diet of food pellets was supplemented with milk, lettuce, and cod liver oil, their hoarding scores were significantly less than when rats were given only the food pellets but in sufficient quantity to maintain their weight. Unfortunately this study may have compounded the factor of deprivation or not enough food with that of nutritional deficiency. It is very plausible that the rats kept on a diet "sufficient to maintain body weight" were in fact being deprived of their normal amount of food. Wolfe may have been comparing supplimented rats with deprived rats which would confuse his results. In any case, he concluded that "the absence of certain food elements provides a distinct motivation for hoarding" (Wolfe, 1939, p. 107).

A similar effect of a supplemented diet on food hoarding in mice was reported by Ross and Smith (1953). They placed mice on an experimental regime of 5 days of satiation (food *ad lib*.) followed by 5 days of satiation plus supplemental lettuce and sugar cubes, and then finally on 5 days of satiation again. During the satiation-supplementation phase hoarding dropped off by 54%, apparently as some undefined need was satisfied. When supplementation was stopped, the amount hoarded in the next 5 days rose by 51%, or to the level at which it had previously been.

Several approaches have been used to study whether deprivation of specific food elements leads to a body tissue deficit which in turn triggers hoarding. Stellar (1943) manipualted the sugar metabolism of rats by injecting insulin, epinephrine, and glucose. It was predicted that insulin would increase hoarding because of its lowering of the blood glucose levels and the production of a glucose "deficit." On the other hand injections of epinephrine (i.e., adrenalin) and glucose were expected to produce the opposite effect on hoarding. Only epinephrine showed the expected effect, and therefore his hypothesis is still equivocal.

Bindra (1948a,b) investigated the importance of specific components of the diet including fats, vitamins, minerals, salts, proteins, and carbohydrates on the hoarding response. He found that hoarding increased when both carbohydrates and proteins were given together. There was no evidence of an effect by any of the other components which were studied.

In an attempt to investigate whether a dietary deficiency was affecting overall metabolism rather than a specific tissue deficit, Stellar (1951) manipulated thyroid functioning in three groups of rats. He proposed two contrasting hypotheses for the role of metabolism on hoarding: (1) that hoarding served as a heat production activity like any other bodily activity, or (2) that hoarding was a heat conservation activity similar to nest building. He also theorized that any condition which would either raise or lower metabolism ought then to affect hoarding. In his experiment one group of rats received a thyroid depressent, one group had their thyroids removed, and one group received thyroid injections. There were no significant differences among the hoarding scores of the three groups and Stellar concluded that "general metabolic changes do not underlie the hoarding behavior of the laboratory rat" (Stellar, 1951, p. 297).

In summary, any general conclusion about the effects of both deprivation and dietary deficiency upon the hoarding response is still equivocal. Clearly there is a need for a more standardized approach to these questions using comparable test conditions and subjects of similar age, weight, sex, and feeding experience.

Sex differences.--Many researchers have reported significant sex differences in the hoarding response (i.e., in rats, Wolfe, 1939, Morgan et al., 1943, Smith & Ross, 1950a; in mice, Smith & Ross, 1953a; and in hamsters, Smith & Ross, 1950b). As already mentioned, hoarding by rats is typically quite high if the animals are kept on some sort of deprivation schedule. However when food is continuously available, a sex difference usually emerges with the females hoarding more than males. Wolfe (1939) attributed this to some sort of malnutrition in females caused by previous lactation, while Calhoun (1963) reported increased hoarding by female rats during lactation. Marx (1950b) proposed that high levels of female hoarding might possibly be due to heightened activity during their estrous cycle. Studies by Lapetite and Soulairac (1951) and Herbert et al. (1972) have also implicated the estrous cycle as being a factor, but not because of an increase in sexual arousal or general activity as Marx predicted. Lapetite and Soulairac (1951) brought female rats into permanent diestrous by the administration of an anti-thyroxine drug called methyl thioruracil and noted increased hoarding. Male subjects showed a decrease in hoarding. Both sexes also decreased their food intake. Lapetite and Soulairac hypothesized that the mechanism underlying hoarding behavior was different in each sex with males hoarding under a physiological condition related to hunger, and females hoarding because of some sort of extra-thyroid condition which might be called "sexual equilibrium."

The study by Herberg *et al*. (1972) also confirmed that female rats tend to hoard more during the diestrous days of their cycle. Apparently when sexual and general activity (i.e., wheelrunning) is maximal, hoarding behavior falls off. This same sort of phenomenon was found by Kinder (1927) for nest building by rats. The greatest amount of nest building was also observed during the diestrous days of the cycle. The possibility that hoarding behavior is modified or displaced nest building was examined by Herberg *et al*. (1972). They found that satiated females hoarded a much greater proportion of cotton-wool pledgets than did food-deprived female and male control groups, although food pellets predominated. As the satiated subjects still preferred food pellets to the nesting material on all but the first 2 test days, it was concluded that hoarding was not simply a manifestation of nest building activity. Instead, Herberg *et al*. (1972) proposed two alternative explanations for the sexual difference seen in hoarding. They hypothesized that perhaps estrogen imposed some sort of restriction on food intake in females, resulting in the release of the hoarding response in much the same fashion as seen in food deprived males. Kennedy (1969) had previously given evidence that estrogen reduces food intake and limits body weight in female rats to a level below males. This hypothesis, however, would seem inconsistent with Lapetite and Soulairac's (1951) observations that their treatment of anti-thyroxine drug resulted in reduced food intake in both sexes but with a resultant increase in only the hoarding of females. The alternative hypothesis offered by Herberg *et al*. (1972) is that the difference in hoarding behavior is yet another "long term repercussion of perinatal androgen activity" (p. 190).

Not surprisingly, consistent sex differences were not observed in several of the reported studies of hoarding behavior. Hunt *et al*. (1947) and Stellar (1951) found that sex differences contributed little if anything to the total variance in their studies. Marx (1951) also found that the percentage of rats which hoard was about the same for both sexes and in fact male rats would hoard more than females when the rats were given only 30 minutes in which to hoard. When given 24 hours, then females tended to hoard more than males. Apparently the experimental situation frequently interacts with sex leading to some of the differences reported in the literature.

Neural control.--One would naturally expect that because the hoarding response depends upon sensory input, any interference with the cortical sensory areas should affect hoarding activity. Both the early and recent research has centered around attempts to isolate areas of cortex directly controlling this response and not surprisingly the results have often been contradictory.

Zubeck (1951) found that small lesions in the neocortex regardless of location increased hoarding in laboratory rats. However, Stamm (1953) found the opposite effect that bilateral cortical lesions reduced the level of hoarding in rats. He also found that small lesions of the median cortical surface affected the level of hoarding to a greater degree than those in other larger areas on the cortical surface (Stamm, 1954a). Vanderwolf (1967) has also demonstrated that anterior thalamic lesions result in the depression of hoarding by rats.

Most recently Wallace and Tigner (1972) have confirmed that neocortical lesions lead to increased hoarding in rats under both _ad lib_. and food deprivation conditions. They explain the apparent contradiction of both Zubeck's and their own findings with that of Stamm's (1953, 1954a) as probably due to Stamm's selection of animals for study which showed maximal preoperative hoarding. As a result these animals would have been less likely to show any further increase after the operation. In contrast, for both the studies of Zubeck (1951) and of Wallace and Tigner (1972), animals were selected under _ad lib_. conditions and probably were hoarding at a very low preoperative level. Appropriate experimental manipulation therefore would be expected to significantly increase hoarding over that of controls. Wallace and Tigner (1972) also found that rats with hippocampal lesions did not hoard significantly more than controls under either _ad lib_. or food deprivation.

Again, however, this is an apparent contradiction of the work by Wishart _et al_. (1969) in which they found the exact opposite effect.

The role of the lateral hypothalamus in food hoarding was first implicated by Herberg and Blundell (1967) when they found that electrical stimulation of that area elicited hoarding in satiated rats. Previous work had already demonstrated the importance of this area on feeding, and lesions there diminish both feeding and hoarding (Blundell, 1970). In another study Herberg and Blundell (1970) also found that although lesions in the ventromedial nucleus of the hypothalamus increased food intake, there was no increase in hoarding. Later when their lesioned subjects became very obese, hoarding could not be elicited even after 16 hours of deprivation. As a consequence of their findings, Herberg and Blundell (1970) have presented a model for hypothalamic control of hoarding. First they propose that hoarding is motivated by long term nutritional needs or "deficits" (i.e., body weight loss or changes in the size of fat reserves) mediated ultimately though the lateral hypothalamus feeding area. Secondly, they propose that hoarding, unlike feeding, is not under the inhibitory control of the ventromedial satiety area which probably responds to elevated blood glucose levels or some other short term change following feeding. Stellar's early work involving the injection of massive doses of glucose and its failure to have any effect on hoarding behavior would seem to give additional support to this model. More recent work by Blundell and Herberg (1973) has likewise tended to support their model as they have demonstrated that electrical stimulation of hypothalamic sites other than the lateral area did not induce hoarding even though locomotor activity was increased.

Whether the model described above by Herberg and Blundell (1970) holds for small mammals other than laboratory rats remains to be seen. In fact, this may not be the case in laboratory mice which, as already noted, do not increase their hoarding after food deprivation (Ross & Smith, 1953). The results of my work with deermice (*Peromyscus*) would also tend to contradict this model, since there was no consistent relationship between weight loss and hoarding.

Learning and early experience.--Wolfe (1939) was the first to study the relative importance of early experience on adult hoarding. He compared rats raised with food pellets to those fed only powdered food, and found that the rats with previous pellet experience hoarded more. Marx (1950a) interpreted these results as suggesting that hoarding was a stimulus-response behavior formed primarily from the fusion of "earlier and independently learned 'homing' and pellet seizure habits" (p. 91) aided by some form of reinforcement. Smith and Ross (1953a) attempted to verify this hypothesis by comparing C3H mice reared on pellet food to those reared on a liquid diet (similar to

Wolfe's original study with rats). When hoarding trials were conducted, the two groups showed no significant difference in the level of hoarding. They concluded that prior experience with the transportation of food was not necessary in mice.

Stellar and Morgan (1943) approached the problem a little differently and instead studied the effect of prior experience with the hoarding apparatus itself. They concluded that "emotional adaptation" to the apparatus was what appeared in their data as "experience." Bindra (1948c) later disagreed with this conclusion and stated that in fact the opposite was true, with some form of anxiety (emotion) being necessary to even produce the hoarding response. More recently and probably much to the chagrin of these earlier workers, Blundell and Herberg (1973) have demonstrated that they can elicit the hoarding response in naïve rats which have never previously hoarded by electrically stimulating the lateral hypothalamus. My own observations of deermice (Peromyscus), indicate they too can hoard almost the instant they are given food to carry even without any sort of prior experience.

The effect of early feeding frustration on hoarding also captured the interest of many workers. Hunt (1941) found evidence that depriving rats in infancy augmented the amount of hoarding exhibited by adults after food deprivation. Later work by Hunt et al. (1947) also provided what was thought to be additional support for such an effect on hoarding. However, McKelvey and Marx (1951) took exception to the statistical procedures used in the original study. In an attempt to repeat Hunt's study, they were unable to find any evidence to support his conclusions. Nonetheless, Marx (1952) proposed that increased rates of hoarding by infantile-deprived rats might be the result of their retention in adulthood of an increased feeding rate with consequent effects on hoarding.

Albino and Long (1951) also repeated Hunt's experiment but modified it by insuring that all groups prior to adult deprivation tests were kept on a satiation schedule long enough to insure equivalence of pre-test "hunger." Their results did agree with Hunt's but they pointed out that their "feeding frustration effect" may have been a consequence of the differential experience their experimental animals had in transporting food. Manosevitz (1970) concurred with this latter explanation and also attempted to replicate Hunt's original study, although this time with inbred strains of mice. He found no evidence to support Hunt's earlier conclusions.

Genetic variation.--For many years there was a continuous debate concerning whether hoarding was instinctive (McDougall, 1923; Morgan, 1947; Thorpe, 1963) or learned (Holland, 1954; Marx, 1950a; Mowrer, 1960). Today, however, one can only conclude that the debate was inconclusive and that more attention needs to be paid to the relative contribution of both the environment and genotype to the hoarding response.

Stamm (1954b) was the first investigator to report strain differences in the amount of hoarding by rats. In 1956, he pursued this further by mating a high hoarding strain with a low hoarding strain and then backcrossed some of the Fl's with the low strain. Although this method was not complete enough to clearly demonstrate the mode of inheritance of this trait, Stamm (1956) did conclude that hoarding was dependent on a single dominant gene. The Fl's were similar in hoarding scores to the high strain and the backcross generation had a bimodal distribution in their hoarding scores. Koski (1963) also reported that a single gene theory could possibly explain inheritance of this trait in golden hamsters. Although he found no significant differences in the scores of the two hamster strains he studied, he did get a bimodal distribution of scores for both strains. Smith and Powell (1955) found a significant difference in the hoarding scores of several inbred strains of mice but attributed this to each strains' characteristic "emotionality."

More recently the contribution of genetic factors to hoarding has been investigated by Lindzey and Manosevitz (1964), in which they too found significant differences in the level of hoarding among several strains of inbred laboratory mice. Significant interactions between genotype and the environment have also been found (Manosevitz, 1965;

Manosevitz *et al.*, 1968). Manosevitz and Lindzey (1970) have emphasized that the environment can influence the "heritability" of the genetic factors involved and that if one attempts to select for high or low strains, the results are dependent upon the specific environmental situation. They concluded that the determinants of hoarding are complex and involve the genotype, components of the environment, and their interaction.

Situational Factors

Competition-social interaction.--The effect of conspecifics on the hoarding response was investigated by Miller and Postman (1946). In their experiment they used a central hoarding bin from which rats from several cages could hoard. When the rats were permitted to hoard simultaneously some preferred to take food from the bin whereas others hoarded more from the cages of the other rats. The rats whose food was stolen showed no resistance to the thefts suggesting that the goal of hoarding is the activity itself rather than the result of such activity (Miller & Postman, 1946).

Hoarding by rats in a group situation was also studied by Ross *et al.* (1950). They found that a dominance-submission relationship was established in which submissive rats hoarded less under the group condition as compared to when they were isolated. The best hoarder was the dominant rat. Denenberg (1952) extended this study and raised rats in a group and then habituated them to individual living conditions. When tested under isolation conditions, they tended to hoard more than they did under the group situation where more time was spent eating than hoarding. Calhoun (1963), however, has found that low ranking Norway rats hoard more than high ranking ones when kept together in large outdoor enclosures.

In another study, Lindzey and Manosevitz (1964) examined the effect of group competition in mice using two experimental conditions of deprivation. One condition consisted of depriving the mice as a group and forcing them to compete for food. For the other condition, mice were deprived while isolated in individual cages. When the mice from the two groups were later tested under identical conditions in individual hoarding cages, there was no significant difference between the two groups' hoarding scores. Lindzey and Manosevitz (1964) concluded that there was little evidence for the direct effect of group competition for food upon the hoarding response.

Recently Terman (1974) has reported on a study of several laboratory populations of prairie deermice (*P. maniculatis bairdi*) and the possible correlation of hoarding behavior and population growth. He observed that hoarding behavior always began prior to population asymptote, and hypothesized that increasing intraspecific competition or social pressure may have been a causative factor. Typically a founding female was the first and most consistent hoarder, although a few other mice also participated in the hoarding. Terman (1974) also speculated that the "establishment and maintenance of the hoard appears to be an effort on the part of the hoarders to spatially organize the populations with respect to the location of food storage and consumption" (p. 144).

Cage, lighting, and familiarity of apparatus.--The importance of lighting or illumination on the hoarding apparatus and its effect on hoarding scores was first noticed by Wolfe (1939). He found that lighting the hoarding alleys more than doubled the number of pellets retrieved by rats. Waddell (1951) also found this to be true when measuring hoarding in hamsters. When he lighted their food bin, the hoarding rate was doubled. Stellar (cited by Morgan, 1947) found that differential lighting of the cage and alley decreased hoarding when the source of light was over the cages. Apparently if the home cage was shaded, hoarding was increased. Manosevitz (1965) likewise found that if the home cage is kept dark, higher hoarding scores can be obtained.

The familiarity of the cage is also important as pointed out by Stellar and Morgan (1943) and Viek and Miller (1944). Optimum hoarding was obtained in their studies of rats when a familiar cage, alley, and food were used. This familiarity was apparently related to olfactory as well as visual cues. They also concluded that rats tend to transport food to places of maximum security, in this case their home cage. Bindra (1948c) also found that the type of alley was important. "Open" alleys increase the frequency of hoarding as compared to "closed" ones. Bindra noticed that the latency to enter the alleys increased with the use of open ones and interpreted this as indicating insecurity or "shyness" in the rats. Partial support for this hypothesis has been provided by Tigner and Wallace (1972) who observed greater hoarding in anosmic rats (olfactory bulb removed) than in sham operated or blind rats. They noticed an increase in the latency to enter the hoarding alley by the anosmic rats and attributed this to their increased shyness.

Several studies have demonstrated that the length of the alley is an important factor affecting the amount of hoarding (Miller & Viek, 1950; Smith & Ross, 1950a, 1953a; Wolfe, 1939). In general shorter alleys result in higher hoarding scores apparently because the distance over which the pellet has to be transported is less. The shorter the alley the less the "anxiety" experienced by the animal as he retrieves the food to his home cage (Ross _et_ _al_., 1955).

Stimulus characteristics.--Several studies have attempted to investigate the stimulus characteristics of hoarded material to see whether there was some sort of relationship between the animal's need and what is hoarded. Although relevance to a need has an effect on the intensity of the food hoarding response in rats (Wolfe, 1939; Stellar & Morgan, 1943), it apparently is not a necessary characteristic of the hoarding stimulus *per se*. Bindra (1948a) found that rats hoarded saccharin flavored food even when not deprived. He also found that they would hoard cotton dental plegets soaked in water when they had been satiated with water (Bindra, 1947). Smith and Ross (1953b) similarly found that laboratory mice would hoard more wet or dry cotton pellets than food pellets, even when they had experienced neither food nor water deprivation. As there was also plenty of nesting material, the explanation that possibly the cotton was needed for nest building seemed unlikely.

The relevance of need as an important characteristic of the hoarded material has been further investigated by McCann *et al*. (1964). They found that food deprived rats hoarded fewer paper strips than did satiated rats. Severe water depression likewise tended to depress hoarding of both paper strips and food. In conclusion they state that severe deprivation of food or water depresses the hoarding of materials which are incapable of alleviating that deprivation. Tigner and Wallace (1972) have similarly found that food deprived rats hoard more food pellets than wooden blocks. When not under food deprivation, they hoard more blocks than food. Licklider and Licklider (1950) in an earlier study, had also shown that non-deprived rats hoarded more tin foil wrapped pellets than plain ones when given a choice. A different finding has been reported for prairie deermice, however, as they apparently will not hoard wooden pellets or cotton balls when non-deprived in the laboratory (Rice, 1972). Although "novelty" seems to be important in rats, this may not be the case in deermice.

The stimulus cues by which an animal might identify objects to be hoarded have also been studied to a limited extent. The role of vision and olfaction has been studied by Tigner and Wallace (1972) in rats. They found that neither visual nor olfactory cues were necessary for the elicitation of hoarding. In fact anosmic rats (olfactory bulbs removed) hoarded significantly more food pellets under both _ad lib_ and deprivation than did blind and sham operated rats. Tigner and Wallace (1972) concluded that several cues are available to an animal and that there is no evidence that cues for only one sensory modality are being used.

Muul (1968, 1970) has observed that flying squirrels use olfactory cues to recognize nuts previously stored by themselves or other individuals. In his study "new" nuts were preferred 4 to 1 over previously stored ones. This behavior apparently prevents the wasteful restoring of food by this species and insures that a large accumulation of nuts will be gathered for winter. This is not the case in prairie deermice, however, for in the laboratory they show no apparent preference for either fresh food pellets or previously hoarded ones, when given a choice of both kinds to hoard (Rice, 1972).

Studies on the stimulus characteristics of objects hoarded by hamsters in the laboratory have implicated novelty or variety as being an important determinant as to what things are preferred for hoarding. Scelfo and Hammer (1969) showed that non-deprived hamsters preferred sucrose pellets to plain chow pellets for hoarding purposes. They concluded that taste was probably responsible for the preference. However, in a follow-up study Hammer (1972) found that variety was probably all that was necessary and that citric acid flavored pellets were preferred over plain chow, sucrose over citric acid, and glass beads even over sucrose. The glass beads were highly preferred. In each test there was a decrease in preference by the fifth day of the experiment indicating that "novelty" was probably important. Hammer (1972) speculated that this apparent "innate liking for (glass beads) and disposition to hoard these articles may be comparable to the reaction to innate releasing stimuli in other behavior systems" (p. 140). In fact these stimuli may even be "super normal releasers" as compared to ordinary food items or nesting materials.

Temperature.--McCleary and Morgan (1946) were the first to investigate the effect of temperature on food hoarding in laboratory rats. In their preliminary work, rats were tested on alternate days either under temperatures between

10°-15°C or between 25°-30°C. When tested under the colder temperature range, the level of hoarding was almost seven times higher than it was under the warmer temperatures. As the experimental procedures were different under the two temperature conditions, the test was repeated except that the lower temperature range was from 25°-30°C and the higher range from 40°-45°C. Again tests were conducted on alternate days with the rats again hoarding more under the lower temperatures (although heat stress was almost certainly an important factor). In their next experiment, they housed 6 animals (4 males and 2 females) in a room where the temperature was allowed to fluctuate with outside ambient temperature with a range from 8°-34°C. The rats were given unlimited food and the number of food pellets carried from an alley into a home cage in a 24 hour period was the measure of hoarding. As predicted they found an inverse linear relationship between the logs of the hoarding scores and the mean daily temperatures. McCleary and Morgan (1946) provided three possible explanations of the observed increases in hoarding. It may have been an attempt on the part of the rats to (1) increase heat production through muscular activity, (2) insure a supply of food to meet increased metabolic demands, or (3) supply insulation material for the home cage. Although McCleary and Morgan raised many interesting questions, their study has apparently never been repeated with rats.

Ross and Smith (1953) did perform a similar experiment to McCleary and Morgan's but with female laboratory mice (C3H) as the subjects. They had predicted that because mice respond differently than rats to the stress of food deprivation, mice would also respond differently to changes in ambient temperatures as it effects their hoarding. Their test temperatures varied from about -2° to 29°C, but there was no relationship between the lowest daily temperature and the highest hoarding scores. In fact on 17 of the 20 days of testing, hoarding varied directly with temperature. Temperatures below approximately 15°C appeared to inhibit hoarding.

The results just reported for the Ross and Smith (1953) study might tend to cast some doubt on the naturalistic interpretation that mice hoard when the temperature drops in order to have food for subsequent cold weather periods. A criticial appraisal of their study suggests, however, several possible explanations for this apparent contradiction to the more classical interpretation. First, their experimental situation consisted of a variable temperature which could fluctuate nearly 27°C from one day to the next. A more appropriate test might have been to keep the test temperature constant to see whether it was temperature change or the temperature per se that was important. Secondly, their subjects, besides being all of one sex (females), were also inbred mice on which the selection for hoarding had been relaxed for many generations.

Genetic variability was greatly diminished in these mice. Lindzey and Manosevitz (1964) have shown that there are strain differences in hoarding by laboratory mice and it is possible that another strain might have demonstrated an opposite effect of temperature. The results of my own work to be discussed later, show that the response of deermice to ambient temperature apparently has some relationship to their latitudinal and climatic origins.

Photoperiod.--Muul (1968) was the first investigator to hypothesize that photoperiod had an effect on hoarding in at least some rodents. In his study of flying squirrels (Glaucomys volans), Muul found that he could increase their level of hoarding by either giving the squirrels an appropriate photoperiod for fall or a shorter than normal one. In fact the level of hoarding was directly related to the length of the dark phase of his light-dark cycle. Time tests indicated, however, that it was not merely a consequence of having more time to hoard. The response appeared to be completely independent of all temperature cues. In fact, cold temperatures tended to inhibit the squirrels' activity and probably would similarly affect their amount of hoarding.

According to Muul (1968, 1970) the capability of sensing photoperiod changes is advantageous because it allows a precise timing of food storage to the time of year when food suitable for hoarding is readily available. In the northern states, hickory nuts and acorns are the main items found in caches made by flying squirrels. This food is used until the next mast season and during the summer, insects and vegetable matter often supplement their diet. During mid-September, the intensity of the storage response increases and reaches a peak in November. Flying squirrels apparently hoard at all times of the year, but the greatest intensity is in these autumn months. Muul proposes that their use of photoperiod changes for a cue to begin intensive hoarding prevents premature gathering of unripe nuts which might spoil or be less nutritional. It also assures that they will not "waste" their energy searching for food that would be unsuitable for storage at other times of the year. The results of my own study of hoarding in deermice (*Peromyscus*) indicates that the response of some subspecies to photoperiod might be a purely opportunistic one in which they use the longer periods of darkness to be active longer.

METHODS AND MATERIALS

Subjects

The mice used in this study represented 5 different taxonomic groups of 3 species (Table 1). Two subspecies were chosen from within both *P. leucopus* and *P. maniculatus* so that north-south comparisons of their hoarding scores could be made. *P. l. castaneus* were selected because of their proximity to the equator, whereas *P. l. noveboracensis* were used because they were available locally from brush and forest habitats around East Lansing, Michigan. Both of these subspecies are found at practically equivalent altitudes. Within *P. maniculatus*, stocks of *P. m. blandus* were available from the deserts of the southwest, whereas *P. m. bairdi* were trapped in cornfields bordering the campus of Michigan State University. *P. eremicus eremicus* were also utilized because they represented an entirely different subgenus than the other two species and are found in the same habitat as *P. m. blandus*. The latitude, elevation, habitat, and climatic conditions from which each of the above stocks was obtained are summarized in Table 2.

Table 1.--Systematic Relationships, Sex and Number of Mice Used in This Study.

Subgeneric Name	Species Group	Specific Name	Subspecific Name	Number	
				Males	Females
Peromyscus	maniculatus	maniculatus	bairdi	64	64
Peromyscus	maniculatus	maniculatus	blandus	64	64
Peromyscus	leucopus	leucopus	noveboracensis	64	64
Peromyscus	leucopus	leucopus	castaneus	64	64
Haplomylomys		eremicus	eremicus	28	12
			Totals	284	268

Table 2.--Description of the Geographical Origins of the Mice Used in This Study.

Subspecies	Origin	Latitude	Altitude (meters)	Habitat Where Captured	Mean Daily Temperatures (°C)		Day Length (Hrs)	
					Max.	Min.	Longest	Shortest
P. *maniculatus bairdi*	E. Lansing, Mi.	42°42' N	271	Cornfields (active)	27.2 (July)	-8.9 (Jan)	15 1/3	9
P. *leucopus noveboracensis*	E. Lansing, Mi.	42°42' N	271	Forest	27.2 (July)	-8.9 (Jan)	15 1/3	9
P. *maniculatus blandus*	Rodeo, New Mexico	32°21' N	1250	Desert	35.8 (July)	-3.1* (Dec)	14 1/3	10
P. *eremicus eremicus*	Rodeo, New Mexico	32°21' N	1250	Desert	35.8 (July)	-3.1* (Dec)	14 1/3	10
P. *leucopus castaneus*	Escárcega and Champoton, Mexico	19°20' N and 18°37' N	Near Sea Level	Cornfields (active & abandoned)	36.5 (Apr)	15.3* (Jan)	13 1/3	11

*For Lordsburg, New Mexico approximately 35 miles north-northeast of Rodeo.

#For Escárcega, Mexico.

All mice were raised under laboratory conditions in the colony maintained on the Michigan State University Campus. The colony temperature was kept at approximately 21°C under a 15:9 hour light-dark cycle. The mice were housed in plastic cages measuring 28.6 cm. X 12.7 cm. X 15.2 cm., provided with 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 always available *ad libitum* from a suspended drop.

Except for *P. l. castaneus* all mice were the first laboratory generation from wild caught parents. *P. l. castaneus* probably consisted of individuals of the 3rd-4th generation of laboratory raised mice. All mice were weaned at approximately 21 days of age and kept in groups of 3-4 of one sex until their use in the experiment. The average ages in days (± 1 standard error) of the mice when placed in the experiment were: *P. l. noveboracensis* 146.3 ± 1.8, *P. l. castaneus* 165.4 ± 4.7 (the ages of 33 of these mice were unknown and were arbitrarily assigned ages of 250 days), *P. m. bairdi* 141.6 ± 1.9, *P. m. blandus* 157.6 ± 4.1, and *P. eremicus eremicus* 146.9 ± 6.5. The average weights in grams (± 1 standard error) of the mice before testing were: *P. l. noveboracensis* 22.6 ± 0.5, *P. l. castaneus* 29.1 ± 0.8, *P. m. bairdi* 17.8 ± 0.3, *P. m. blandus* 27.0 ± 0.5, and *P. e. eremicus* 26.0 ± 0.8.

Apparatus

The hoarding apparatus was similar in design to that described by Smith and Ross (1953a). The test cages were the same as those in which the mice were raised and had hardware cloth (1/4-in. mesh) alleys approximately 43 cm. long and 7.62 cm. square attached to them. Access to the alleys was provided by a hole (2.54 cm. in diameter) drilled in the end of each cage. A hardware cloth food bin measuring about 7.62 X 7.62 X 2.54 cm. was placed at the opposite end of each alley from the test cage and filled with food. The food pellets were of the same type (Wayne Mouse Breeder Blox) as used for rearing and had been previously sorted to a uniform size of about 3.67 ± 0.07 grams each. All food was removed from the normal food hoppers atop the cage during experiments.

Procedure

The experimental situation was designed so that the effects of four variables on food hoarding could be studied: (1) ambient temperature, (2) acclimation to temperature, (3) photoperiod, and (4) latitude or subspecies.

Four weeks prior to testing, a group of mice (normally about 48) were randomly selected from the various available stocks and divided into four equal experimental groups. Each mouse was weighed and housed singly in a plastic cage of the same type used for previous rearing. One group of mice was then maintained at 7.0 ± 0.8°C and under a 15:9

hour light-dark photoperiod (henceforth to be called a "long" day photoperiod); a second group at 7.0 ± 0.8°C and under a 9:15 hour light-dark photoperiod (a "short" day photoperiod); a third group at 26.7 ± 1.0°C and under a long day photoperiod; and a fourth group at 26.7 ± 1.0°C and under a short day photoperiod. Both of the "warm" temperature groups (27°C) were kept in separate rooms with independent light control systems and with the temperature controlled by a single thermostat. The two "cold" temperature groups (7°C) were kept in a refrigerated chamber with the shelves for both groups again having their own independent light control systems. The cages were kept on steel and wood shelving, with approximately 12.7 cm. between cages. Lighting was provided by two 60 watt light bulbs approximately 43 cm. above each shelf of 6-8 cages. A 7 1/2 watt red bulb provided the only light in each room during the dark phase of the photoperiods. Relative humitity in the warm rooms was approximately 40-50% and in the cold rooms 75-85%. Food and water were available *ad libitum*.

In order to distinguish between the effects of immediate ambient temperature at the time of testing versus the effects of a long term acclimation to the warm or cold temperatures, each of the above four experimental groups were further subdivided on the day before testing so that half of the animals would be tested at the opposite temperature (but the same photoperiod) to which they had been acclimated for the previous 4 weeks. This resulted in a total of 8 experimental groups (4 temperature groups under each of the 2 photoperiods). This design is outlined in Table 3.

On the day prior to testing, the appropriate cages were switched from one temperature control room to another as outlined above and the hardware cloth alley was attached to the end of each cage. All food was removed from the normal food hoppers atop the cages. On the first day of testing, the number of food pellets that had been carried into the home cage during the previous night was recorded. Good pellets that were not appreciably eaten were returned to the food bins at the end of the alleys and if necessary additional fresh pellets were added to keep the bins full. Any pellets left in the alley but not in the bins were also replaced (but not counted) and any nesting material in the alley was removed. This procedure was followed for seven consecutive days while the mice had continued access to the alleys and the food. At the end of the test, all mice were again weighed and then destroyed.

A total of 552 mice were tested using the above procedure from January 1973 to March 1974. An attempt was made to randomize the months during which individuals of any one stock were tested. As equal numbers of mice of suitable ages from the same stock were not always available, the test periods necessarily contained disporportionate numbers of mice from various stocks. The only exception to

Table 3.--The Experimental Design for This Study.[a]

Photoperiod	15 Light: 9 Dark								9 Dark: 15 Light							
Acclimation Temperature	7°C				27°C				7°C				27°C			
Test Temperature	7°C		27°C		7°C		27°C		7°C		27°C		7°C		27°C	
Sex	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Days 1																
2																
3																
4																
5																
6																
7																
Number of Animals	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8

[a] Used for all groups except *P. eremicus*, see methods section.

this procedure was the testing of the *P. eremicus* mice which were all tested simultaneously from November to December 1973 because of their unavailability earlier in the study. The small number of avilable *P. eremicus* also necessitated their testing under the same temperature to which they had been acclimated in order to insure an adequate sample size for the comparisons of interest.

Analysis

The dependent variable chosen for analysis within each subspecies was the number of food pellets hoarded on each of the seven days of testing. For comparisons among the various subspecies an average daily hoarding score (i.e., the sum of all pellets hoarded by each mouse divided by 7 days) was used. In both cases the common logarithm of the score plus 1 was taken in order to reduce the variance among scores and to prevent negative scores (Morgan, 1945). In summary, for all comparisons within a subspecies involving days as a factor, the log $(X + 1)$ for each mouse was used; for comparisons among subspecies the log $(\bar{X} + 1)$ was analyzed. The latter procedure results in slightly higher mean scores, but the relationship between them remains the same.

The experimental design for the comparisons within *P. l. noveboracensis*, *P. l. castaneus*, *P. m. bairdi*, and *P. m. blandus* represented a 2x2x2x2x7 factorial arrangement of treatments with one repeated measure for each taxonomic group (2 sexes x 2 acclimation temperatures x 2 photoperiods x 2 test temperatures x 7 days) (Winer, 1962). For the comparisons among these same subspecies the design was a 4x2x2x2x2 factorial (4 subspecies x 2 sexes x 2 acclimation temperatures x 2 photoperiods x 2 test temperatures). The hoarding data for P. eremicus were analyzed in a 2x2 (2 test temperatures x 2 photoperiods). The actual analysis was done on Michigan State University's CDC 6500 computer using the MSU Stat System Version 3.04 Program for Analysis of Variance. Interaction cell means were compared using t tests. Simple correlation coefficients were also calculated using the MSU Stat System's Bastat Program. Homogeneity of variance was tested by using both the Bartlett's Test (Sokal and Rohlf, 1969) and Cochran's Test (Winer, 1962).

The change in body weight of the mice during the experiment was also analyzed. A score for each mouse was obtained by subtracting the initial weight of each mouse from their final weight after testing, and adding 20.00 to this difference in order to prevent negative values. Scores less than 20.00 therefore indicate a loss of weight during the 35 days of the experiment, and scores greater than 20.00 indicate a gain in weight for the same period. The experimental design for all the subspecies of P. maniculatus and P. leucopus again represented a 4x2x2x2x2 factorial arrangement of treatments (4 subspecies x 2 sexes x 2 acclimation temperatures x 2 photoperiods x 2 test temperatures). For the analysis of weight change in P. eremicus, the design was simply a 2x2 factorial (2 temperatures x 2 photoperiods) because of the small sample size.

RESULTS

The following description of the results has been divided into three basic parts to coincide with my three original hypotheses. First, the effects of the treatments on each subspecies will be examined, followed by comparisons among all the subspecies. Special emphasis will be placed on comparisons between the northern and southern subspecies of both P. leucopus and P. maniculatus. Finally the results of the analysis of the weight changes under the various experimental conditions will be examined. The complete analysis of variance tables are given in the appendix.

Comparisons Within Each Subspecies

The analysis of variance of the daily hoarding scores of P. l. noveboracensis indicated a highly significant main effect of test temperature ($F=6.39$, $df=1/112$, $p=0.01$), with mice hoarding more under 7°C than under 27°C (Table 4). Neither photoperiod nor any of the other main effects between subjects gave a significant F value. However, the within subjects factor of days was highly significant ($F=12.76$, $df=6/672$, $p<0.001$) and is graphed in Figure 1.

Table 4.--Mean Daily Log Hoarding Scores for the Main Effects of Sex, Acclimation Temperature, Photoperiod, and Test Temperature. Each Mean Represents the Average of 64 Animals, Except in *P. eremicus* in Which Only 20 Animals Are Represented. (*Indicates the Two Means are Significantly Different.)

	P. l. noveb.	*P. l. castaneus*	*P. m. bairdi*	*P. m. blandus*	*P. eremicus*
Sex					
Male	.5057	.4468	.5528	.4154	. .
		*			
Female	.5830	.5550	.5470	.3989	. .
Accl. Temp.					
7°C	.5815	.4886	.5818	.4387	. .
27°C	.5072	.5131	.5180	.3756	. .
Photoperiod					
Short	.5765	.4780	.6161	.4381	.7998
			*		
Long	.5122	.5237	.4836	.3762	.5666
Test Temp.					
7°C	.6268	.4754	.5470	.3400	.7067
	*			*	
27°C	.4619	.5264	.5527	.4743	.6597

Figure 1. Mean log hoarding scores for the two subspecies of both *P. leucopus* and *P. maniculatus* on each of the seven test days. Each point represents the average of 128 animals over all experimental conditions.

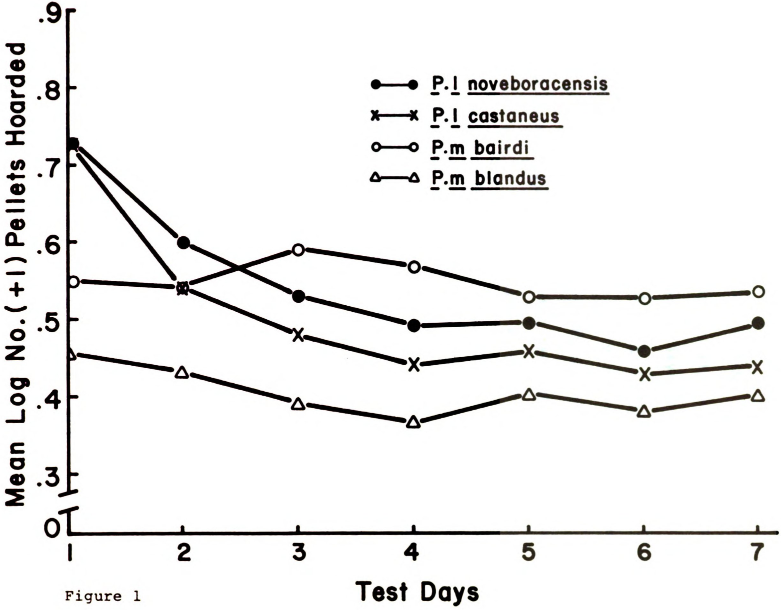
Mean Log No.(+1) Pellets Hoarded
.9
.8
.7
.6
.5
.4
.3
0
1
2
3
4
5
6
7
Test Days
●—● P.l noveboracensis
x—x P.l castaneus
o—o P.m bairdi
△—△ P.m blandus

Figure 1

The scores for the first two days were typically the highest and then leveled off at a lower level for the remaining days of testing. None of the interactions either between or within subjects was significant, although the interaction of test temperature x days was graphed (Figure 2) for comparison with _P_. _l_. _castaneus_.

The analysis of the mean daily hoarding scores for _P_. _l_. _castaneus_ revealed a significant main effect of sex (F=4.03, df=1/112, p=0.05), with females hoarding more than males (Table 4). Both the main effects of temperature and photoperiod were nonsignificant, although the within subject factor of days was again significant (F=23.19, df=6/672, p<0.001). As already pointed out for _P_. _l_. _noveboracensis_, the mean daily hoarding scores for _P_. _l_. _castaneus_ were highest in the first two days of testing with a leveling off in the remaining five days (Figure 1). There was also a highly significant interaction between days and test temperature (F=4.52, df=6/672, p<0.001; Figure 3). On day 1 of testing, mice under 7°C, hoarded significantly more than those under 27°C (Table 5). However, on all subsequent days, more hoarding was done under the warmer temperature with the difference becoming significant on the last three days of testing.

The interaction of sex x acclimation temperature in _P_. _l_. _castaneus_ was also significant (F=6.31, df=1/112, p=0.01; Figure 4a). After acclimation to 7°C, females hoarded significantly more than males (t=3.20, df=62,

Figure 2. Mean daily log hoarding scores for *P. l. noveboracensis* under the two test temperatures. Each point represents the average of 64 animals.

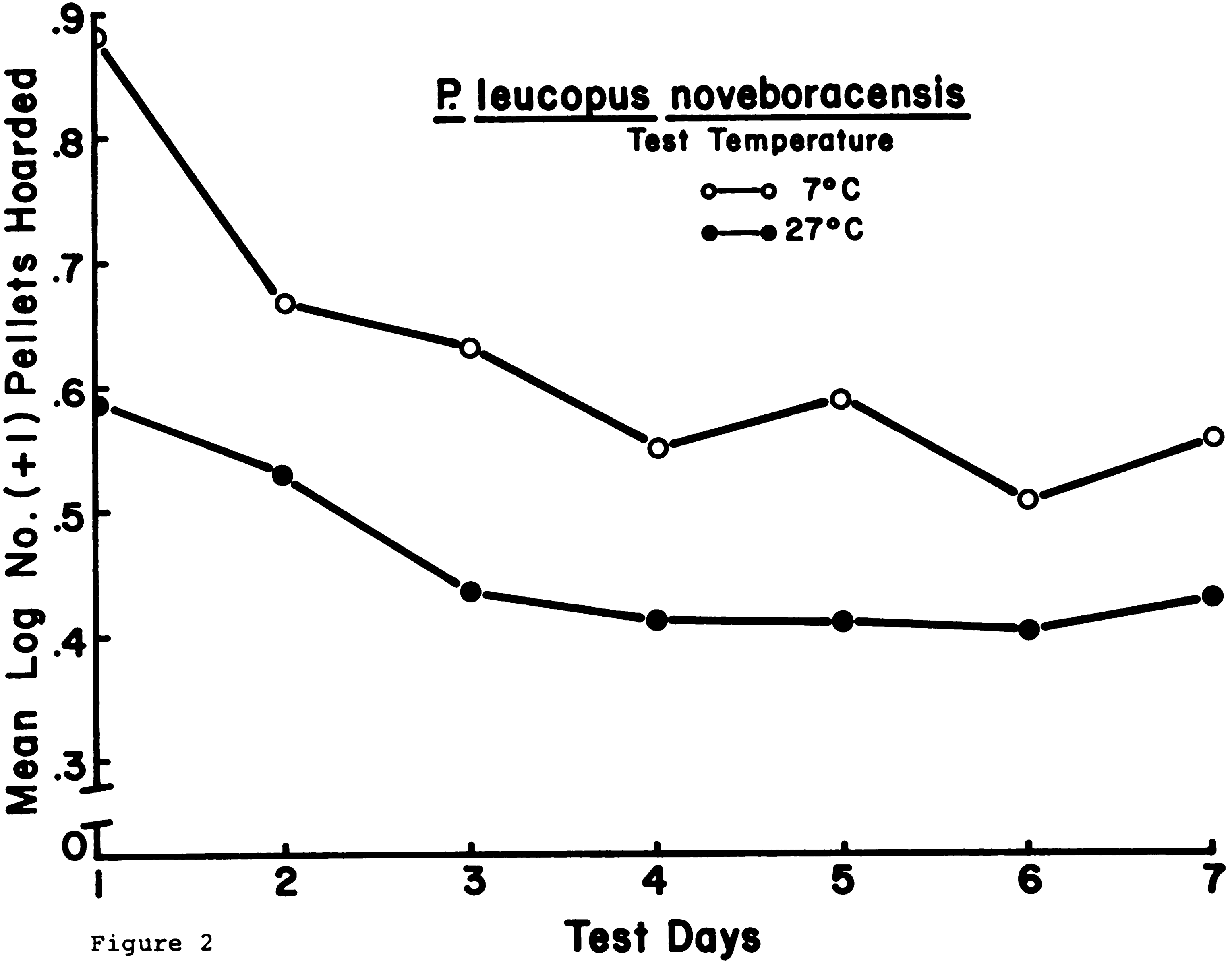
P. leucopus noveboracensis
Test Temperature
○—○ 7°C
●—● 27°C
Mean Log No. (+1) Pellets Hoarded
.9
.8
.7
.6
.5
.4
.3
0
1
2
3
4
5
6
7
Test Days

Figure 2

Figure 3. Mean daily log hoarding scores for *P. l. castaneus* under the two test temperatures. Each point represents the average of 64 animals.

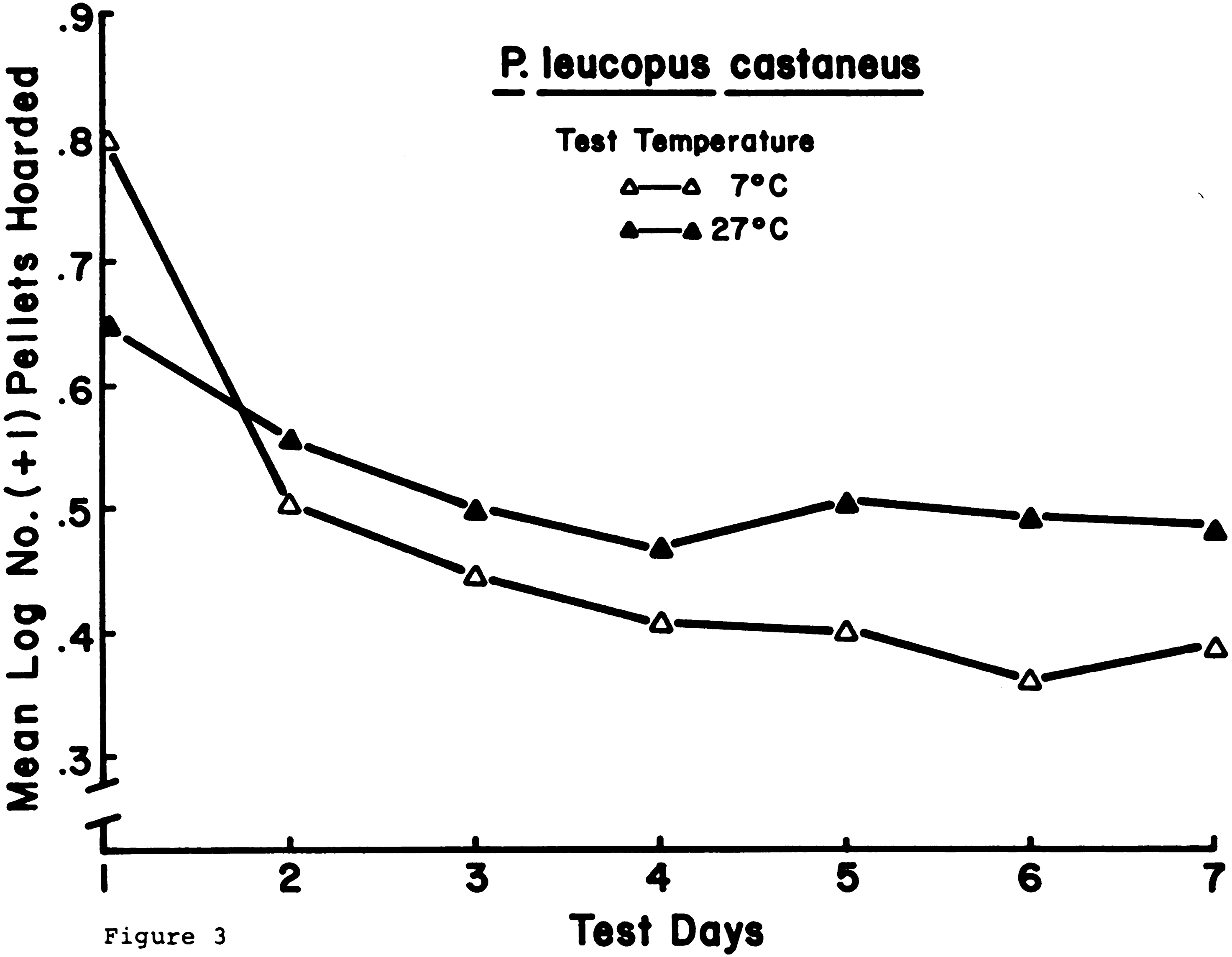
P. leucopus castaneus
Test Temperature
△—△ 7°C
▲—▲ 27°C
Mean Log No. (+1) Pellets Hoarded
.9
.8
.7
.6
.5
.4
.3
1
2
3
4
5
6
7
Test Days

Figure 3

Table 5.--Student's t Tests of the Difference Between the Mean Daily Log Hoarding Scores Under 7°C and the Mean Scores Under 27°C for Both Subspecies of *P. leucopus* and *P. maniculatus*. Negative Values Indicate More Hoarding Was Done Under 27°C Than Under 7°C. The Level of Significance is Given in Parenthesis Beside Each t Value; df=126.

	P. l. noveboracensis		*P. l. castaneus*	
Days	$\bar{X}$ Difference	t Value	$\bar{X}$ Difference	t Value
1	.2874	5.38(.001)	.1526	3.42(.01)
2	.1401	2.62(.02)	-.0576	1.29(N.S.)
3	.1879	3.51(.001)	-.0529	1.19(N.S.)
4	.1357	2.53(.02)	-.0625	1.40(N.S.)
5	.1700	3.18(.01)	-.1107	2.49(.02)
6	.0962	1.80(.10)	-.1358	3.05(.01)
7	.1291	2.41(.02)	-.0901	2.02(.05)

	P. m. bairdi		*P. m. blandus*	
Days	$\bar{X}$ Difference	t Value	$\bar{X}$ Difference	t Value
1	.1234	2.38(.05)	.0433	.86(N.S.)
2	-.0247	.48(N.S.)	-.1535	3.04(.01)
3	.0444	.86(N.S.)	-.1972	3.91(.001)
4	.0229	.44(N.S.)	-.2086	4.13(.001)
5	-.0951	1.83(.10)	-.1602	3.17(.01)
6	-.0476	.92(N.S.)	-.1674	3.31(.01)
7	-.0629	1.21(N.S.)	-.0963	1.91(.10)

Figure 4. Mean daily log hoarding scores of P. l. castaneus for the significant interactions of (a) sex x acclimation temperature, and (b) photoperiod x acclimation temperature. Each point represents the average of 32 animals.

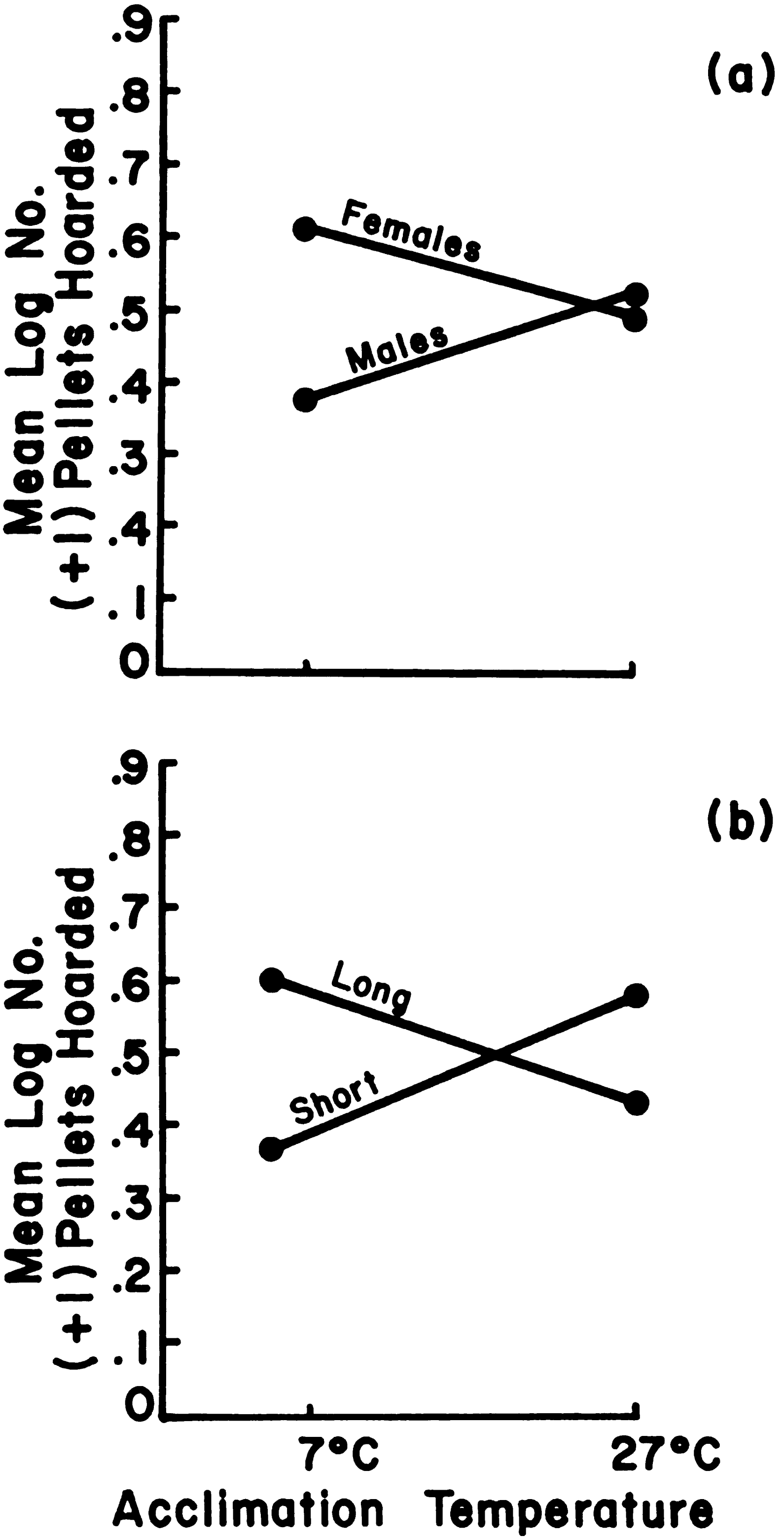
.9
.8
.7
.6
.5
.4
.3
.4
.1
0
Mean Log No.
(+1) Pellets Hoarded
(a)
Females
Males
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
Mean Log No.
(+1) Pellets Hoarded
(b)
Long
Short
7°C
27°C
Acclimation Temperature

Figure 4

p=0.01), although after 27°C there was no significant difference between their scores. The interaction of acclimation temperature x photoperiod was likewise highly significant (F=11.52, df=1/112, p=0.001; Figure 4b). Under a short photoperiod, *P. l. castaneus* hoarded significantly more after acclimation to 27°C than after 7°C (t=2.72, df=62, p=0.01). However, under a long photoperiod just the opposite was true (t=2.08, df=62, p=0.05). Further examination of this interaction will follow when *P. l. castaneus* and *P. l. noveboracensis* are compared with each other.

The analysis of variance of the hoarding scores of *P. m. bairdi* showed that photoperiod had a significant main effect (F=4.01, df=1/112, p=0.05), with mice hoarding more under a short day photoperiod than under a long day one (Table 4). There was, however, no significant difference in the rate of their hoarding (i.e., the log number of pellets hoarded plus 1 divided by the number of hours of darkness available to hoard them) in contrast to the amount under either photoperiod ($\bar{X}$ rate=.0411 per hr. under short, versus $\bar{X}$=.0537 per hr. under long). The main effect of test temperature was non-significant. Unlike both *P. l. noveboracensis* and *P. l. castaneus*, *P. m. bairdi* did not differ in hoarding across days. The interaction of test temperature x days was, however, on the borderline of significance (F=2.06, df=6/672, p=0.056) and is graphed in Figure 5. There was a significant difference between the scores for mice tested under 7°C and those under 27°C only

Figure 5. Mean daily log hoarding scores for *P. m. bairdi* under the two test temperatures. Each point represents the average of 64 animals.

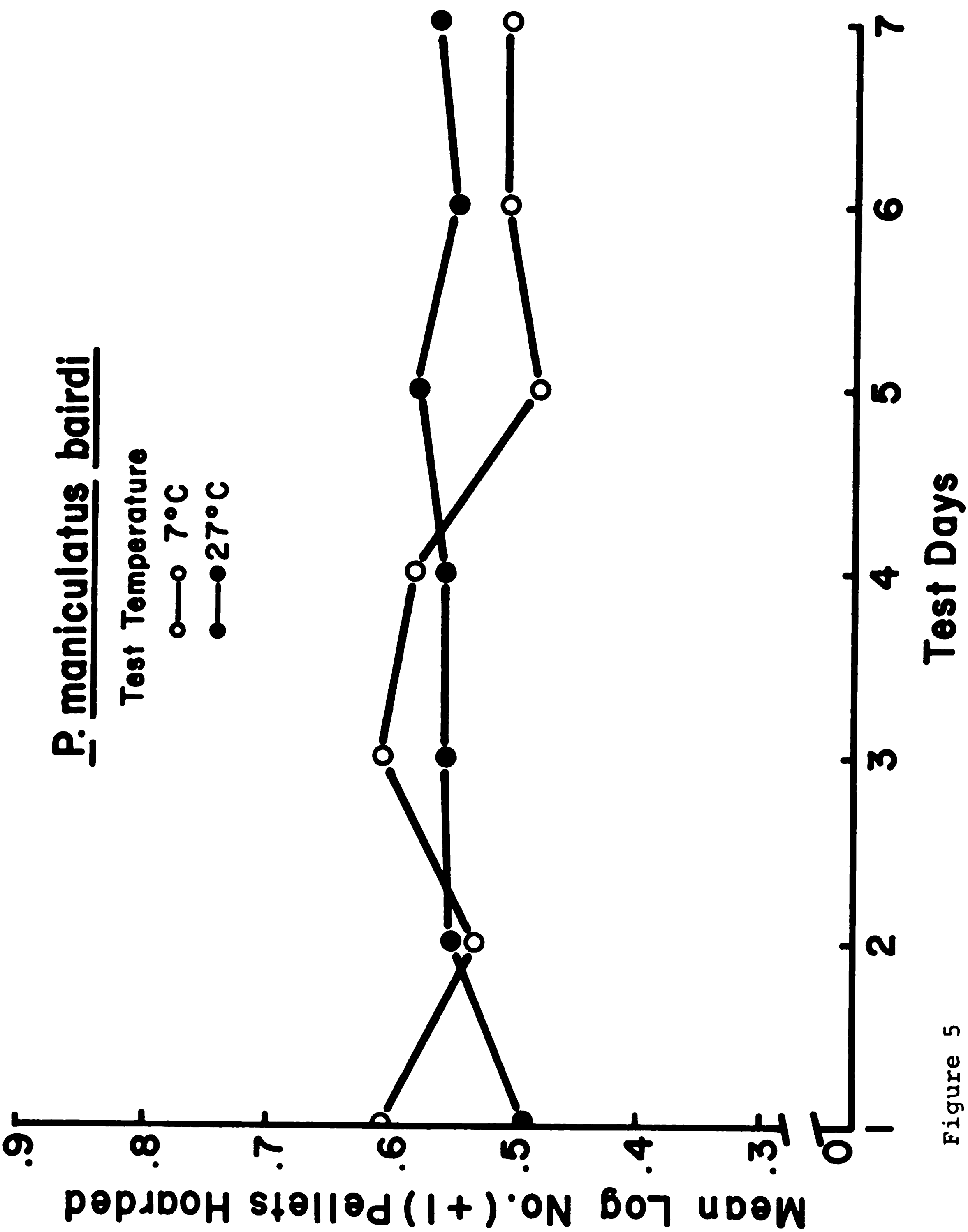
P. maniculatus bairdi
Test Temperature
7°C
27°C
Mean Log No. (+1) Pellets Hoarded
.9
.8
.7
.6
.5
.4
.3
0
1
2
3
4
5
6
7
Test Days

Figure 5

on the first day of testing (Table 5). None of the other interactions for *P. m. bairdi* was significant.

The results of the analysis of variance for *P. m. blandus* disclosed that test temperature had a significant main effect (F=6.77, df=1/112, p=0.01), with mice tested under 27°C hoarding more than those under 7°C (recall that this is the exact opposite of what was found for *P. l. noveboracensis*). Like *P. m. bairdi*, there was no significant effect across days, although the interaction of test temperature x days was highly significant (F=2.92, df=6/672, p=0.008; Figure 6). On every test day but the first, *P. m. blandus* hoarded more under the warm 27°C temperature than under the cold 7°C temperature (Table 5). This is very similar to what was found for *P. l. castaneus*. No attempt was made to interpret the significant four way interaction of sex x acclimation temperature x photoperiod x days (F=2.21, df=6/672, p=0.05).

The analysis of variance of the mean hoarding scores for *P. eremicus eremicus* indicated that both main effects of temperature and photoperiod were non-significant, as was their interaction. The within subjects factor of days was not analyzed because of the small sample size and simpler experimental design (see "Methods" section).

Comparisons Among Subspecies

The analysis of variance for the combined hoarding scores for all subspecies except *P. eremicus* indicated a

Figure 6. Mean daily log hoarding scores for *P. m. blandus* under the two test temperatures. Each point represents the average of 64 animals.

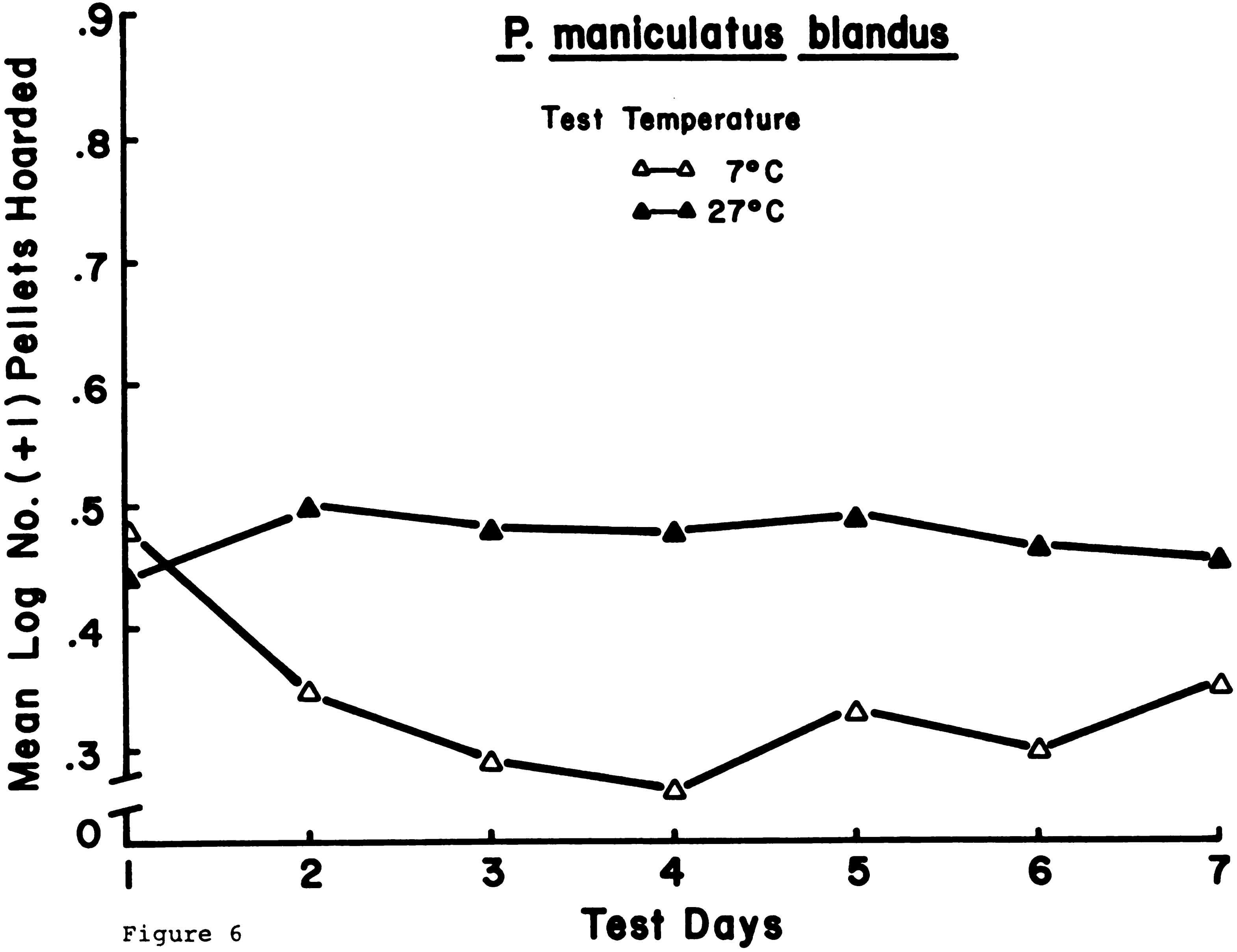
P. maniculatus blandus
Test Temperature
△—△ 7°C
▲—▲ 27°C
Mean Log No. (+1) Pellets Hoarded
.9
.8
.7
.6
.5
.4
.3
0
1
2
3
4
5
6
7
Test Days

Figure 6

highly significant main effect of subspecies (F=4.41, df=3/448, p=0.005). The highest mean hoarding score was for *P. l. noveboracensis*, with *P. m. bairdi*, *P. l. castaneus*, and *P. m. blandus* following in that order (Figure 7). Comparisons of these means using the Student-Newman-Keul's Test and a lsd test for the mean of *P. eremicus* (because of its much smaller sample size) indicated that *eremicus* hoarded significantly more food than both *P. l. castaneus* and *P. m. blandus* (Table 6). The mean scores for *P. l. noveboracensis*, *P. m. bairdi*, and *P. l. castaneus* were all significantly greater than the mean for *P. m. blandus*, but were not significantly different from each other.

Table 6.--Multiple Comparisons Among the Mean Log Hoarding Scores (i.e., Log ($\bar{X}$+1) for Each Mouse)±1S.E. for All Subspecies of *Peromyscus* Used in This Study. Any Two Means Not Joined by the Same Vertical Line Are Significantly Different at the .05 Level.

Subspecies	Mean ±1 S.E.		
P. eremicus	.7123 ± .0586	│	│
P. l. noveboracensis	.6435 ± .0360	│	│
P. m. bairdi	.6331 ± .0359	│	│
P. l. casataneus	.5794 ± .0299		│
P. m. blandus	.4964 ± .0290		

The interaction of subspecies x test temperature was also highly significant (F=4.85, df=3/448, p=0.002; Figure 8). Consistent with my original hypothesis, *P. l. noveboracensis* hoarded significantly more than *P. l.*

Figure 7. Comparisons of the mean log hoarding scores per test day for all five stocks of Peromyscus studied. Each bar represents the average for 128 animals, except for P. eremicus in which 40 animals are represented. The vertical lines are ±1 standard error.

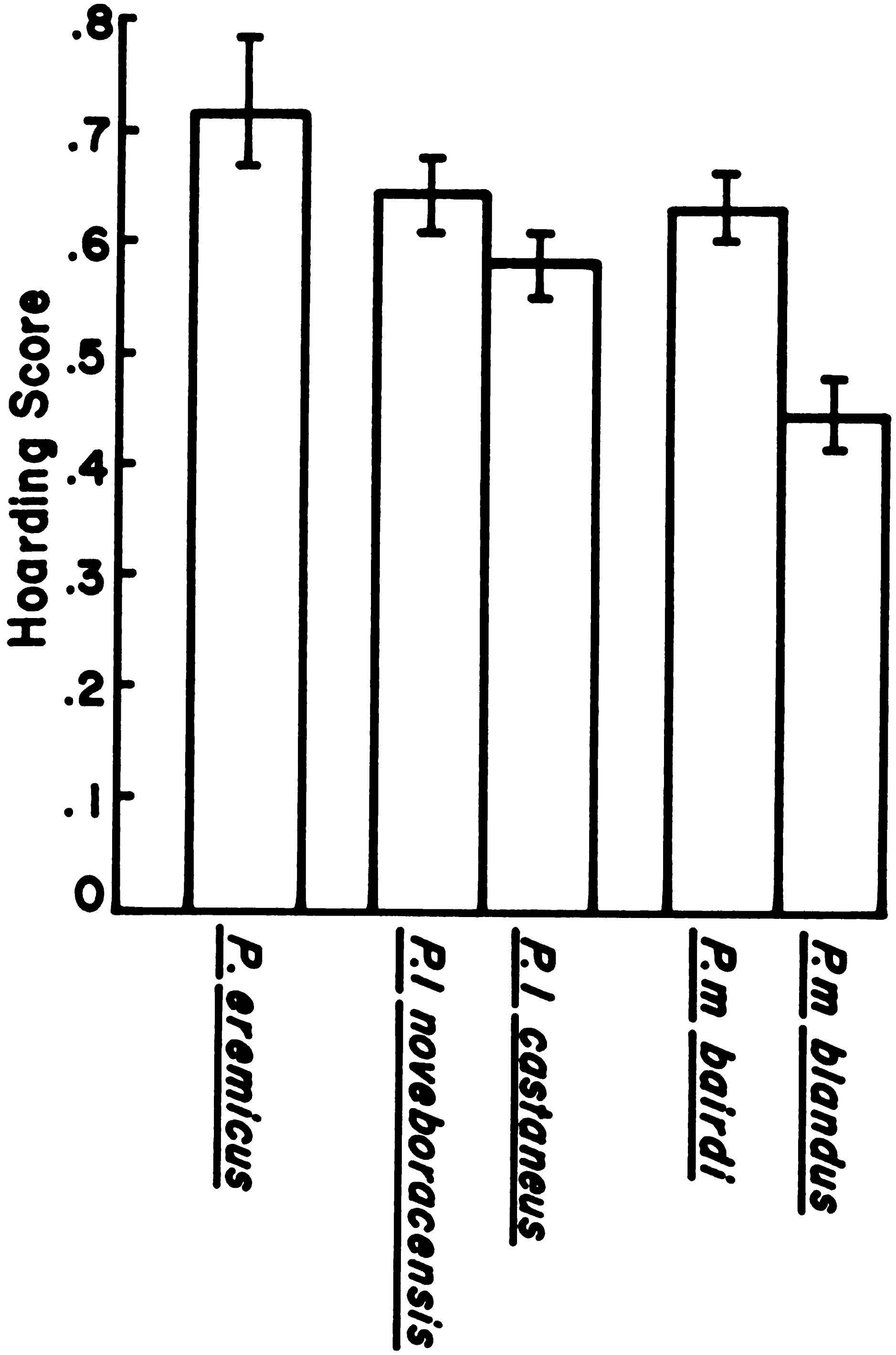
Hoarding Score
.8
.7
.6
.5
.4
.3
.2
.1
0
P. eremicus
P.l noveboracensis
P.l castaneus
P.m bairdi
P.m blandus

Figure 7

Figure 8. Graphs of the mean log hoarding scores per test day for the interaction of subspecies x test temperature. Each point represents the average of 64 animals.

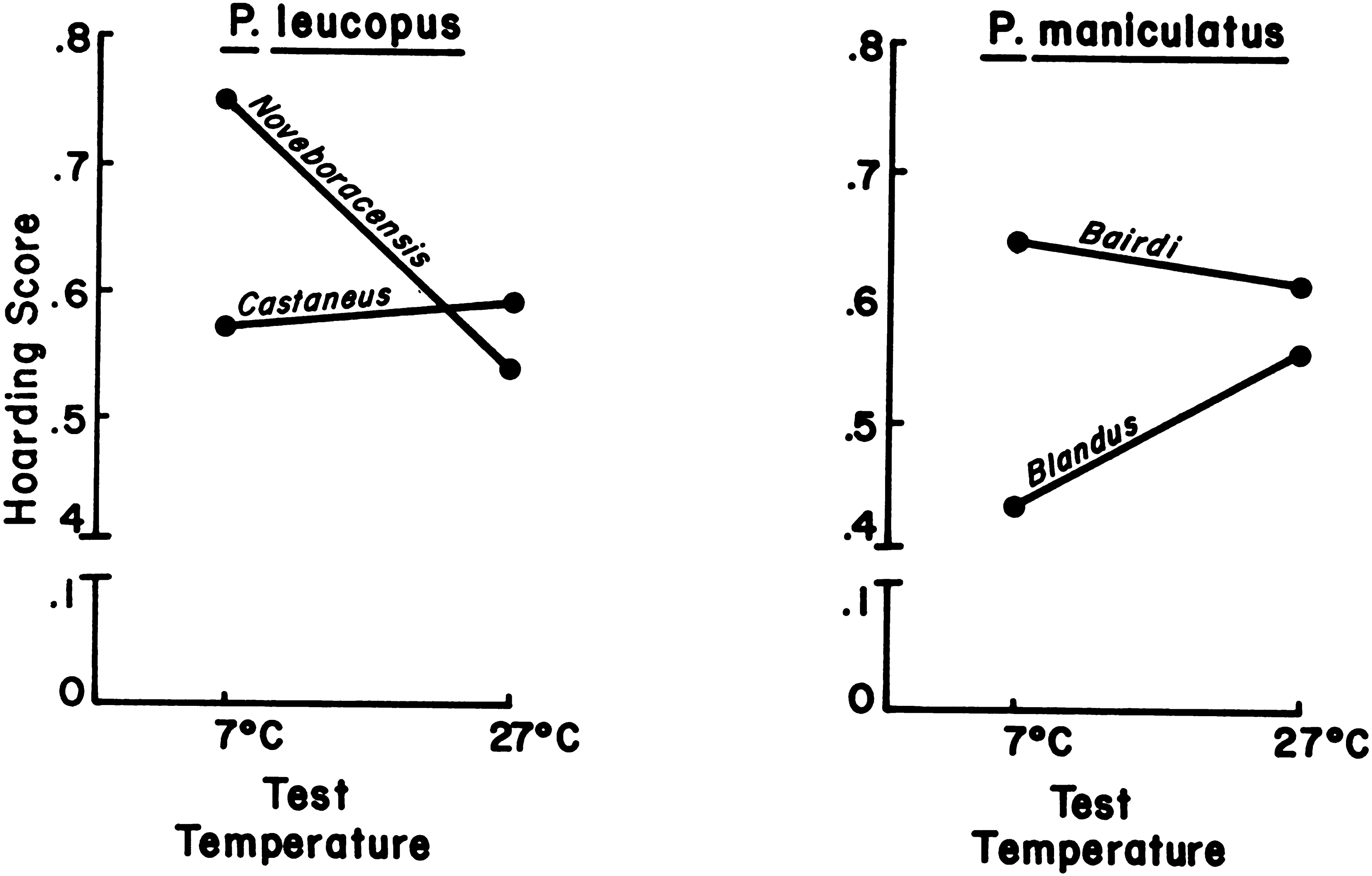
P. leucopus
Hoarding Score
.8
.7
.6
.5
4
.1
0
Noveboracensis
Castaneus
7°C
27°C
Test Temperature
P. maniculatus
.8
.7
.6
.5
.4
.1
0
Bairdi
Blandus
7°C
27°C
Test Temperature

Figure 8

castaneus under a test temperature of 7°C (t=2.79, df=126, p=0.01). As might be predicted, there was no difference between the subspecies under the warm, 27°C, test temperature. As already pointed out in the preceding section, *P. l. noveboracensis* hoarded significantly more under the cold test temperature than it did under the warm temperature. In contrast, test temperature had no significant effect on the hoarding scores of *P. l. castaneus*.

Comparisons of the hoarding scores for both subspecies of of *P. maniculatus* under the two test temperatures (Figure 8) revealed that under 7°C, *P. m. bairdi* also hoarded significantly more than its southern subspecies, *P. m. blandus* (t=3.36, df=126, p=0.01). The difference between their scores under 27°C was not significant. As previously pointed out, test temperature had no effect within *P. m. bairdi*, although it did within *P. m. blandus*.

The interactions of subspecies x acclimation temperature x photoperiod (F=3.44, df=3/448, p=0.02) and subspecies x sex x acclimation temperature x photoperiod (F=2.76, df=3/448, p=0.05) were both significant. Only the three way interaction was examined because no hypotheses had been formulated to explain possible interactions with sex, and secondly, the level of significance was greater in the three way interaction than in the four way interaction. The cell means for this interaction are graphed in Figures 9 and 10. As illustrated in Figure 9a, under a short day photoperiod and after acclimation to cold temperature,

Figure 9. Graphs of the mean log hoarding scores per test day for the significant interaction of subspecies x photoperiod x acclimation temperature in *P. leucopus* under (a) a short photoperiod, and (b) a long photoperiod. Each point represents the average of 32 animals.

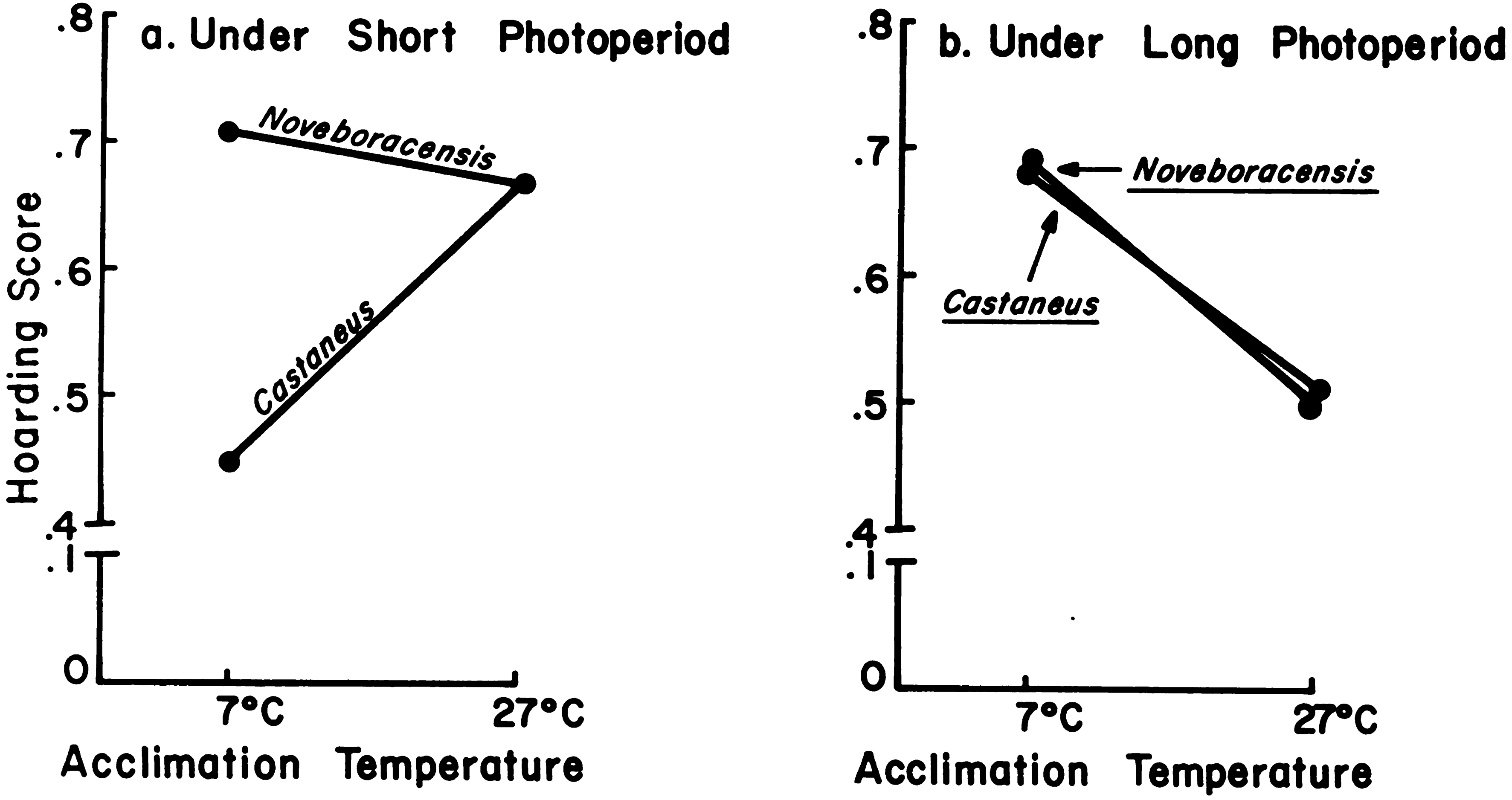

Figure 9

P. leucopus

Figure 10. Graphs of the mean log hoarding scores per test day for the significant interaction of subspecies x photoperiod x acclimation temperature in P. maniculatus under (a) a short photoperiod, and (b) a long photoperiod. Each point represents the average of 32 animals.

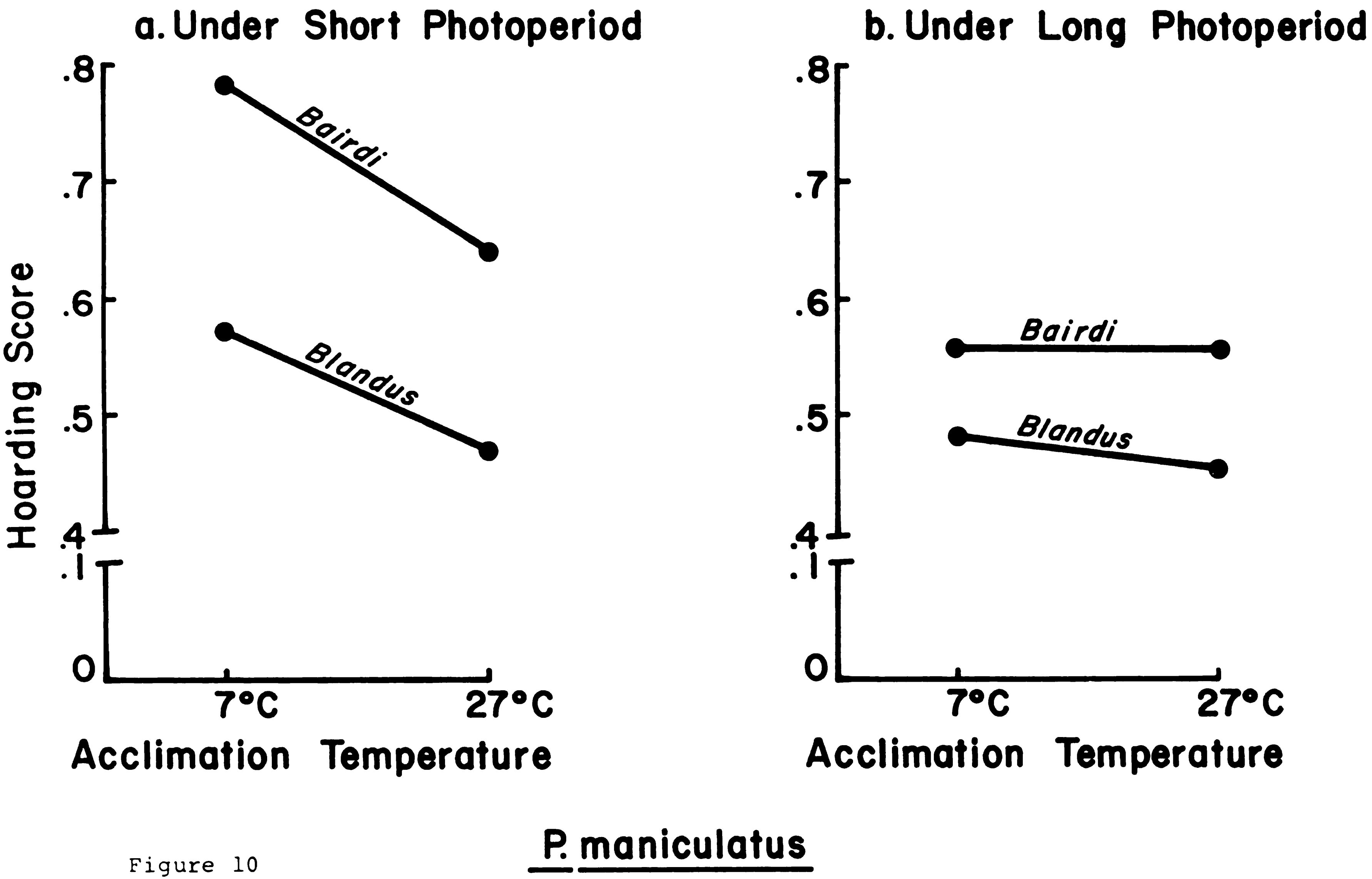
a. Under Short Photoperiod
b. Under Long Photoperiod
Hoarding Score
.8
.7
.6
.5
.4
.1
0
Bairdi
Blandus
7°C
27°C
Acclimation Temperature
P. maniculatus

Figure 10

P. l. noveboracensis hoarded significantly more than *P. l. castaneus* (t=2.93, df=62, p=0.01). After acclimation to the warm temperature (27°C) no difference was found between their scores. *P. l. castaneus* also hoarded more after acclimation to 27°C than after acclimation to 7°C (t=2.65, df=62, p=0.02), while the hoarding of *P. l. noveboracensis* was apparently unaffected by prior temperature acclimation under this photoperiod. Under a long day photoperiod (Figure 9b) previous temperature acclimation had more of an effect on the hoarding of both subspecies. Although both subspecies tended to hoard more after acclimation to 7°C, the effect was only significant in *P. l. noveboracensis* (t=2.07, df=62, p=0.05).

Figure 10a illustrates the means for both subspecies of *P. maniculatus* under a short day photoperiod. As in *P. leucopus*, the northern subspecies, *P. m. bairdi*, hoarded significantly more than the southern subspecies, *P. m. blandus*, after acclimation to 7°C (T=2.22, df=62, p=0.05). However, the difference between their scores after acclimation to 27°C was not significant at the .05 level (t=1.91, df=62, p=0.10). Under a long photoperiod (Figure 10b), there was no significant difference between any of the means for both *P. m. bairdi* and *P. m. blandus*.

My original hypotheses (see "Introduction") suggested several *a priori* comparisons that could be made independently of the AOV design and regardless of the significance level of the F values obtained (Steel & Torrie, 1960). The means of mice tested under 7°C and a short photoperiod were compared individually by subspecies with the means for mice tested under 27°C and a long photoperiod (Tables 7 and 8). Consistent with my original hypotheses, both *P. l. noveboracensis* and *P. m. bairdi* hoarded significantly more under a short day photoperiod and cold temperature than under a long day photoperiod and a warm temperature. The means within *P. l. castaneus*, *P. m. blandus*, and *P. eremicus* under these two test conditions were not significantly different.

The simple correlation coefficients between the mean hoarding scores for all subspecies and their age, initial weight, weight change, and final weight are given in Table 9. There were no significant correlations with age since this variable was fairly well controlled for in this study. There were also no significant correlations with either initial or final weight in any of the subspecies. There was, however, a significant correlation between the mean hoarding score of *P. m. bairdi* and their weight change (r=-0.21, p=0.05). The correlation indicated that there was a tendency for hoarding scores to increase slightly with loss in weight in this subspecies.

Analysis of Weight Changes

The combined analysis of variance of the weight changes of all the subspecies except *P. eremicus* revealed that the main effects of both acclimation temperature (F=6.40,

Table 7.--Mean Log Hoarding Scores (i.e., Log ($\bar{X}$+1) for Each Mouse) for the Five Stocks of *Peromyscus* Under All Possible Combinations of Test Temperature and Photoperiod. Each Mean Represents the Average of 32 Animals, Except in *P. eremicus* in Which 10 Animals are Represented. Means in Parenthesis are for Mice Acclimated and Tested at the Same Temperature.

Photoperiod	Test Temperature	
	7°C	27°C
P. l. noveboracensis		
Short	.7705(.7541)	.6064(.5450)
Long	.7320(.7955)	.4651(.3407)
P. l. castaneus		
Short	.5239(.3922)	.5895(.6802)
Long	.6207(.6615)	.5835(.4657)
P. m. bairdi		
Short	.7004(.7179)	.7114(.5943)
Long	.6004(.5837)	.5203(.5049)
P. m. blandus		
Short	.4078(.4344)	.6316(.5502)
Long	.4621(.4675)	.4842(.4697)
*P. eremicus**		
Short	.7596	.6872
Long	.8346	.5678

*For *P. eremicus*, all mice were tested at the same temperature to which they had been acclimated.

Table 8.--Planned Comparisons of the Mean Log Hoarding Scores (i.e., Log ($\bar{X}$+1) for Each Mouse) of Mice Tested Under a Short Photoperiod and 7°C With Those of Mice Tested Under a Long Photoperiod and 27°C.

Subspecies	$\bar{X}$(7°+short)	$\bar{X}$(27°+long)	t Value(prob.)[a]
P. l. noveboracensis	.7705	.4651	3.60(.001)
P. l. castaneus	.5239	.5835	.66(N.S.)
P. m. bairdi	.7004	.5203	1.99(.05)
P. m. blandus	.4078	.4842	1.14(N.S.)
P. eremicus	.7596	.5678	1.15(N.S.)

[a] df=62 for all subspecies except *P. eremicus* in which df=18.

Table 9.--Correlation Coefficients Between the Hoarding Scores of All Five Stocks of *Pereomyscus* and Their Age, Initial Weight, Weight Change, and Final Weight (*Indicates Significance at the .05 Level).

	P. l. noveboracensis	*P. l. castaneus*	*P. m. bairdi*	*P. m. blandus*	*P. eremicus*
Age	-.070	-.024	.050	-.099	-1.96
Initial Weight	.074	.096	.065	.028	-1.81
Weight Change	-.009	-.066	-.205*	.042	.028
Final Weight	.088	.081	-.116	.075	-.187

df=1/448, p=0.01) and subspecies (F=22.68, df=3/448, p=0.001) were significant as was their interaction (F=5.14, df=3/448, p=0.002; Figure 11). Although both _P_. _l_. _noveboracensis_ and _P_. _l_. _castaneus_ lost weight under the two acclimation temperatures, they lost significantly more weight under 7°C than under 27°C (Table 10). There was also a significant correlation in both subspecies between their initial weight and weight change (r=-0.62, p=0.01, for _P_. _l_. _noveboracensis_; r=-0.58, p=0.01, for _P_. _l_. _castaneus_) indicating that the greater the initial weight the larger the loss. The negative sign should be ignored as it is a result of the method in which the weight changes were scored (see "Methods" section). The change in weight of _P_. _eremicus_ was also significantly different under the two acclimation temperatures (F=7.98, df=1/36, p=0.008) with individuals losing weight if acclimated to 7°C, but gaining weight under 27°C. The correlation between initial weight and weight change was also significant (r=-0.51, p=0.01). The difference in weight change for both _P_. _m_. _bairdi_ and _P_. _m_. _blandus_ were non-significant (Table 10), but again the correlation between initial weight and weight change was significant (r=-0.56, p=0.01 for _P_. _m_. _bairdi_; r=-0.61, p=0.01 for _P_. _m_. _blandus_).

The interaction of subspecies x sex x acclimation temperature was also significant (F=2.74, df=3/448, p=0.05) and is graphed in Figure 12. Comparisons of the means using t tests indicated that it was the females of

Figure 11. Graphs of the mean weight changes for all five stocks of *Peromyscus* after acclimation to either 7°C or 27°C.

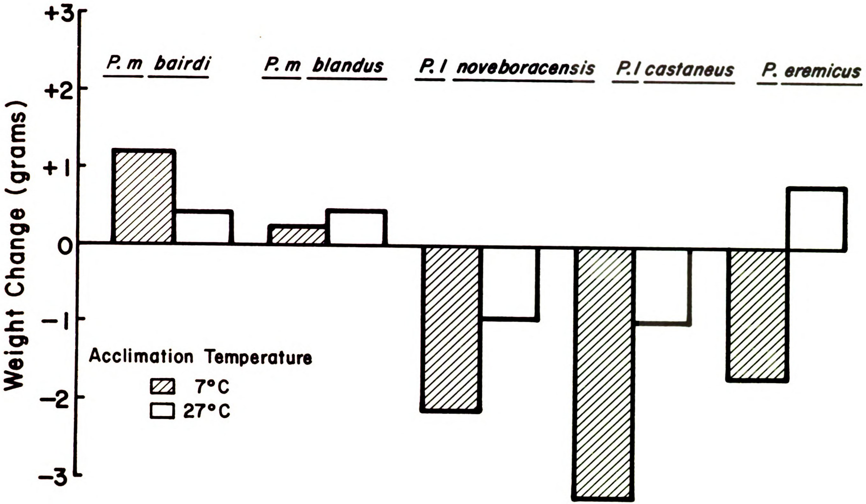
+3
+2
+1
0
−1
−2
−3
Weight Change (grams)
P. m bairdi
P. m blandus
P. l noveboracensis
P. l castaneus
P. eremicus
Acclimation Temperature
▨ 7°C
☐ 27°C

Figure 11

Figure 12. Graphs of the mean weight changes for the significant interaction of subspecies x sex x acclimation temperature.

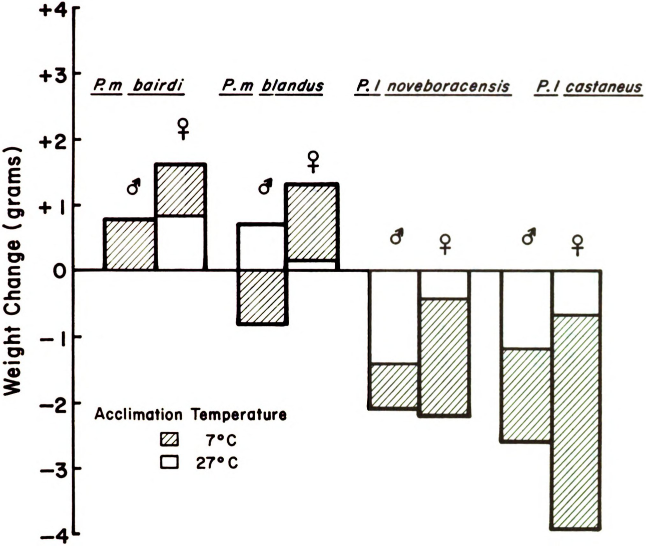
+4
+3
+2
+1
0
−1
−2
−3
−4
Weight Change (grams)
P.m bairdi
P.m blandus
P.l noveboracensis
P.l castaneus
♂
♀
♂
♀
♂
♀
♂
♀
Acclimation Temperature
▨ 7°C
☐ 27°C

Figure 12

Table 10.--Student's t Test Comparisons of the Mean Weight Changes (In Grams) After Acclimation to 7°C and 27°C for the Significant Interaction of Subspecies x Acclimation Temperature.

Subspecies	$\bar{X}$(7°C)	$\bar{X}$(27°C)	t Value(prob.)
P. l. noveboracensis	-2.16	-0.92	2.09(.05)
P. l. castaneus	-3.26	-0.92	3.94(.001)
P. m. bairdi	+1.20	+0.41	1.35(N.S.)
P. m. blandus	+0.24	+0.46	.38(N.S.)
P. eremicus	-1.72	+0.79	2.83(.01)

both subspecies of *P. leucopus* which accounted for the significantly greater loss in weight under the colder of the two acclimation temperatures (t=2.13, df=62, p=0.05 for female *P. l. noveboracensis*; t=3.88, df=62, p=0.001 for female *P. l. castaneus*). The losses in weight observed in males of both of these subspecies were not significantly different under either of the two acclimation temperatures. Consistent with what was mentioned above, acclimation temperature also had no significant effect within either sex of *P. m. bairdi* or *P. m. blandus*, although female *P. m. blandus* gained weight under 7°C, while males lost weight under the same temperature (t=2.48, df=62, p=0.01).

The interaction of subspecies x sex x photoperiod was significant (F=3.53, df=3/448, p=0.02) and the means are graphed in Figure 13. Photoperiod had no significant effect on weight change in either subspecies of *P. leucopus*

Figure 13. Graphs of the mean weight changes for the significant interaction of subspecies x sex x photoperiod.

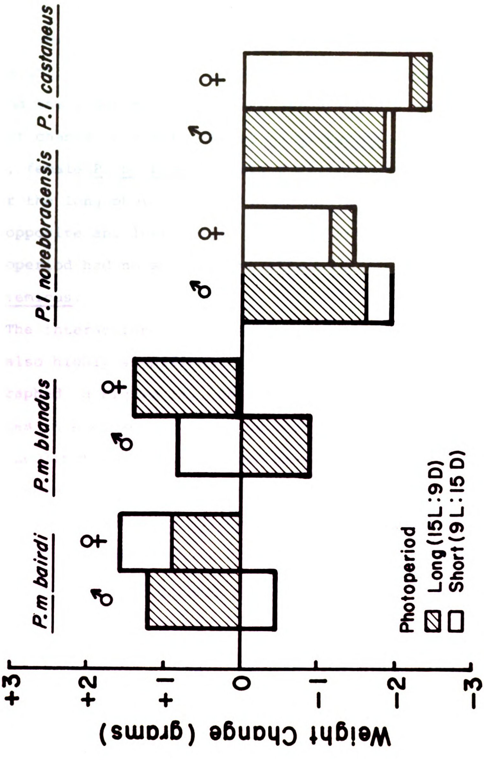
P.m bairdi
P.m blandus
P.l noveboracensis
P.l castaneus
♂
♀
♂
♀
♂
♀
♂
♀
Weight Change (grams)
+3
+2
+1
0
−1
−2
−3
Photoperiod
▨ Long (15L:9D)
☐ Short (9L:15D)

Figure 13

but did interact with sex in both *P. m. bairdi* and *P. m. blandus*. Under a short photoperiod female *P. m. bairdi* gained weight, whereas males showed a small average loss in weight (t=2.35, df=62, p=0.05). Under a long photoperiod there was no significant difference in the amount of weight change in either sex of *P. m. bairdi*. On the other hand, female *P. m. blandus* gained significantly more weight under the long photoperiod than males, which reacted just the opposite and lost weight (t=2.72, df=62, p=0.01). Photoperiod had no significant effect on weight change in *P. eremicus*.

The interaction of subspecies x sex x test temperature was also highly significant (F=5.29, df=3/448, p=0.001) and is graphed in Figure 14. One would normally expect that changes in body weight would be more influenced by the 4 week acclimation period to each temperature than by the final seven days of testing. This was in general true for all groups except *P. m. blandus*, which did show some significant adjustment in their weight during the seven days of the testing. *P. m. blandus* males which had lost weight during acclimation to 7°C, tended to gain it back if tested at 27°C. Likewise, females which had gained weight under 7°C, tended to lose it if tested at 27°C. The same sort of changes went on in the other groups but not to the same extent. Apparently more than seven days is needed before an adjustment is complete in these groups and therefore Figure 14 may be misleading. The weight changes of

Figure 14. Graphs of the mean weight changes for the significant interaction of subspecies x sex x test temperature.

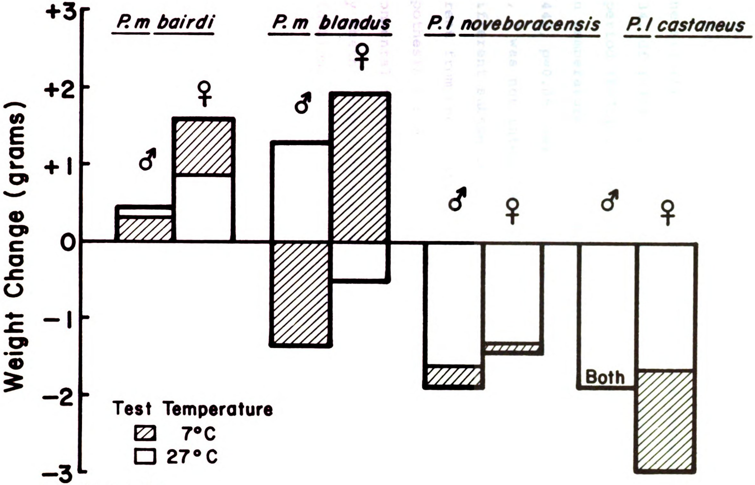
Weight Change (grams)
+3
+2
+1
0
−1
−2
−3
P.m bairdi
P.m blandus
P.l noveboracensis
P.l castaneus
♂
♀
♂
♀
♂
♀
♂
♀
Both
Test Temperature
▨ 7°C
☐ 27°C

Figure 14

all mice under the various combinations of acclimation temperature and test temperature are shown in Table 11, which serves to illustrate this point.

The significant interactions of sex x test temperature (F=4.34, df=1/448, p=0.05), sex x acclimation temperature x photoperiod (F=7.11, df=1/448, p=0.008), and sex x acclimation temperature x photoperiod x test temperature (F=4.38, df=1/448, p=0.05) were not examined for several reasons. First, I was not interested in "average" changes over all the different subspecies, but only those significantly different from one subspecies to the next. Second, I had no hypothesis concerning weight change under various environmental conditions. The relationship of interest, namely whether hoarding and weight change are related in some fashion, will be discussed in the next section.

Table 11.--Weight Changes (In Grams) of Mice Under All Combinations of Acclimation and Test Temperature.

Acclimation Temperature	Test Temperature 7°C	Test Temperature 27°C	$\bar{X}$
<u>P</u>. <u>l</u>. <u>noveboracensis</u>			
7°C	-2.28	-2.04	-2.16
27°C	-0.99	-0.86	-0.92
$\bar{X}$	-1.64	-1.45	
<u>P</u>.<u>l</u>. <u>castaneus</u>			
7°C	-2.98	-3.54	-3.26
27°C	-1.85	0.00	-0.92
$\bar{X}$	-2.42	-1.77	
<u>P</u>. <u>m</u>. <u>bairdi</u>			
7°C	+1.53	+0.88	+1.20
27°C	+0.43	+0.38	+0.41
$\bar{X}$	+0.98	+0.63	
<u>P</u>. <u>m</u>. <u>blandus</u>			
7°C	+0.12	+0.35	+0.24
27°C	+0.51	+0.41	+0.46
$\bar{X}$	+0.31	+0.38	
<u>P</u>. <u>eremicus</u>			
7°C	-1.72	. .	-1.72
27°C	. .	+0.79	+0.79
$\bar{X}$	-1.72	+0.79	

DISCUSSION

The thesis of this study has been that deermice are capable of utilizing multiple environmental cues to "anticipate" seasonal changes in their food supplies by beginning intensive hoarding. Five taxonomic groups representing three species of *Peromyscus* were studied under laboratory conditions of photoperiod and temperature simulating fall and summer to mice from northern latitudes. My three working hypotheses and their fates upon testing were: (1) both photoperiod and temperature affect the amount of food stored by deermice. This hypothesis was confirmed in regards to test temperature, but the evidence for photoperiod was only conclusive in one subspecies of *P. maniculatus*. (2) The effect of photoperiod and test temperature will vary depending upon the latitudinal and climatic origins of the subspecies being studied. This hypothesis was confirmed since the northern subspecies of both *P. maniculatus* and *P. leucopus* hoarded significantly more under experimental conditions simulating fall or early winter than under summer conditions. The two southern subspecies did not show this difference, but did hoard more under a warm test temperature than under a cold one, except during the first day of testing. (3) The hoarding of food by deermice is not related to changes in their body weight. This hypothesis was confirmed in all groups except *P. m. bairdi*, in which the relationship may have been spurious.

Test Temperature

The effect of ambient temperature upon the hoarding behavior of two subspecies of *P. leucopus* was consistent with the original hypothesis that their response would be predictable on the basis of their latitudinal or climatic origins. *P. l. noveboracensis*, a northern subspecies found predominantly in forest-type habitats, hoarded significantly more under the cold temperature (7°C) than under the warm temperature (27°C). The southern subspecies, *P. l. castaneus*, which inhabits an entirely different habitat of cultivated cornfields in tropical Mexico, did not show a significant difference in the average amount hoarded under either temperature. However, when the hoarding of *P. l. castaneus* was analyzed on a day by day basis it was found that the mice on day 1 hoarded significantly more under 7°C than under 27°C. On all subsequent days, their hoarding under the cold dropped so that by the fifth day it was below the amount hoarded in the warm temperature. The interaction of acclimation temperature and test temperature was non-significant in both subspecies and indicated that these two factors acted independently of each other.

The effect of temperature on the two subspecies of *P. maniculatus* contrasted with what was found in *P. leucopus*. *P. m. bairdi*, the northern subspecies which occurs predominantly in cultivated fields and grassland habitats, did not show the same consistent response to test temperature that *P. l. noveboracensis* did. Only on the first day of testing did *P. m. bairdi* hoard significantly more under the cold temperature than under the warm. On the remaining six days, hoarding was approximately the same under both temperatures with a slight tendency to hoard more under the warmer temperature, especially in the last three days. *P. m. blandus*, the southern subspecies which occupies the desert-shrub habitat of the southwest, hoarded even more consistently in the warm temperature. On all days but the first, *P. m. blandus* hoarded significantly more under the warm temperature. When the two subspecies were compared under both test temperatures, it was found that *P. m. bairdi* hoarded significantly more than *P. m. blandus* under 7°C as would be predicted on the basis of my hypothesis. Under 27°C there was no significant difference between their scores. The absence of any significant interaction of test temperature and acclimation temperature again illustrated the independence of these two factors.

Several possible explanations might be proposed to interpret the effects of test temperature on hoarding in deermice: (1) hoarding is directly related to food consumption under all ambient temperatures, (2) hoarding scores reflect changes in general activity under various ambient temperatures, (3) ambient temperatures act as cues to the mice to begin intensive hoarding at certain times of the year. The first proposal that hoarding is related to food consumption under all ambient temperatures is not supportable in light of my findings. The metabolic rate of rodents, and hence their food consumption, varies inversely with ambient temperature except while in torpor or hibernation (see Hart, 1971). If changes in metabolic rate were responsible for hoarding, one would expect then a similar inverse relationship between food storage and temperature. However, my results indicate that in deermice the effect of test temperature varies with both subspecies and species, even though its effect on their metabolic rates is in general the same (Hart, 1953; McNab & Morrison, 1963). The finding that a cold temperature increases hoarding in *P. l. noveboracensis* but has the opposite effect on *P. m. blandus* would tend to contradict any explanation of hoarding based solely on metabolic rates. This agrees with the earlier findings by Stellar (1951) that metabolic rate, at least when manipulated through experimental interference of thyroid functioning, has little effect on hoarding.

The second proposal that hoarding scores reflect changes in activity with ambient temperature cannot be entirely refuted by my study and may account for some of the observed subspecific differences. It is possible that in *P. l. castaneus*, the cold test temperature was sufficiently stressful so as to inhibit their hoarding under the cold temperature on all days except the first, when they hoarded more under 7°C than 27°C. During the early stages of this study, several *P. l. castaneus* (approximately 7 out of 135) died when placed under the cold temperature, indicating that they may lack the ability to adjust as quickly to cold as does *P. l. noveboracensis*, in which no deaths were observed. The deaths of *P. l. castaneus* always took place 24-48 hours after being placed at 7°C and apparently were due to their inability to construct a nest in a sufficiently short period of time to provide adequate insulation from the cold. When *P. l. castaneus* individuals were given sufficient time to construct a nest in the test cage before being placed at 7°C, no deaths were observed. The latter procedure was incorporated into the experiment as soon as this fact became known.

An explanation similar to the one suggested above for *P. l. castaneus* could possibly be used to interpret my findings for *P. m. blandus*. The overall level of hoarding in *P. m. blandus* was low, and perhaps their hoarding under the cold temperature was inhibited sufficiently to cause a significant difference in their scores under the two test temperatures. Winter nights in the southwestern deserts from which the original stocks of *P. m. blandus* were obtained are cool, with minimum temperatures falling below freezing much of the time from mid-November through early March (Lordsburg, New Mexico Weather Station, U.S. Department of Commerce). My results sugest that *blandus* might be less active during these periods.

The failure of *P. m. bairdi* to respond to either test temperature except on the first day, probably indicates temperature was not significantly affecting their activity. Stinson (1952; cited by Falls, 1968) has reported that laboratory reared *P. m. bairdi* tended to be most active between 15°C and 27°C and this may account for the slightly greater hoarding response under 27°C test temperature in the last three days of testing.

If inhibition of activity by cold is used to interpret the results in *P. l. castaneus* and perhaps *P. m. blandus*, it cannot be used to explain the effect of cold temperature on the hoarding of *P. l. noveboracensis*. In fact the opposite may be true in this subspecies. Orr (1959) has reported that *P. l. noveboracensis* kept in outdoor enclosures showed the greatest amount of activity in crossing treadles between approximately 4° and 10°C, which encompass the cold test temperature of my own study. It is possible that the increases in food storage by this particular subspecies under 7°C were a consequence of their increased activity at that temperature. This finding agrees with what has already been reported on the hoarding behavior of laboratory rats (McCleary & Morgan, 1946), but remains contrary to observations on laboratory mice

(Ross & Smith, 1953). The response of _P_. _m_. _blandus_ to test temperature is in more agreement with the latter study.

By far the most interesting explanation of the effect of test temperature on hoarding is that it acts as a cue to the mice to begin intensive hoarding during certain seasons of the year. The substantial difference between the two subspecies of _P_. _leucopus_ under 7°C and the significant effect of cold temperature on the hoarding of _P_. _l_. _noveboracensis_ strongly suggests that cold ambient temperatures are at least in part responsible for initiating the intensive food storage reported for this species during the fall and early winter in the northern latitudes. Mean daily temperatures in the area of Michigan from which the stocks of _P_. _l_. _noveboracensis_ were derived, do undergo seasonal changes from a high of about 27°C in July to a low of -9°C in January (East Lansing, Michigan Weather Station, U.S. Department of Commerce). Mean daily temperatures for the fall months of September, October, and November range between 3° and 16°C. Consistently low temperatures could, therefore, serve as a reliable cue to begin intensive food hoarding.

The failure of _P_. _m_. _bairdi_ to be similarly affected by cold temperature is surprising, considering that both _P_. _m_. _bairdi_ and _P_. _l_. _noveboracensis_ are sympatric in Michigan. Whether this difference has any relationship to their different habitats remains to be resolved. The greater influence of photoperiod on *P. m. bairdi* than on *P. l. noveboracensis* will be discussed in the next section.

The response of *P. m. blandus* to the warm test temperature might also be explained on the basis that a hot temperature may be a cue to begin intensive hoarding in its habitat. The continental climate of the southwestern deserts is characterized by large annual and diurnal ranges in temperature, but with distinct seasonal temperature changes. Summers are quite warm with mean daily maximum temperatures ranging above 32°C from mid-May until September (Lordsburg, New Mexico Weather Station, U.S. Department of Commerce). Half the yearly moisture normally falls in the summer months of July and September, providing good stands of grasses and other annual plants. It is probably during this time of year that *P. m. blandus* does the most hoarding, although there is no field evidence to either support or refute this conclusion. It is reasonable to assume that the long photoperiod and warm temperature under which the *P. m. blandus* were tested may have simulated summer conditions to them and the need to hoard in preparation for the relatively mild but dry winter season. Another possibility that will be discussed more thoroughly later is that both *P. eremicus* and *P. m. blandus* may hoard during certain seasons so as to have food for use during prolonged periods of torpor induced by extremes in daily temperature.

Photoperiod

Day length had by far the greatest effect on *P. m. bairdi,* which hoarded significantly more under the short day photoperiod than under the long one. All other groups, except *P. l. castaneus*, showed small but non-significant increases in hoarding under the short day photoperiod. These findings do suggest that at least one northern subspecies, *P. m. bairdi*, may be using the length of the photoperiod as a cue to increase hoarding. However, an alternative explanation might be that the longer nights could have afforded a longer period of time in which to hoard, since there was no significant difference in the rate of hoarding (in contrast to the amount) by *P. m. bairdi* under the two photoperiods. This is contrary to Muul's (1968) finding that flying squirrels do increase their rate of hoarding under a shortened photoperiod.

If *P. m. bairdi* hoard whenever food and time are available, their accumulation of food during autumn and early winter may be a fortuitous consequence of their remaining active under longer periods of darkness. Both *P. m. bairdi* and *P. l. noveboracensis* do show longer periods of nocturnal activity in the winter than in the summer (Johnson, 1926; Orr, 1959). During the winter, the nocturnal activity pattern of *P. m. bairdi* is characterized by two major peaks in activity both early and late in the night (Falls, 1968). In contrast, during the summer (when nights are shorter) the activity of *P. m. bairdi* is more continuous, with only a single major peak early in the night. If their fall and early winter hoarding activity follows a similar pattern, the two peaks in activity would result in larger caches of food at that time of the year. In fact, Falls (1968) has suggested the two peaks probably represent a feeding pattern which would further suggest a relationship to their hoarding.

The activity of *P. l. noveboracensis* also shows two peaks during winter nights, although the second peak is typically not as high as the first (Orr, 1959). In *P. m. bairdi* both peaks are substantial and this may account for the failure to find any significant difference in the amount of hoarding done by *P. l. noveboracensis* under either photoperiod. The small but non-significant increase in the amount of hoarding under a short day photoperiod in all the other groups, except *P. l. castaneus*, may also suggest a similar pattern of nocturnal activity and hoarding in these mice. However, the failure of *P. l. castaneus* to show this trend suggests that a study of their activity patterns might be fruitful.

Obviously, the above offered explanation for the increase in hoarding under a short day photoperiod does not explain the intensive food storage by many diurnal rodents during the shortening days of fall and early winter. A study on the hoarding behavior of such species as chipmunks, ground squirrels, or one of the diurnal tree squirrels under a natural photoperiod would provide conclusive evidence of whether the mechanism which has been proposed as acting in flying squirrels (Muul, 1968) has any generality among the other rodents or even in other sciurids. It will also be absolutely essential that all learning be controlled for, as this was the one weakness of Muül's study in which he used wild caught animals.

Possible Physiological Mechanism for Hoarding

Both *P. l. noveboracensis* and *P. m. bairdi* showed a significant difference in the amount of food hoarded under experimental conditions simulating autumn or early winter as compared to the amount hoarded under summer conditions. The highly significant response of *P. l. noveboracensis* to the "fall" conditions in my study, agrees well with the finding by Lynch (1973) that this subspecies when kept under a short photoperiod (9L:15D) and a cold temperature (5°C) will show physiological changes associated with the fall of the year. Starting approximately 4 weeks after acclimation to these conditions, some of the mice in Lynch's study began to show both a "fall" molt and gonadal regression. Photoperiod was apparently the more important influence, since cold tended to accelerate molting (as compared to groups under the same photoperiod but at 27°C) but had no appreciable effect on the rate of gonadal regression. Both males and females responded similarly to the photoperiod and temperature conditions in regards to both their molting and gonadal regression. Weight changes, if any, were not reported. Lynch (1973) proposed this as case in which multiple environmental cues permit a more reliable assessment of critical changes in the environment leading to a higher probability of survival. Since some of the *P. l. noveboracensis* in my own study (exactly 50% of those tested) were also acclimated under a 9L:15D photoperiod and under 7°C, it is reasonable to assume that the physiological changes reported by Lynch were occurring. Table 7 illustrates that under a short photoperiod, *P. l. noveboracensis* kept at 7°C over a period of 5 weeks hoarded more than twice as much as those mice kept at 27°C and under a long photoperiod. The finding that test temperature had more of an influence than photoperiod appears to be the one major difference in the findings of Lynch and this study. Obviously, there is yet insufficient evidence to suggest that the physiological mechanisms underlying molt and gonadal regression are the same as those for hoarding. Additional study is also needed on *P. m. bairdi* to see whether similar changes occur in this species under controlled laboratory conditions of photoperiod and temperature.

Torpor and Food Hoarding

The high level of hoarding by *P. eremicus* even in contrast to the northern subspecies, *P. l. noveboracensis* and *P. m. bairdi*, is at first a little perplexing. I have attributed the intensive hoarding of both *P. l.*

noveboracensis and *P. m. bairdi* as being a necessary response in the northern latitudes where seasonal fluctuations in food supplies can be severe. The fact that food supplies in other environments may also fluctuate has only been given brief mention up to now. Food supplies in the desert habitats from which both *P. eremicus* and *P. m. blandus* were derived to undergo seasonal changes, although at different times of the year than in the northern latitudes. MacMillen (1965) has reported that *P. eremicus* will enter torpor during both the winter and summer in their habitat. During the winter, torpor can only be induced through food restriction, but during the summer either food restriction or negative water balance is capable of inducing it. MacMillen has proposed that summer torpor probably allows *P. eremicus* to remain in its humid burrows for several weeks, if necessary, to avoid the demanding external desert environment. He also mentions that torpor could be one method of prolonging the food stores which are needed during these periods of forced inactivity. Unfortunately, no field evidence exists to confirm whether *P. eremicus* hoard prior to summer torpor. The exceptionally high level of hoarding of this species in the present study suggests, however, that this trait has been heavily selected for. This species' obligatory restriction to burrows during the summer would be a strong selection pressure on the development of the hoarding habit. As pointed out earlier, the fact that *P. m. blandus* hoard significantly more under a warm temperature than under a cold one, may indicate that it, too, hoards for periods of forced inactivity during the exceptionally hot summer months. Until someone studies whether torpor is also the normal response of *blandus* to food and water deprivation in both winter and summer, the reasoning given here remains viable. Whether the presence of daily torpor in both *P. m. bairdi* (Fuller, Stebbins, & Dyke, 1969) and *P. l. noveboracensis* (Gaertner, Hart, & Roy, 1973) also has any relationship to their hoarding behavior remains to be investigated. Apparently both of these species will undergo temperature induced torpor even in the presence of stored food (Howard, 1951; Gaertner *et al.*, 1973).

Weight Change and Hoarding

The finding that *P. l. noveboracensis* lose weight during acclimation to a cold temperature appears to be consistent with what has already been reported for this subspecies (Hart, 1953). Although in this study both *P. l. noveboracensis* and *P. l. castaneus* lost weight under both acclimation temperatures, they did lose significantly more weight under 7°C than under 27°C. The general loss in weight under both temperatures could have been a response to the experimental conditions, perhaps induced by their social isolation while in the experiment. Animals that were obese showed the greatest changes in weight in all the subspecies. The increases in weight of *P. m. bairdi* under the two acclimation temperatures demonstrate, however, the diversity of responses possible within this genus to both temperature and social isolation. The slightly greater gain in weight by bairdi under 7°C is in agreement with Sealander's finding that laboratory raised members of this subspecies show a significant increase in weight when acclimated to 8.5°C versus 30.5°C (Sealander, 1951). The highly significant loss in weight by P. eremicus under the cold acclimation temperature and their gain under the warm temperature indicates a lack of stability in their body weight that may have some ecological significant in their desert environment. The inconsistent effect of acclimation temperature and sex on weight change in P. m. blandus, a sympatric species with P. eremicus, deserves further investigation.

The results of this study suggest that there is little evidence of any relationship between weight change (either weight loss or gain) and hoarding behavior in deermice. The correlation between weight change and hoarding in P. m. bairdi was small, whereas the correlations in the other groups were all non-significant. There was also no apparent relationship between the factors which influenced weight change and the factors influencing hoarding. Under a short day photoperiod, P. l. castaneus hoarded significantly more after acclimation to 27°C than after 7°C, even though it lost more weight under the colder temperature. P. l. noveboracensis, which had similarly lost weight under the cold temperatures, failed to show any significant difference in the amount of food hoarded after acclimation to either temperature under the same photoperiod. Test temperature, which could have only a minimal effect on weight change because it lasted for only 7 days, had more of an influence on hoarding than acclimation temperature in all the groups. Changes in weight under the two photoperiods also tended to be an equally poor predictor of hoarding. *P. m. bairdi* hoarded significantly more under the short day photoperiod than under the long, but tended to gain weight under the longer photoperiod. These findings would appear to contradict the model of Herberg and Blundell (1970) in which they proposed that hoarding in rats at least, is motivated by long term nutritional needs or "deficits" (i.e., losses in body weight or changes in the size of fat reserves) acting through the lateral hypothalamus. The report that *P. l. noveboracensis* apparently gain weight during fall and early winter (Sealander, 1951) when they would be most actively hoarding, tends to further dispute their model.

Conclusions

The hypothesis that the hoarding behavior of deermice is under the influence of environmental factors has been confirmed by my study. The two northern subspecies of both *P. leucopus* and *P. maniculatus* found in Michigan do hoard more under laboratory conditions of a low temperature and short photoperiod, than they do under a high temperature and long photoperiod. A similar response in the wild would lead to the accumulation of food in the fall of the year which could then be used during a winter scarcity. Similarly, my results suggest that the response of *P. m. blandus* to a warm temperature may have some relationship to the seasonal changes in its food supplies in the southwestern deserts.

My results also indicate that temperature and photoperiod are not of equal importance to both *P. leucopus noveboracensis* and *P. maniculatus bairdi*. *P. m. bairdi* was more influenced by photoperiod than by temperature, but in *P. l. noveboracensis* just the opposite was true. As both of these species are sympatric in Michigan, further research is needed to see whether this finding has any relationship to their habitat requirements.

There remains a great deal of work to be done on the hoarding behavior of *Peromyscus*, especially in regards to the collection of good field data. With one exception (Howard & Evans, 1961), field reports of food storage by members of this genus have been only casual in nature with little information as to how much food is hoarded, when or where it is hoarded, or by how many individuals. The lack of experimental interest in their hoarding up till now is surprising in view of the considerable attention given to other aspects of the behavioral ecology of this genus (for example, see King, 1968). However, recent advances in the use of radioactive tracers ought to facilitate field studies of hoarding as radioactively labeled food could be provided and then relocated after storage. This technique could be used in a variety of habitats with equal efficiency and might provide answers to the many questions raised in this dissertation.

SUMMARY

1. Five taxa of deermice including *P. l. noveboracensis*, *P. l. castaneus*, *P. m. bairdi*, *P. m. blandus*, and *P. eremicus* were tested in the laboratory for the amount of food hoarded on seven consecutive days under various combinations of test temperature (7°C or 27°C) and photoperiod (9L:15D or 15L:9D).

2. The two northern subspecies of both *P. leucopus* and *P. maniculatus* hoarded significantly more food under a low temperature and a short day photoperiod than they did under a high temperature and long day photoperiod. A similar response to these environmental variables in the wild would lead to a higher level of hoarding in the fall of the year than in the summer.

3. Comparisons of *P. l. noveboracensis* with *P. l. castaneus*, and *P. m. bairdi* with *P. m. blandus* revealed that in both cases the northern subspecies hoarded significantly more than the southern one under the cold test temperature. Under the warm test temperature, there was no significant difference between their scores.

4. Photoperiod and temperature were not of equal importance to both *P. l. noveboracensis* and *P. m. bairdi*. Test temperature had more of an effect than photoperiod on the hoarding of *P. l. noveboracensis*, while in *P. m. bairdi* photoperiod was the more important factor. Test temperature also had a significant effect on *P. m. blandus* which hoarded more under the 27°C test temperature than under 7°C.

5. The high level of hoarding by *P. eremicus* in contrast to the other groups studied, may be related to the occurrence of summer torpor in this species and its restriction to burrows during extremes in temperature in its desert habitat.

6. In all of the groups studies, except perhaps *P. m. bairdi*, there was no evidence found to support a model of food hoarding in deermice based on long term nutritional needs or deficits (i.e., losses in body weight) as proposed by Herberg and Blundell (1970) for laboratory rats. In *P. m. bairdi* there was only a small correlation between weight change and hoarding scores. In all other groups this correlation was non-significant.

APPENDIX

Table 12.--Analysis of Variance of the Log Hoarding Scores of *P. leucopus noveboracensis*.

Source of Variance	df	MSS	F	Prob.
Between Subjects				
Sex	1	1.3383	1.4034	.239
Accl. Temp.	1	1.2347	1.2949	.258
Photoperiod	1	.9278	.9730	.326
Test Temp.	1	6.0909	6.3875	.013
Sex x Accl. Temp.	1	.0314	.0329	.856
Sex x Photop.	1	.0283	.0297	.863
Sex x Test Temp.	1	.2119	.2222	.638
Accl. Temp. x Photop.	1	1.4556	1.5264	.219
Accl. Temp. x Test Temp.	1	2.4868	2.6079	.109
Photop. x Test Temp.	1	.3847	.4034	.527
Sex x Accl. Temp. x Photop.	1	2.9956	3.1414	.079
Sex x Accl. Temp. x Test Temp.	1	.7922	.8308	.364
Sex x Photop. x Test Temp.	1	.1690	.1772	.675
Accl. Temp. x Photop. x Test Temp.	1	.1192	.1250	.724
Sex x Accl. Temp. x Photop. x Test Temp.	1	.2375	.2491	.619
Error	112	.9536		

Table 12.--continued.

Source of Variance	df	MSS	F	Prob.
Within Subjects				
Days	6	1.1672	12.7589	<.0005
Sex x Days	6	.0601	.6573	.684
Accl. Temp. x Days	6	.1016	1.1108	.354
Photop. x Days	6	.0245	.2673	.952
Test Temp. x Days	6	.1247	1.3627	.227
Sex x Accl. Temp. x Days	6	.0555	.6067	.725
Sex x Photop. x Days	6	.0486	.5315	.785
Sex x Test Temp. x Days	6	.0925	1.0109	.417
Accl. Temp. x Photop. x Days	6	.0518	.5665	.757
Accl. Temp. x Test Temp. x Days	6	.0798	.8724	.515
Photop. x Test Temp. x Days	6	.1164	1.2721	.268
Sex Accl. Temp. x Photop. x Days	6	.0985	1.0767	.375
Sex x Accl. Temp. x Test Temp. x Days	6	.0593	.6487	.691
Sex x Photop. x Test Temp. x Days	6	.0106	.1154	.995
Accl. Temp. x Photop. x Test Temp. x Days	6	.0805	.8801	.509
Sex x Accl. Temp. x Photop. x Test Temp. x Days	6	.0837	.9149	.483
Error	672	.0915		
Total	895	(SS=200.3108)		

Table 13.--Analysis of Variance of the Log Hoarding Scores of *P. leucopus castaneus*.

Source of Variance	df	MSS	F	Prob.
Between Subjects				
Sex	1	2.6227	4.0335	.047
Accl. Temp.	1	.1336	.2055	.651
Photoperiod	1	.4666	.7175	.399
Test Temp.	1	.5826	.8960	.346
Sex x Accl. Temp.	1	4.1030	6.3100	.013
Sex x Photop.	1	1.5196	2.3370	.129
Sex x Test Temp.	1	1.1225	1.7263	.192
Accl. Temp. x Photop.	1	7.4910	11.5204	.001
Accl. Temp. x Test Temp.	1	.7044	1.0833	.300
Photop. x Test Temp.	1	.3801	.5846	.446
Sex x Accl. Temp. x Photop.	1	.0804	.1236	.726
Sex x Accl. Temp. x Test Temp.	1	.0000	.0000	.993
Sex x Photop. x Test Temp.	1	1.6297	2.5062	.116
Accl. Temp. x Photop. x Test Temp.	1	.2086	.3209	.572
Sex x Accl. Temp. x Photop. x Test Temp.	1	1.0076	1.5495	.216
Error	112	.6502		

Table 13.--continued.

Source of Variance	df	MSS	F	Prob.
Within Subjects				
Days	6	1.4744	23.1871	<.0005
Sex x Days	6	.0498	.7839	.583
Accl. Temp. x Days	6	.0624	.9820	.436
Photop. x Days	6	.0181	.2845	.944
Test Temp. x Days	6	.2875	4.5217	<.0005
Sex x Accl. Temp. x Days	6	.0293	.4604	.838
Sex x Photop. x Days	6	.0549	.8629	.522
Sex x Test Temp. x Days	6	.0736	1.1579	.327
Accl. Temp. x Photop. x Days	6	.0433	.6812	.665
Accl. Temp. x Test Temp. x Days	6	.0228	.3579	.905
Photop. x Test Temp. x Days	6	.0515	.8092	.563
Sex x Accl. Temp. x Photop. x Days	6	.0645	1.0141	.415
Sex x Accl. Temp. x Test Temp. x Days	6	.0789	1.2416	.283
Sex x Photop. x Test Temp. x Days	6	.0824	1.2962	.257
Accl. Temp. x Photop. x Test Temp. x Days	6	.0372	.5856	.742
Sex x Accl. Temp. x Photop. x Test Temp. x Days	6	.0968	1.5215	.168
Error	672	.0636		
Total	895	(SS=152.7749)		

Table 14.--Analysis of Variance of the Log Hoarding Scores of *P. maniculatus bairdi*.

Source of Variance	df	MSS	F	Prob.
Between Subjects				
Sex	1	.0076	.0078	.930
Accl. Temp.	1	.9124	.9316	.337
Photoperiod	1	3.9295	4.0125	.048
Test Temp.	1	.0072	.0074	.932
Sex x Accl. Temp.	1	1.9706	2.0123	.159
Sex x Photop.	1	.3376	.3447	.558
Sex x Test Temp.	1	.0219	.0219	.883
Accl. Temp. x Photop.	1	1.3783	1.4074	.238
Accl. Temp. x Test Temp.	1	.4548	.4644	.497
Photop. x Test Temp.	1	.2131	.2175	.642
Sex x Accl. Temp. x Photop.	1	1.2986	1.3260	.252
Sex x Accl. Temp x Test Temp.	1	.0430	.0439	.834
Sex x Photop. Test Temp.	1	.6259	.6391	.426
Accl. Temp. x Photop. x Test Temp.	1	.0800	.0817	.776
Sex x Accl. Temp. x Photop. x Test Temp.	1	1.2745	1.3015	.256
Error	112	.9793		

Table 14.--continued.

Source of Variance	df	MSS	F	Prob.
Within Subjects				
Days	6	.0599	.6942	.654
Sex x Days	6	.1495	1.7337	.111
Accl. Temp. x Days	6	.1125	1.3036	.253
Photop. x Days	6	.0298	.3458	.912
Test Temp. x Days	6	.1780	2.0628	.056
Sex x Accl. Temp. x Days	6	.0086	.0994	.996
Sex x Photop. x Days	6	.1347	1.5610	.156
Sex x Test Temp. x Days	6	.1082	1.2542	.277
Accl. Temp. x Photop. x Days	6	.0672	.7790	.587
Accl. Temp. x Test Temp. x Days	6	.0299	.3468	.912
Photop. x Test Temp x Days	6	.0881	1.0217	.410
Sex x Accl. Temp. x Photop. x Days	6	.0218	.2528	.958
Sex x Accl. Temp. x Test Temp. Days	6	.0781	.9057	.490
Sex x Photop. Test Temp. x Days	6	.0832	.9640	.449
Accl. Temp. x Photop. x Test Temp. x Days	6	.1469	1.7023	.118
Sex x Accl. Temp. x Photop. x Test Temp. x Days	6	.1159	1.3437	.235
Error	672	.0863		
Total	895	(SS=188.6874)		

Table 15.--Analysis of Variance of the Log Hoarding Scores of *P. maniculatus blandus*.

Source of Variance	df	MSS	F	Prob.
Between Subjects				
Sex	1	.0611	.1025	.749
Accl. Temp.	1	.8940	1.4986	.223
Photop.	1	.8583	1.4387	.233
Test Temp.	1	4.0390	6.7706	.011
Sex x Accl. Temp.	1	.1210	.2029	.653
Sex x Photop.	1	.2751	.4612	.498
Sex x Test Temp.	1	1.1721	1.9647	.164
Accl. Temp. x Photop.	1	.2066	.3464	.557
Accl. Temp. x Test Temp.	1	.0150	.0251	.874
Photop. x Test Temp.	1	1.2532	2.1007	.150
Sex x Accl. Temp. x Photop.	1	.2506	.4201	.518
Sex x Accl. Temp. x Test Temp.	1	.0127	.0212	.884
Sex x Photop. x Test Temp.	1	.5474	.9176	.340
Accl. Temp. x Photop. x Test Temp.	1	.2163	.3626	.548
Sex x Accl. Temp. x Photop. x Test Temp.	1	.3625	.6076	.437
Error	112	.5966		

Table 15.--continued.

Source of Variance	df	MSS	F	Prob.
Within Subjects				
Days	6	.1189	1.4569	.191
Sex x Days	6	.0202	.2481	.960
Accl. Temp. x Days	6	.0726	.8895	.502
Photop. x Days	6	.0675	.8272	.549
Test Temp. x Days	6	.2379	2.9151	.008
Sex x Accl. Temp. x Days	6	.0707	.8660	.519
Sex x Photop. x Days	6	.0744	.9111	.486
Sex x Test Temp. x Days	6	.0586	.7180	.635
Accl. Temp. x Photop. x Days	6	.0270	.3310	.921
Accl. Temp. Test Temp. x Days	6	.0728	.8918	.500
Photop. x Test Temp. x Days	6	.0603	.7394	.618
Sex x Accl. Temp. x Photop. x Days	6	.1800	2.2055	.041
Sex x Accl. Temp. x Test Temp. x Days	6	.0267	.3269	.923
Sex x Photop. x Test Temp. x Days	6	.0124	.1519	.989
Accl. Temp. x Photop. x Test Temp. x Days	6	.1312	1.6080	.142
Sex x Accl. Temp. x Photop. x Test Temp. x Days	6	.1002	1.2276	.290
Error	672	.0816		
Total	895	(SS=139.9269)		

Table 16.--Analysis of Variance of Log Hoarding Scores of *P. eremicus eremicus*.

Source of Variance	df	MSS	F	Prob
Temperature[a]	1	.0049	.0357	.851
Photoperiod	1	.2876	2.0797	.158
Acclimation Temp. x Photoperiod	1	.0944	.6828	.414
Residual error	36	.1383		
Total	39	(SS=5.3647)		

[a] All mice were tested at the same temperature to which they had been acclimated.

Table 17.--Combined Analysis of Variance for the Mean Log Hoarding Scores (i.e., Log ($\bar{X}$+1) for Each Mouse) of *P. l. noveboracensis*, *P. l. castaneus*, *P. m. bairdi*, and *P. m. blandus*.

Source of Variance	df	MSS	F	Prob.
Subspecies	3	.5795	4.4134	.005
Sex	1	.2217	1.6887	.194
Subspecies x Sex	3	.1858	1.4152	.238
Accl. Temp.	1	.3704	2.8212	.094
Subspecies x Accl. Temp.	3	.1230	.9371	.423
Sex x Accl. Temp.	1	.0409	.3114	.577
Subspeciex x Sex x Accl. Temp.	3	.2689	2.0477	.106
Photoperiod	1	.4476	3.4083	.065
Subspecies x Photop.	3	.2080	1.5845	.192
Sex x Photop.	1	.0634	.4829	.487
Subspecies x Sex x Photop.	3	.1220	.9288	.427
Accl. Temp. x Photop.	1	.1803	1.3729	.242
Subspecies x Accl. Temp. x Photop.	3	.4516	3.4395	.017
Sex x Accl. Temp. x Photop.	1	.0769	.5860	.444
Subspecies x Sex x Accl. Temp. x Photop.	3	.3618	2.7553	.042
Test Temp.	1	.1018	.7753	.379
Subspecies x Test Temp.	3	.6374	4.8545	.002
Sex x Test Temp.	1	.0458	.3486	.555
Subspecies x Sex x Test Temp.	3	.1782	1.3571	.255
Accl. Temp. x Test Temp.	1	.4084	3.1102	.078
Subspecies x Accl. Temp. x Test Temp	3	.0092	.0703	.976

Table 17.--continued.

Source of Variance	df	MSS	F	Prob.
Sex x Accl. Temp. x Test Temp.	1	.0126	.0959	.757
Subspecies x Sex x Accl. Temp. x Test Temp.	3	.0316	.2407	.868
Photop. x Test Temp.	1	.4967	3.7827	.052
Subspecies x Photop. x Test Temp.	3	.0213	.1626	.922
Sex x Photop. x Test Temp.	1	.0942	.7177	.397
Subspecies x Sex x Photop. x Test Temp.	3	.1552	1.1819	.316
Accl. Temp. x Photop. x Test Temp.	1	.0177	.1347	.714
Subspecies x Accl. Temp. x Photop. x Test Temp.	3	.0160	.1220	.947
Sex x Accl. Temp. x Photop. x Test Temp.	1	.2864	2.1812	.140
Subspecies x Sex x Accl. Temp. x Photop. x Test Temp.	3	.0576	.4390	.725
Residual Error	448	.1313		
Total	511			

Table 18.--Combined Analysis of Variance for the Mean Weight Changes in *P. l. noveboracensis*, *P. l. castaneus*, *P. m. bairdi*, and *P. m. blandus*.

Source of Variance	df	MSS	F	Prob.
Subspecies	3	255.6920	22.6762	.0005
Sex	1	21.2063	1.8807	.171
Subspecies x Sex	3	10.8070	.9584	.412
Accl. Temp.	1	72.1500	6.3987	.012
Subspecies x Accl. Temp.	3	57.9114	5.1359	.002
Sex x Accl. Temp.	1	.1188	.0105	.918
Subspecies x Sex x Accl. Temp.	3	30.9308	2.7431	.043
Photoperiod	1	.8945	.0793	.778
Subspecies x Photop.	3	3.0120	.2671	.849
Sex x Photop.	1	.1070	.0095	.922
Subspecies x Sex x Photop.	3	39.7912	3.5289	.015
Accl. Temp. x Photop.	1	.4395	.0390	.844
Subspecies x Accl. Temp. Photop.	3	15.6312	1.3863	.246
Sex x Accl. Temp. x Photop.	1	80.1695	7.1099	.008
Subspecies x Sex x Accl. Temp. x Photop.	3	15.0153	1.3316	.263
Test Temp.	1	2.3926	.2122	.645
Subspecies x Test Temp.	3	5.3758	.4768	.699
Sex x Test Temp.	1	48.8813	4.3351	.038
Subspecies x Sex x Test Temp.	3	59.6087	5.2864	.001
Accl. Temp. x Test Temp.	1	13.1970	1.1704	.280
Subspecies x Accl. Temp. x Test Temp.	3	12.3776	1.0977	.350

Table 18.--continued.

Source of Variance	df	MSS	F	Prob.
Sex x Accl. Temp. x Test Temp.	1	17.0382	1.5110	.220
Subspecies x Sex x Accl. Temp. x Test Temp.	1	28.1301	2.4947	.059
Photop. x Test Temp.	1	.1876	.0166	.897
Subspecies x Photop. x Test Temp.	3	24.7451	2.1945	.088
Sex x Photop. x Test Temp.	1	17.9251	1.5897	.208
Subspecies x Sex x Photop. x Test Temp.	3	1.8783	.1666	.919
Accl. Temp. x Photop. x Test Temp.	1	11.8220	1.0484	.306
Subspecies x Accl. Temp. x Photop. x Test Temp.	3	18.0512	1.6009	.188
Sex x Accl. Temp. x Photop. x Test Temp.	1	49.3770	4.3790	.037
Subspecies x Sex x Accl. Temp. x Photop. x Test Temp.	3	7.2797	.6456	.586
Residual Error	448	11.2758		
Total	511			

Table 19.--Analysis of Variance of the Weight Change in *P. eremicus*.

Source of Variance	df	MSS	F	Prob.
Temperature[a]	1	62.7503	7.9834	.008
Photoperiod	1	2.6523	.3374	.565
Temperature x Photoperiod	1	26.0823	3.3183	.077
Residual Error	36	7.8601		
Total	39	(SS=374.4478)		

[a] All mice were tested at the same temperature to which they had been acclimated.

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