THE WATER REQUIREMENTS OF THE AUSTRALIAN RODENTS, NOTOMYS ALEXIS, N. MITCHELLI AND PSEUDOMYS MINNIE

by

JANICE R. SMITH
B. Sc. (Hons.)

DEPARTMENT OF ZOOLOGY,
UNIVERSITY OF ADELAIDE,
SOUTH AUSTRALIA

A thesis submitted to the University of Adelaide
for the Degree of Master of Science.

FEBRUARY 1971.

TABLE OF CONTENTS.

SUMMARY

A study was made of the water requirements of three species of Australian rodents. The two desert species Notomys alexis and Pseudomys minnie were independent of drinking water when kept in the laboratory on a diet of hulled oats (10 percent water by weight) and at a temperature of 21°C and relative humidities between 30 and 60 percent. Notomys mitchelli, a species from the semi-arid parts of southern Australia, kept under the same conditions, was less tolerant to water deprivation with almost half of this species dying by the 30th day without water.

When denied water, all rodents lost between 15 and 20 percent of their body weight during the first 5 days. But thereafter, N. alexis and P. minnie gained weight so that after 60 days without water they had very nearly returned to their original weight. However, the N. mitchelli were still losing weight after 30 days without water.

Food intake, faecal water loss and faeces production all dropped markedly when the rodents were initially denied water, but increased again after the 10th day without water. However, the recovery of the food intake and faecal water

loss of N. mitchelli was much less than that of N. alexis and P. minnie.

Urine osmotic concentrations of all species reached a maximum after 3 days without water. Urine samples collected until the 7th day showed no further increase in concentration. Whether fed hulled oats or sunflower seed, N. alexis produced the most concentrated urine of the three species. Feeding the rodents sunflower seed, a food higher in protein than hulled oats, resulted in higher urine concentrations from only N. alexis and N. mitchelli. Apparently the Notomys were better able to concentrate urea than P. minnie. N. alexis fed sunflower seed produced urine with the highest osmotic and urea concentrations measured in this study with means of 4511 mOsm/l and 2985 mM/l respectively.

Associated with the increase in urine concentrations was a marked decrease in urine volumes. Mice denied water yielded only 3 to 7 percent of the urine of mice drinking. The Notomys, which concentrated their urine more than P. minnie, voided less urine per gram body weight.

When denied water, the N. alexis initially decreased their running in activity wheels on the average by 78 per cent. However, after 20 days without water, activity had risen to 50 percent of its initial level.

From these changes in body weight, food intake, urine concentrations and volumes, faecal water loss, faeces production and activity, it appears that the rate of metabolism of mice denied water initially decreased and so lessened the drain of water from their bodies. The first 3 to 5 days without water were a critical stage in their water balance, since it took this time for the major mechanism for conserving water, that of concentrating the urine, to reduce water loss to a minimum. As the withdrawal of water was sudden, this saving of water during the initial few days was important. This economy appeared to be accomplished by reducing metabolism.

Once urine concentrations reached their maximum, the rodents safely increased their food intake so avoiding possible starvation. The failure of N. mitchelli, the species least independent of drinking water, to recover its appetite completely further showed that food intake and hence metabolism, decreased in response to the severe stress placed on their water metabolism. Only when water balance was maintained did food intake remain normal.

Thus N. alexis, the desert species, is best equipped for living under conditions of extreme aridity. This species lost the least weight when denied water, was the quickest to regain this lost weight, and produced the

most concentrated urine. N. mitchelli, however, continued to lose weight while denied water, suffered the greatest mortality, and was less able to concentrate its urine. This latter feature is most likely responsible for the lower tolerance of N. mitchelli to water deprivation. P. minnie, though not able to concentrate its urine any more than N. mitchelli, survived without water as well as N. alexis. This somewhat paradoxical situation may be elucidated further by studying the evaporative water losses of these species.

The ability of N. alexis to concentrate its urine more than P. minnie may be a result of their longer time living under arid conditions, thus supporting Tate's (1951) suggestion of an early evolution of the Notomys in the desert and the Pseudomys in the more temperate south.

DECLARATION

This thesis does not contain any material previously accepted for the award of any degree or diploma at any University. Nor to the best of my knowledge does it contain any material previously published or written by any other person without due acknowledgement.

ACKNOWLEDGEMENTS.

I would like to thank the following for their help during the course of my study: Mr. Peter Aitken for supplying me with the *Notomys mitchelli*; Dr. Chris Watts and the Royal Zoological Society of South Australia for enabling me to go to Central Australia to collect *Pseudomys minnie* and *N. alexis*; Dr. S. Barker and all my fellow students for their valuable advice; Dr. G. Crowcroft for supervising the first year of my work; my husband, Robert, for help with the statistical methods and figures; and Mrs. Wanda Redell for typing the thesis.

I would especially like to thank my supervisor, Dr. M.E.B. Smyth, for his helpful criticism and guidance throughout my studies, particularly in preparing this thesis.

I am also grateful to Professor H.G. Andrewartha for allowing me to undertake this study in the Department of Zoology at the University of Adelaide. This study was made possible through a University Research Grant administered by the University of Adelaide.

1. INTRODUCTION

1. INTRODUCTION.

Rodents are found in all the major deserts of the world. Being mostly nocturnal and fossorial, these desert rodents can avoid the high ambient temperatures of their environment by remaining in their cooler burrows during the day and coming out to feed only at night when temperatures are more moderate. As they are, therefore, rarely exposed to temperatures where heat regulation is necessary, they do not often use water for regulating their body temperatures. Nevertheless, even without this additional drain on their water, desert rodents are still often faced with the problem of obtaining enough water for their bodily needs.

Over the last twenty years, many workers have investigated how desert rodents overcome this problem. Perhaps the most notable and intensive studies have been those by the Schmidt-Nielsens and their co-workers (1948, 1950a, and b, 1951, 1952) on the kangaroo rats, Dipodomys, which inhabit the deserts of south-western United States. From these and subsequent studies have emerged a knowledge of the various ways desert rodents can minimise their water loss so that their low intakes can be matched with equally low outputs.

For animals to function satisfactorily they must maintain a water balance; that is, the total water input

must equal the total water output over a period that is physiologically tolerable to the animal. Any complete study of water balance requires that all avenues of water gain and loss be considered.

A desert rodent can gain water in three ways:

1. From the free water present in the environment. In the wild, this is available only on the rare occasions after rain or dew. But in the laboratory, most rodents will drink when given water.

2. From the free water present in the food. For desert rodents this is often the main source of water. Succulent vegetation contains considerable water, but even seeds contain 10 to 20 percent water by weight.

3. From the water of oxidation or metabolic water that is potentially present in the food eaten. This water is formed when hydrogen is oxidised in the body tissues.

Water is lost from the body in three ways:

1. Through the urine in excreting the nitrogenous waste products. The kidneys are the most important organs regulating the water content of the body. They excrete any excess water, or retain water when intakes are scant.

2. With the faeces. In rodents, this accounts for the least loss of water.

3. By evaporation from the skin and lungs. This

pulmocutaneous water loss is usually the major water loss in desert rodents.

Any decreases in water input or increase in water loss can seriously upset water balance. If this balance is to be maintained the decrease in water intake must be compensated for by a corresponding decrease in water loss. In experimental work, denying animals water to drink is a simple way of decreasing their total water intake. A comparative study of both animals denied water and those given it shows how tolerant the species is to aridity and reveals the mechanisms involved in conserving water under these conditions. This approach has been used by numerous workers including Schmidt-Nielsen and Schmidt-Nielsen (1951), Hudson (1962); Church (1966), Carpenter (1966), Getz (1968) and MacMillen and Lee (1969). They have studied, as it were, the long-term response to aridity, that is, how long the animals survive without water, the minimum amount of water required to maintain a constant body weight, the maximum urine concentrations reached, and faecal and evaporative water loss, all measured a considerable time after water deprivation.

One of the most striking physiological adaptions of desert rodents to aridity to emerge from such studies is their ability to produce a highly concentrated urine, this

often being by far the greatest saving of water available to the animal. In addition to their efficient kidneys, desert rodents generally produce drier faeces and have lower evaporative water losses than other rodents, both of which contribute further to reducing water output.

When studying the physiological adaptations which enable desert rodents to live in their arid environments, many workers have compared the performance of the desert species denied water with the performance of another species usually one closely related phylogenetically, but from a less arid climate, the inference being that those features which enable the desert species to survive beyond the limits of the other species represent adaptation to the desert environment. The ability of the desert kangaroo rat, Dipodomys merriami, to live without free water or succulent food is well known from the work of the Schmidt-Nielsens, but this ability is not characteristic of the entire genus. In a comparative study of the water metabolism of the desert kangaroo rat, D. merriami, and the chaparral kangaroo rat, D. agilis, Carpenter (1966) found that D. agilis requires free water or succulent food to survive while D. merriami does not. Correlated with the differences in the water requirements of these species are differences in their ability to concentrate their urine; D. merriami can concentrate its urine 20 percent more than D. agilis.

Yet Carpenter (1966) found that both species lose little water through their pulmocutaneous surfaces. Church (1969) suggests that the similar low pulmocutaneous water loss of Dipodomys spp may be remnant of an overall preadaptation to the desert of the primitive Dipodomys, which speciated in the evolving deserts of south western United States. Yet the concentrating ability of their kidneys appears to have been modified during their evolution, with those kangaroo rats now occupying the desert being able to concentrate their urine much more than those species occupying the non-desert environment. Thus such comparative studies show both the physiological features common to a particular taxon, and therefore those likely to be phylogenetically primitive, such as the low pulmocutaneous water loss of the Dipodomys, and those that have been modified by the ecological selection pressures impinging upon the animal, and therefore likely to be important for the survival of the animal in its particular environment, such as the marked ability of D. merriami to concentrate its urine.

Like the members of the genus Dipodomys, rodents within the subfamily Gerbillinae of the Cricetids show different abilities to conserve water. Gerbillus gerbillus

is able to survive on a dry diet and produces a very concentrated urine (Burns, 1956). However, another gerbil, Meriones unguiculatus, is barely able to maintain weight without free water and produces a urine less concentrated than G. gerbillus (Winkelman and Getz, 1962). Instead, this rodent seeks out succulent vegetation to get the water is needs. Psammomys obesus, yet another of the gerbils, while capable of producing a very concentrated urine, prefers to eat large quantities of salty juicy vegetation (Gottschalk and Mylle, 1959). To excrete the large amount of salt ingested, it produces a urine extraordinarily high in electrolytes. Thus within the Gerbillinae, three desert species have developed different ways of coping with their arid environment.

Showing further that desert rodents are not equal in their ability to exist on a dry diet, Shkolnik (reported in Shkolnik and Borut, 1969) demonstrated the different abilities of six sympatric species of desert rodents to subsist on a dry diet. Four species, all gerbils, were able or very nearly able to maintain weight on the dry diet, while two murids of the genus Acomys could not maintain weight. From the maximum urine concentrations attained by these six sympatric species, it is apparent that the four species of gerbils, when fed the dry diet,

survived by virtue of their great ability to concentrate their urine, while the Acomys spp lost weight rapidly when fed the same diet because of their more limited powers of concentrating their urine. However, Shkolnik and Borut (1969) showed from field studies that Acomys spp survived as well as the gerbils in the desert, not by producing a very concentrated urine and cutting down water loss as many other desert rodents do, but by increasing water intake by eating succulent vegetation for food.

From such comparative studies, it has become clear that the most important physiological feature enabling desert rodents to subsist solely on dry food is their exceptional ability to concentrate their urine. Such rodents include D. merriami, D. spectabils, Perognathus baileyi, Microdipodops pallidus, Jaculus jaculus, Gerbillus gerbillus and Meriones crassus. Generally this great ability to concentrate urine is not shared by their non-desert relatives, such as D. venustus, D. agilis and P. flavescens, and, not unexpectedly, these rodents cannot survive long without water. Thus it seems likely that the exceptional ability of some desert rodents to concentrate their urine when fed a dry diet is a specific adaptation to enable them to survive in their arid environment.

The relationship between pulmocutaneous water loss and aridity of habitat is less clearcut. The low evaporative water losses common to both desert and non-desert Dipodomys may be phylogenetically primitive features surviving from the time when the Dipodomyines were evolving in the deserts. As pointed out by Church (1966), low pulmocutaneous water loss of the order of that of the Dipodomys can only reduce water loss by a small amount compared with the saving possible by concentrating the urine. Thus the advantage of a lower evaporative water loss to a desert species would be a minor component of its overall adaption to aridity. Consequently, it is not surprising that rodents from the same taxon, irrespective of their habitat, are more likely to have similar evaporative water losses than rodents from similar habitats (Chew, 1965). However, in a few cases, it appears that habitat does have some bearing on evaporative water loss. Some of the non-desert Murids (for example Microtus californicus) have greater evaporative water losses than desert Murids. Interestingly, wild Mus musculus has a comparatively low evaporative water loss. However, although not usually considered a desert species, several workers (Haines and Schmidt-Nielsen, 1967; Koford, 1969; Fertig and Edmonds, 1969) have found it quite tolerant to arid

conditions, even more tolerant than many other non-desert species.

Not all desert rodents owe their success in the desert to their ability to produce a highly concentrated urine. The desert wood-rat of America, Neotoma lepida, cannot concentrate its urine any more than coastal Neotoma spp (Lee, 1963). Instead it, and others such as Acomys cahirinus and A. russatus, survive in the desert by selecting succulent vegetation as food.

While quite a lot is now known of how rodents survive in the deserts of the northern hemisphere, very little is known of the rodents living in the deserts of Central Australia. To further this knowledge I have investigated the water requirements of three species of Australian rodents, Notomys alexis, N. mitchelli and Pseudomys minnie. N. alexis and P. minnie are found in the arid centre, while N. mitchelli inhabits the semi-desert areas of southern Australia.

These three species of rodents are members of the subfamily Pseudomyinae (Simpson, 1961) within the family Muridae. Simpson (1961) considers that the Pseudomyines have developed from a common ancestor which arrived in Australia no later than Miocene. The Notomys spp are now almost completely confined to Central Australia, and are

found only in desert or semi-desert areas. The Pseudomys spp, however, are more widely distributed with representatives also in south-eastern Australia and Tasmania. This present distribution of the Notomys and the Pseudomys indicates that they may have arisen fairly early in the radiation of the Pseudomyines. The karyotypes of the Pseudomys and Notomys also suggest that these two genera are phylogenetically not very closely related (Kennedy, 1969). Unfortunately, however, no fossils which might resolve their origin further have yet been found.

Still, it seems likely that the Notomys evolved in the North of Australia during a time of extreme aridity, when the continent was even drier than it is today (Tate, 1951), and then spread south to the central desert areas it now inhabits. The Pseudomys, however, appear to have radiated northwards from the southern part of the continent. Therefore it is likely that the two desert species N. alexis and P. minnie have different evolutionary backgrounds, N. alexis belonging to a genus which evolved in a desert, while P. minnie is a derivative of a genus which apparently radiated in a temperate or semi-arid climate. A study of the water balance of these species will indicate whether or not they have independently developed similar ways of coping with the aridity of the desert and what are

the most important factors enabling them to overcome this problem. It was also of interest to study the tolerance of N. mitchelli to aridity to see if there is any feature of its water metabolism which may be limiting its distribution to the semi-desert areas it now occupies.

The comparison of the water metabolism of the three species of rodents was based on the usual comparative approach used by previous workers. The rodents were all fed the same diet, kept under the same laboratory conditions and their avenues of water intake and water loss studied both while they were allowed to drink and when they were denied water.

But I also investigated the immediate response of rodents to the sudden withdrawal of water, a feature of water metabolism largely ignored by other workers. Although the long-term response to aridity shows the overall ability of the animal to survive in the desert and the physiological mechanisms important for conserving water, they do not show how the animal overcomes the critical stage in its water balance, the time when it is adjusting to the new, more arid conditions. In an environment where the heat from the sun is intense and surface evaporation great, the amount of water available may change greatly from day to day. Rapid adjustment to decreased

water rations and the ability to restore water balance quickly if water momentarily becomes available must also be important for survival in the desert. A study of the daily changes in body weight, food intake, water loss and activity will show how well and how quickly these rodents can adjust to acute water deprivation, and how quickly they can return to normal water balance when given water again. In this study I have investigated these immediate responses to see how they are related to each other, and to the overall ability of the rodents to survive without water.

2. DISTRIBUTION AND HABITAT

2. DISTRIBUTION AND HABITAT.

2.1 Notomys alexis.

This species is widely distributed throughout Central Australia and occurs as far north as Tennant Creek, Northern Territory, and south to the Musgrave Ranges in northern South Australia. Much of this country is desert with very hot summers and an irregular rainfall averaging less than 10 inches a year.

The mice dig their burrows in the red sand of lightly-wooded, grassy plains, where the dominant grass, Triodia pungens (Spinifex), grows in dense tussocks about a yard apart. The entrance to the burrow is a hole about two inches in diameter dug between the tussocks and it leads to a vertical shaft which flattens out into a horizontal passage about two feet below the ground. Along this passage, or in an offshoot from it, there is a nest chamber lined with finely shredded grass. Often the offshoots from the main passage end in their own vertical shaft and pophole, so that one burrow may have up to five entrances.

2.2 Notomys mitchelli.

Originally this species was plentiful on the inland plains of southern New South Wales and northern Victoria, and across South Australia into south Western Australia. Now it is rare near settled areas and is mostly known from

the Murray Mallee and Eyre Peninsula. These localities have moderately warm summers and an annual rainfall of about 15 inches.

The mice dig burrows in grey sandy soil which supports a dense vegetation of mallees (Eucalyptus spp.), broombush (Melaleuca uncinata) and many smaller shrubs and grasses including the tea tree, Leptospermum coriaceum, and spinifex. The burrows are very similar to those of N. alexis, though often less complicated and with fewer entrances.

2.3 Pseudomys minnie.

This species occurs chiefly in northern South Australia and its range extends from Marlo Bore in the west to the Queensland border in the east. This area includes some of the driest parts of Australia and has an average rainfall of less than 5 inches a year.

The mice prefer the open gibber plains where the soil is brown, heavy in texture and relatively saline. The vegetation is sparse and includes the grass Agrostis spp. and the chenopods bluebush (Kochia spp.) and saltbush (Atriplex spp.). After rain, annuals such as Helipterum spp. and Bassia spp. are prominent.

Burrows I have dug out had several entrances and were usually found under shrubs. They were shallow with the

nest chamber never more than a foot below the surface. The passages extended obliquely into the ground and frequently changed direction, making the burrows more complex than those of either N. alexis or N. mitchelli.

2.4 Food.

Observations in the field and analyses of stomach contents show that these three species of mice eat mainly seeds supplemented with some green herbage and a few insects (Finlayson, 1939a and b, 1940; Watts, 1970).

In captivity, the mice thrive on a diet of hulled oats, sunflower seed and mixed birdseed.

2.5 Reproduction.

Both N. alexis and P. minnie, and probably N. mitchelli, are opportunistic rather than seasonal breeders. Finlayson (1940) caught pregnant N. alexis and P. minnie in both summer and winter, but more frequently after good rain.

In captivity, so long as the mice are given ample food and moisture, they continue to breed throughout the year.

3. EXPERIMENTAL ANIMALS

3. EXPERIMENTAL ANIMALS.

3.1 Capture.

During a trip to Central Australia in July 1968, Dr. C. Watts and I collected *N. alexis* and *P. minnie*. *N. alexis* were plentiful near Yuendumu Settlement, 185 miles W.N.W. of Alice Springs, Northern Territory. We caught *P. minnie* near Marlo Bore, 80 miles west of Oodnadatta, South Australia.

The *N. mitchelli* were collected from Cleve and Kyancutta, both on Eyre Peninsula, South Australia, by Mr. P.F. Aitken, Curator of Mammals at the South Australian Museum.

All mice were caught either by digging out their burrows during the day or by netting animals illuminated by a spotlight at night.

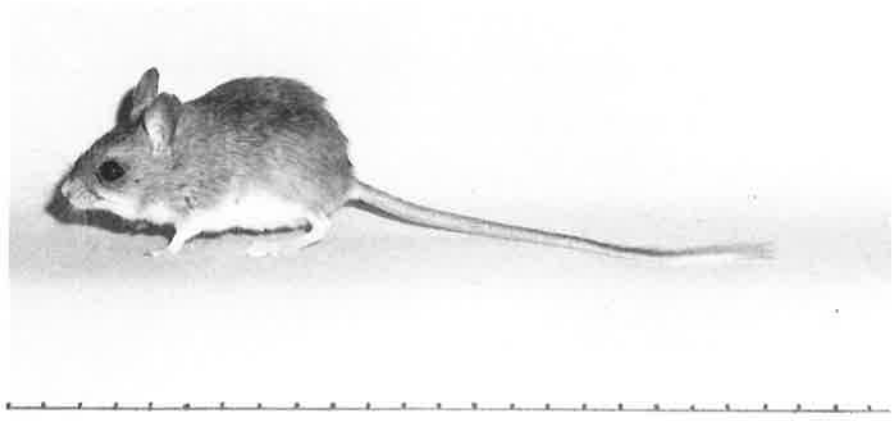
N. alexis is the smallest of the three species studied, the adults weighing between 25 and 35 g. (see fig. 1A). They are very like the jerboas found in deserts of the old world, with very long hind feet, a long tail with a tuft of hair at its tip, and large ears and eyes. When moving slowly they go on all fours like the less specialised murids, but when moving quickly, they are bipedal (Finlayson 1940).

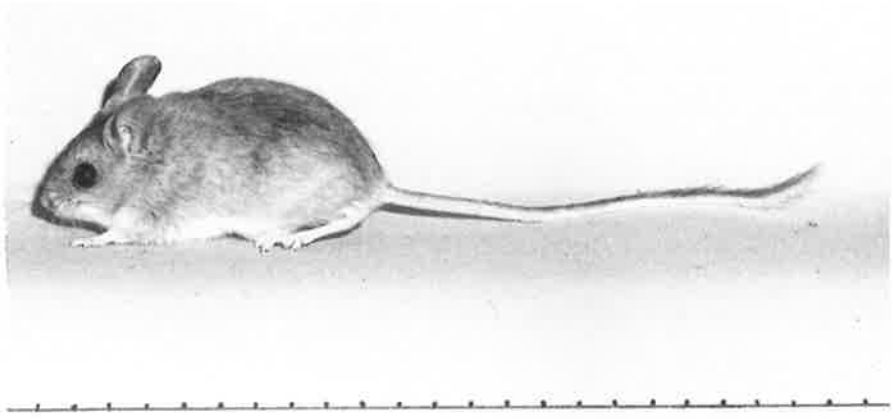
FIG. 1. One scale division represents 1 cm.

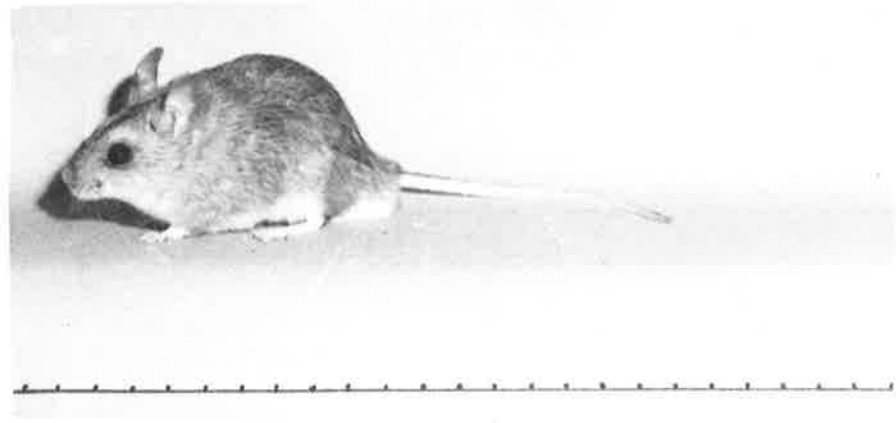
A. Adult male *N. alexis*.

B. Adult female *N. mitchelli*.

C. Adult male *P. minnie*.







N. mitchelli is very similar to N. alexis but is slightly larger, adults weighing between 40 and 50 g. (see fig. 1B).

P. minnie resembles a small brown rat except for its larger ears and eyes, and softer fur (see fig. 1C). Adults weigh between 45 and 60 g.

3.2 Caging.

The mice were housed individually in 52x35x22 cm metal cages which contained ample food, water, a wooden nest box lined with strips of paper, and an activity wheel. The floor of the cage was covered with a layer of sand about one centimeter deep.

The cages were kept in a constant temperature room which was lit by natural light. The ambient temperature of the room was 21 $\pm$ 1 ^{o}C and the relative humidity varied between 30 and 60 percent.

Equal numbers of males and females were used in experiments, and wherever possible an individual was used in only one experiment.

Details of each experiment are described in the appropriate section.

4. WATER CONSUMPTION.

4. WATER CONSUMPTION.

It is often suggested that how much water an animal drinks in the laboratory reflects how much water it requires in the wild, which in turn depends partly on the aridity of the environment. Odum (1944), Lindeborg (1952), and Carpenter (1966) have already correlated the amount of water drunk by a number of rodents with the aridity of their habitats; in their studies animals from moist habitats drank more water than those from dry habitats.

However, this relationship between water intake and aridity is by no means universal. For example, desert species of Neotoma drank approximately twice as much water as coastal Neotoma (Lee, 1963). MacMillen (1964a) was also unable to verify this relationship with Peromyscus species.

As a guide to how much water an animal can be expected to drink, many workers, including Hudson (1962), Lee (1963), and Chew (1965) have used an equation derived by Adolph (1949) to predict water intake from body weight alone. This equation is purely empirical as it is based on the measured water intake of more than fifty mammals ranging from shrews to elephants. Adolph plotted water consumption, I (cc water/g/day), against the logarithm of body weight, W (g), and obtained the equation $I=0.24\ W^{-0.12}$.

Hudson (1962) compared water intakes predicted from this equation with the measured amount of water drunk by 14 species of rodents. These data further show no fixed trend relating water intake to differences in habitat. In addition, there was little agreement between the predicted and measured intakes. It is apparent from these collected data that a comparison of water intakes of different species is complicated by the variety of conditions under which the data were collected. Humidity, temperature, moisture content of the food, activity, and nutritional state all affect the amount of water an animal drinks in the laboratory. More than one study on the same species often shows the extent to which different conditions can alter water intakes. For example, Hudson (1962) reported that Dipodomys agilis drank 12.1 percent of its body weight per day while Carpenter (1966) reported a value of 28.4 percent.

It appears, therefore, that how much water an animal drinks in the laboratory is of limited value. At best, only in the same study where conditions are as uniform as possible can water intakes be compared with any confidence at all.

Adolph's equation also has limited use, since it gives only a rough guide to water intake. His equation was designed to show the relationship between water intake and

body weight of animals ranging in size from a mouse to an elephant. It is not sensitive enough when used over weights ranging from 20 to 100 grams, since variations due to other influences quash any difference due to body weight.

4.1 Methods.

To measure how much water the mice drank in the laboratory, graduated drinking tubes (modified 50 ml burettes) filled with tap water were attached to the cages so that the mice could reach only the open mouths of the tubes. Any water spilt by the mice fell into petri dishes beneath the tubes. Readings were taken only when no spillage occurred.

The mice were allowed a week to become accustomed to drinking from the tubes. One drinking tube was used to measure evaporation. Each day for 10 days the amount of water drunk by the mice was measured to the nearest 0.1 ml, and every second day the mice were weighed to the nearest 0.1g. Throughout the experiment the mice were fed hulled oats which had a moisture content of 10 percent.

4.2 Results.

N. mitchelli drank on the average almost twice as much water per gram of body weight as either N. alexis or P. minnie (table 1). There was no significant difference between the amounts drunk by N. alexis and

P. minnie. The higher water intake of N. mitchelli was also more variable than the relatively lower intakes of N. alexis and P. minnie. This greater variability could not be attributed to greater differences in body weight (table 1), or to age or sex, since equal numbers of adult males and females from each species were used.

TABLE 1

Water intake and body weight of

N. alexis, N. mitchelli and P minnie.

Species	Sample size	Water intake[a] (% body wt./day)	Body weight[a] (g)
N. alexis	23	7.9 ± 1.1	32.2 ± 1.4
N. mitchelli	11	13.7 ± 4.0	37.5 ± 2.0
P. minnie	24	7.3 ± 1.2	46.8 ± 1.8

a. Mean ± 2 S.E.

4.3 Discussion.

The two desert species of rodents, N. alexis and P. minnie drank significantly less water than N. mitchelli. When the amount of water the rodents drank was compared with that predicted from Adolph's equation, N. alexis and P. minnie drank about half that predicted, while N.mitchelli

drank only slightly less than predicted (table 2).

TABLE 2.

Measured water intakes of N. alexis, N.mitchelli and P. minnie compared with the water intake predicted from body weight (Adolph, 1949)

Species	Water intake (percent body weight per day)	
	Measured	Predicted[a]
N. Alexis	7.9	15.8
N. Mitchelli	13.7	15.5
P. minnie	7.3	15.2

a. Calculated from the equation

$I\ (cc\ H_2O/g/day) = 0.24\ W(g)^{-0.12}$

where I is the amount of water drunk

and W is the body weight of the animal.

These results support the proposed relationship between water intake in the laboratory and aridity of the environment, and suggest that N. alexis and P. minnie need less water and are physiologically better adapted to an arid environment than N. mitchelli.

However, MacMillen and Lee (1969) have also studied the water requirements of N. alexis. They reported that their N. alexis drank on the average 14 percent of their body weight per day (range 10 to 70 percent), a value almost twice as much as the value I obtained. This discrepancy underscores further the variability of water drunk in the laboratory, and even though my results do suggest a relationship between water intake and aridity, I still consider that little value should be placed on how much an animal drinks in the laboratory when deciding whether or not it is well adapted to live in an arid environment. A far better and more direct method is to see how long the animal survives when given no water to drink.

5. WATER DEPRIVATION.

5. WATER DEPRIVATION.

Some desert rodents when given no water to drink can survive in the laboratory indefinitely on a dry seed diet. They include the kangaroo rat, Dipodomys spectabilis (Schmidt-Nielsen et al., 1948a), the pocket mouse, Perognathus baileyi (Bartholomew and Cade, 1957), the kangaroo mouse, Microdipodops pallidus (Bartholomew and MacMillen, 1961), the Egyptian gerbil, Gerbillus gerbillus (Burns, 1956), and the Mongolian jerboa, Meriones unguiculatus (Robinson, 1959). This ability indicates that these rodents need only a small amount of water to survive.

Although denying an animal water to drink is rather an extreme procedure, how long it survives does reflect the extent to which it is adapted to limited amounts of water. The purpose of this next experiment was to study the effect of water deprivation on the Australian mice.

5.1 Methods.

The mice were kept individually in the cages described previously and were fed only hulled oats. Initially, they were given water to drink, but once they had maintained a constant body weight for a fortnight, this water was removed. N. alexis and P. minnie were not given water again until 60 days later, while N. mitchelli were denied it for 30 days.

Throughout the experiment, I weighed the mice to the nearest 0.1 g. every second day, and recorded any deaths. However, if an animal was obviously going to die (i.e. it could no longer feed itself), I attempted to revive it, but recorded it as dead in the results. Unfortunately, though, only 2 out of 11 such animals recovered.

Ten mice from each species were given water throughout the experiment and acted as controls.

5.2 Results.

5.2.1 Mortality of mice deprived of water.

Of 20 N. alexis denied water, only one died during the experiment, 12 days after the water was removed, while 4 of the 20 P. minnie died, on respectively the 18th, 25th, 43rd and 54th days. N. mitchelli had the greatest mortality with 4 of 10 animals dying 5, 21, 25 and 29 days after deprivation. On the 30th day, because of the large number of deaths and because it seemed unlikely that the remaining 6 mice would survive much longer, I ended the experiment by giving them water to drink. Even so, 2 of these mice failed to recover and died 10 days later.

Table 3 which summarises the deaths of mice shows that the N. mitchelli which died could not withstand as great a loss of weight as the P. minnie. Figure 2 shows the changes in body weight of some of the mice which died. All of these mice lost weight rapidly until their death.

FIGURE 2.

Changes in body weight of some of the mice which died when denied water. Each line represents the change in weight of an individual animal.

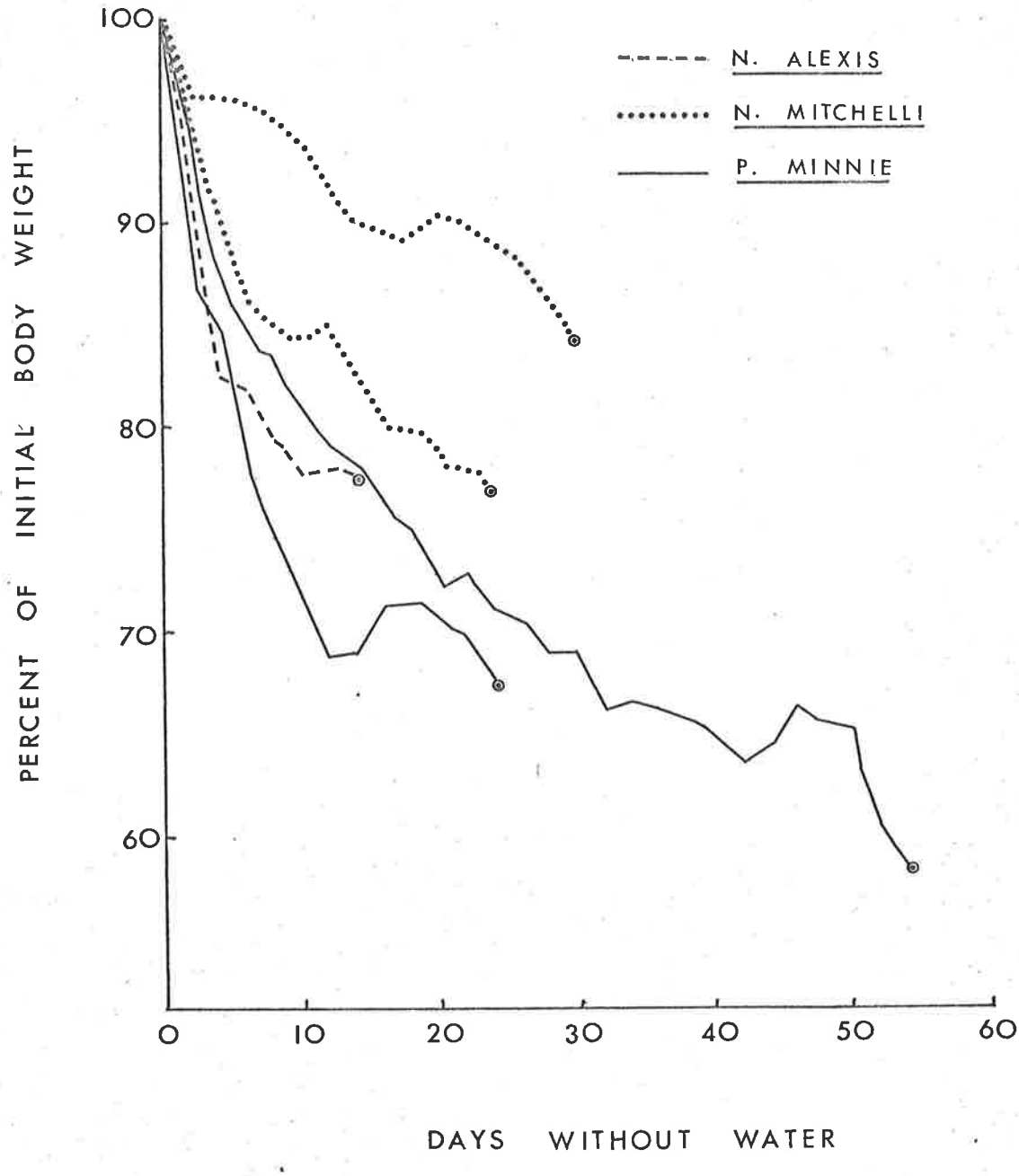

N. ALEXIS
N. MITCHELLI
P. MINNIE
PERCENT OF INITIAL BODY WEIGHT
100
90
80
70
60
0
10
20
30
40
50
60
DAYS WITHOUT WATER

TABLE 3

Mortality of Mice Deprived of Water

Species	Sample Size	No.dead 30 days after water deprivation	% Mortality	% initial body weight at death
N. alexis	20	1	5	77.8
P. minnie	20	2	10	62.2(58.2-67.7)
N. mitchelli	10	4	40	78.0(65.8-85.8)

Values in parenthesis indicate the range.

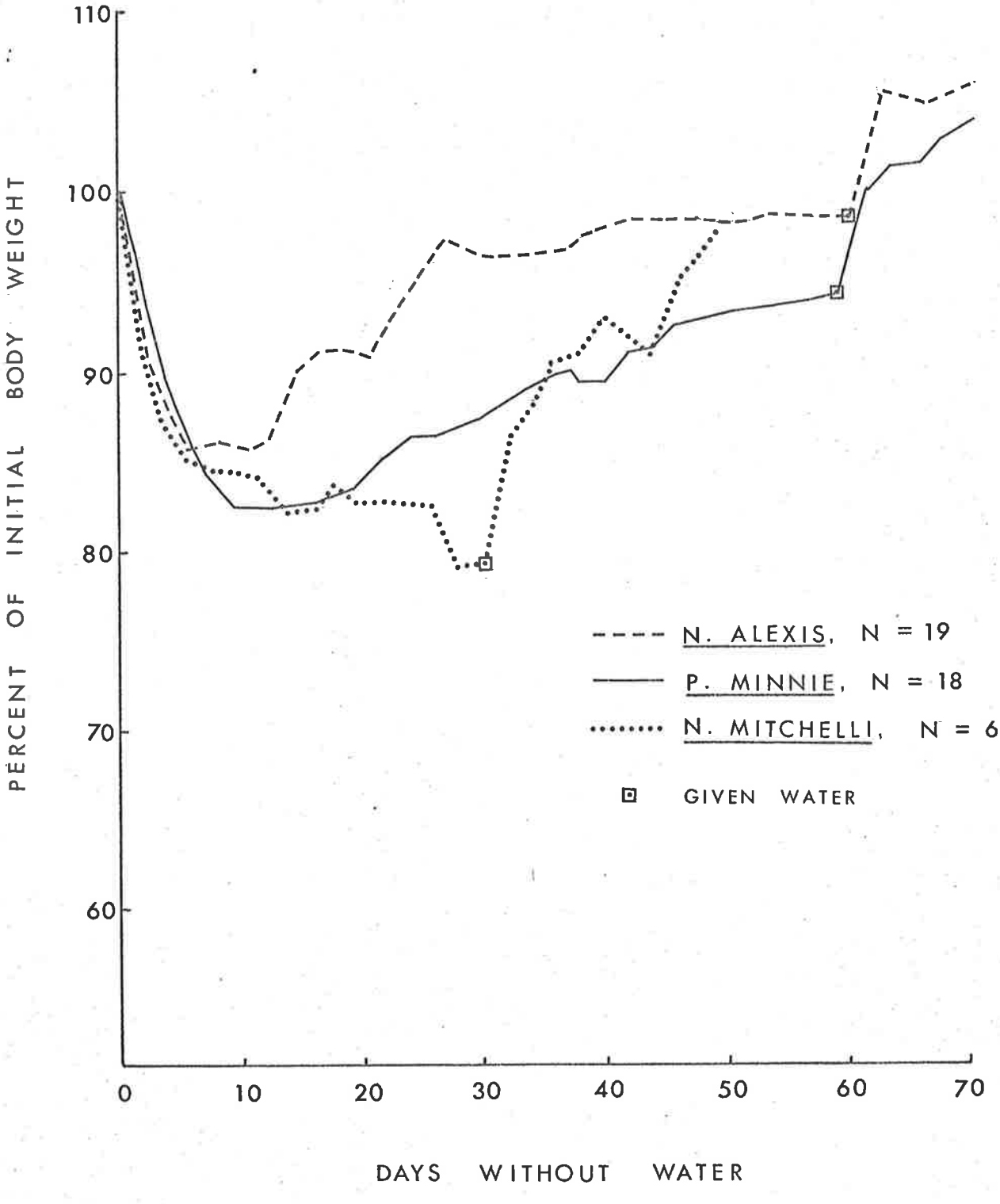
5.2.2 Changes in weight of mice deprived of water

Changes in body weight of those mice which survived the experiment are shown in table 4 and figure 3. During the first 10 days, the mice lost weight rapidly. N. alexis and P. minnie thereafter gained weight slowly and by the 60th day they had returned almost to their original weight. However, N. mitchelli continued to slowly lose weight throughout the experiment, so that by the 30th day they had lost over 20 percent of their original weight.

When the mice were given water at the end of the experiment, they all rapidly increased in weight by about

FIGURE 3.

Changes in body weight of the mice which survived when denied water. N. is the sample size. Each point represents the average body weight of the mice from each species expressed as a percent of the initial average body weight of the same mice at various times after water deprivation.


PERCENT OF INITIAL BODY WEIGHT
110
100
90
80
70
60
0
10
20
30
40
50
60
70
DAYS WITHOUT WATER
N. ALEXIS, N = 19
P. MINNIE, N = 18
N. MITCHELLI, N = 6
GIVEN WATER

4 to 8 percent during the first 2 days. Twenty days later, most of the mice had returned to their original weight.

TABLE 4.

Changes in Body Weight of Mice deprived of Water

Species	Sample Size	% initial body weight at various times after water deprivation.			% initial weight after given water for 20 days
		10 days	30 days	60 days	
N. alexis	19	85.9	96.1	98.7	107.0
P. minnie	18	81.9	85.5	94.1	104.8
N. mitchelli	6	84.4	79.3	-	98.5

5.2.3 Body weight and mortality of mice given water.

Of the 10 mice from each species given water throughout the experiment, one N. alexis, one N. mitchelli and two P. minnie died. Except for one P. minnie, which accidentally drowned, the cause of their deaths is not known. The body weights of these control animals remained fairly constant throughout the experiment (table 5).

TABLE 5

Changes in Body Weight of Mice given Water

Species	Sample Size	Percent of initial body weight		
		10 days	30 days	60 days
N. alexis	9	97.5	99.7	102.8
P. minnie	8	98.0	101.7	105.3
N. mitchelli	9	101.0	99.7	-

5.3 Discussion.

The N. alexis and most P. minnie survived for more than 60 days in the laboratory when fed hulled oats with no water to drink. However, almost half of the N. mitchelli had died after 30 days without water. This difference in survival indicates that N. mitchelli require relatively more water than either N. alexis or P. minnie.

The changes in body weight when the mice are denied water are similar to those reported for other desert rodents (Lindeborg, 1952; MacMillen and Lee, 1967, 1969; Koford, 1968). The sudden, initial weight loss and subsequent recovery is most probably due to some physiological adjustment to the reduced water intake. One obvious

factor affecting body weight is the amount of food eaten. Changes in food intake have been investigated in the next section.

A comparison of the survival of these Australian desert mice on a dry seed diet with other similar studies is again complicated by the variety of conditions under which the experiments were done. However, it seems likely that N. alexis and P. minnie are physiologically as well adapted for living in a desert environment as are many of the North American species of rodents, while N. mitchelli needs free water or at least some succulent vegetation to survive.

However, though the response of mice denied water indicates their ability to live under conditions of extreme aridity, it does not explain the mechanisms involved. In the following pages, I have investigated these mechanisms by studying how animals denied water maintain a water balance. In particular, I have studied food intake, urine output, faecal water loss, and activity.

6. FOOD INTAKE

6. FOOD INTAKE.

The only water available to an animal on a dry diet is the free water present in the food and the water formed when the food is oxidised in the body. It is obvious that juicy fruits and green plant material contain considerable free water, but even dry seeds contain 10 to 20 percent water by weight which may benefit an animal.

The value of water from oxidation for desert animals has been pointed out by several authors (Howell and Gersh, 1935; Schmidt-Nielsen and Schmidt-Nielsen, 1952). Although there are no obscure metabolic pathways that produce 'additional' oxidation water as pictured by some earlier authors, it is still sometimes suggested that animals may benefit if they produce more water of oxidation by increasing their rate of metabolism.

However, to form water of oxidation, food and oxygen are required. These, in turn, cause a loss of water in eliminating waste products and in ventilating the lungs, and so any attempt to increase the water of oxidation at the same time increases water loss. Thus a net gain of water is only possible if this loss is less than the water obtained from oxidation. Kangaroo rats, and possibly some other desert rodents, can obtain sufficient water from oxidation alone to balance their losses, but since they are

already in water balance, increasing metabolism to produce more water is unnecessary (Schmidt-Nielsen and Schmidt-Nielsen, 1952). Other mammals, however, which lose more water than they can obtain from oxidation, would only increase their rate of water loss by increasing their metabolism. Therefore, it is no advantage for any animal to increase its metabolism by eating more food.

A decrease in metabolism by eating less food, however, may be of considerable benefit. The decreased metabolic rate spreads the water loss over a longer time, allowing the animal to survive longer than if its metabolism had remained normal. In the extreme case of dormant or aestivating mammals, this decreased metabolic rate results in considerable advantages to water balance.

In support of the latter argument, there are many reports that restricting water intake reduces food intake. When water is suddenly withheld from pocket mice, feeding on the first day drops 37-40% of normal (Chew, 1951; French, 1956), in Rattus norvegicus 48-69% (Chitty, 1954), in white rats 60% (Adolph, 1943) and in Setonyx brachyurus 63% (Bentley, 1960). With continued deprivation, food intake becomes less and less, until almost no food at all is eaten.

Even moderately restricting water intake reduces food intake. White mice given half their normal water intake eat barely enough to maintain their weight at a reduced level (Chew and Hinegardner, 1957). White rats denied water for 22 hours each day eat only 66% of their normal intake (Lepkovsky et al., 1957).

Camels, however, are unusual in that their appetite remains normal until they have lost water equal to 20-25% of their weight; this is an important factor in their adaptation to desert life (Schmidt-Nielsen et al., 1956). The only other mammals which maintain their food intake on a dry diet are those desert rodents highly adapted to desert conditions, e.g. Perognathus penicillatus (Lindeborg, 1952) and Dipodomys merriami (Schmidt-Nielsen, 1964).

But reduced food intake at the same time increases the assimilation of the food that is eaten. Cows restricted to 60% of their normal water intake eat less, but digest their food better so that they obtain the same amount of energy (Balch et al., 1953). Rats also better digest their food when given less to eat (Quimby, 1948). Coprophagy, which is quite common in small herbivores, may be the means by which digestion is increased. In addition, coprophagy will further benefit animals by reducing the amount of undigested material to be excreted,

with the consequent reduction in water loss.

Measuring weight loss is one of the standard techniques used to study the adaptation of animals to a reduced water intake. The total weight lost is a complex result of the weight lost through evaporation and excretion, and the weight lost by reducing food intake. Measuring food intake shows the extent to which changes in body weight of mice denied water are due to changes in the food intake.

6.1 Methods.

Each day I measured how much food the mice ate, and every second day I weighed the mice. For the first ten days the mice were given water, but thereafter they were denied it. N. alexis and P. minnie were deprived for 50 days and N. mitchelli for 30 days.

Because the mice spilt their food on the floor of their cage, I put each food dish in a plastic carton, 15x10x8 cm. Generally this stopped most spillage, but if any mice still littered the floor of the cage, they were omitted from the experiment.

The hulled oats used as food were stored in large plastic bins in the laboratory. I determined the water content of the grain by drying duplicate samples for 24 hours at 105°C. From the amount of food eaten per day, the water content of the oats, their composition, and the

amount of water formed when the various constituents are oxidised, I calculated the free water and the water of oxidation gained from the food.

6.2 Results.

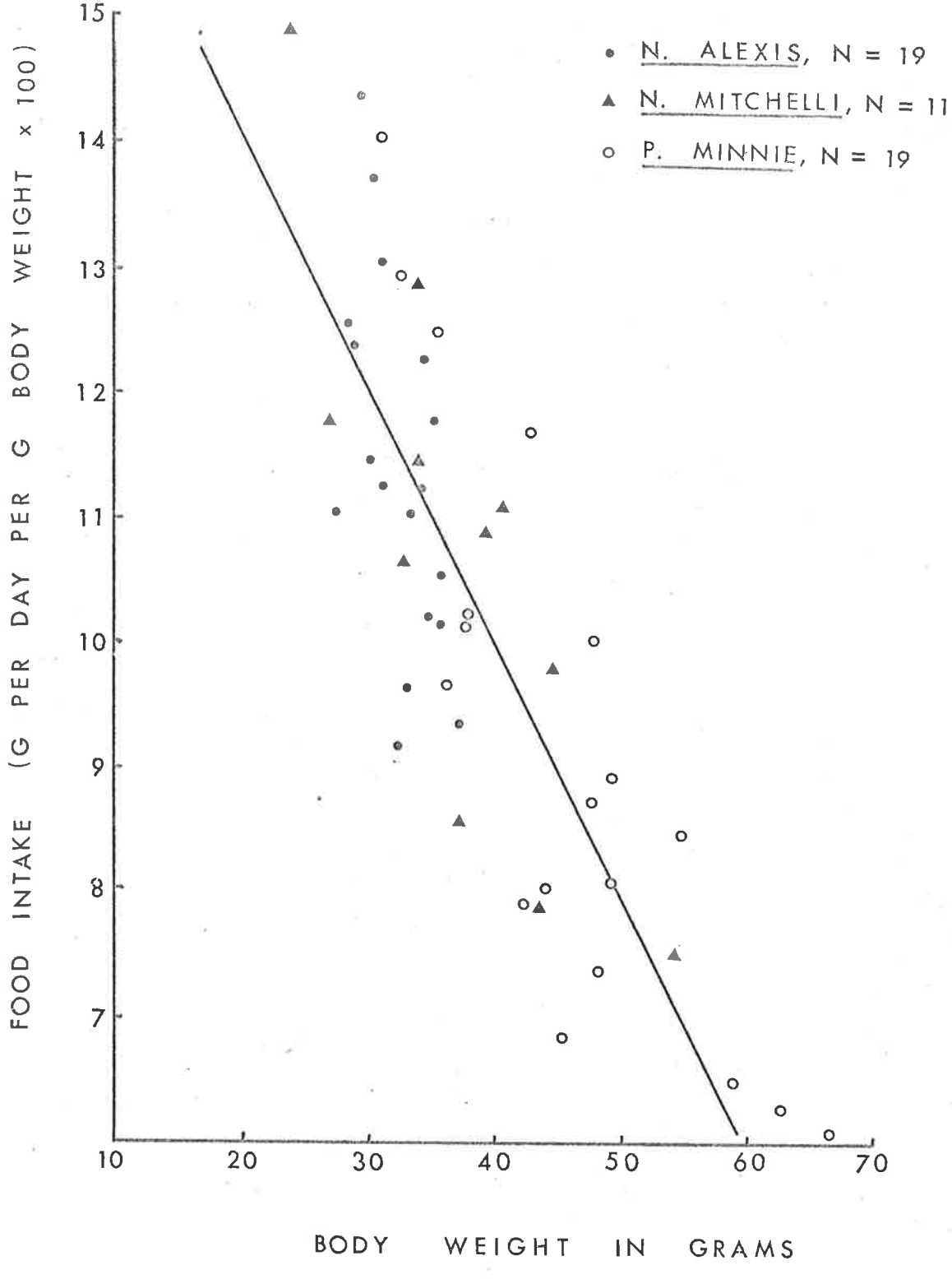
6.2.1 Variation of food intake with body weight.

The amount of food eaten per day per gram of body weight showed an inverse regression on body weight according to the equation $y = 17.98 - 0.20 x$. This equation fitted to the data is shown in figure 4. A large and significant portion of the variance of food intake was explained by the regression ($F = 80.7$, $P < 0.001$), and the regression coefficient differed significantly from zero ($t = 8.97$, $P < 0.001$).

Thus, relative to body weight, small mice eat more food than large mice. This is expected because small animals have a greater metabolic rate per unit body weight than large animals. Recent results on mammals, ranging from mice to cattle, indicate that metabolic rate divided by the three-fourth power of body weight becomes independent of body size (Kleiber, 1961). Since there seems to be no valid objection to applying this correction within species as well as between species, I have expressed the amount of food eaten by the mice in terms of their body weight to the three-fourth power. This expression of food intake should then be independent of the weight of the mice.

FIGURE 4.

Variation of food intake with body weight of *N. alexis*, *N. mitchelli* and *P.minnie* given water. The regression equation, Y = 17.98 - 0.20X, was calculated from the data by the method of least squares.


N. ALEXIS, N = 19
N. MITCHELLI, N = 11
P. MINNIE, N = 19
FOOD INTAKE (G PER DAY PER G BODY WEIGHT x 100)
BODY WEIGHT IN GRAMS
15
14
13
12
11
10
9
8
7
10
20
30
40
50
60
70

6.2.2. Food intake of mice given water.

Table 6 shows the food intake, based on the average daily consumption throughout a 10-day period, of mice given water.

TABLE 6

Amount of Food eaten by Mice given Water.

Species	Sample Size	Average body weight (g)	Average Food Intake (g food/day/$g^{0.75}$)
N. alexis	21	32.0	0.271 ± 0.020
N. mitchelli	10	35.9	0.251 ± 0.025
P. minnie	19	45.3	0.228 ± 0.024

The amount of food eaten by *N. mitchelli* did not differ significantly from that eaten by either of the other two species, but *P. minnie* ate significantly less food than *N. alexis* ($t = 2.8$, $P < 0.01$).

This difference is probably because the *N. alexis* were lean and active animals, while the *P. minnie* were rather fat and lethargic.

6.2.3. Changes in food intake of mice denied water.

Mice denied water decreased their food intake on the average by 40 percent during the first five days without water. This decrease was the same for all species (see figure 5), and was highly significant in each case (see table 7).

During the next 30 days, food intake increased slowly although only in P. minnie did it rise to its original level. In the five days before the mice were given water, N. alexis and N. mitchelli were still eating significantly less food than they were initially.

Five days after the mice were again given water, N. alexis and N. mitchelli had increased their food intake by 19 and 17 percent respectively. P. minnie showed a smaller increase of 5 percent. Ten days later all mice had returned to their normal food intake.

FIGURE 5.

Changes in the food intake of mice denied water. The food was hulled oats. Each point represents the mean daily food intake of each species during the previous 5 days. All mice were denied water on day 10. *N. alexis* and *P. minnie* were given water again on day 60 and *N. mitchelli* was given water again on day 45.

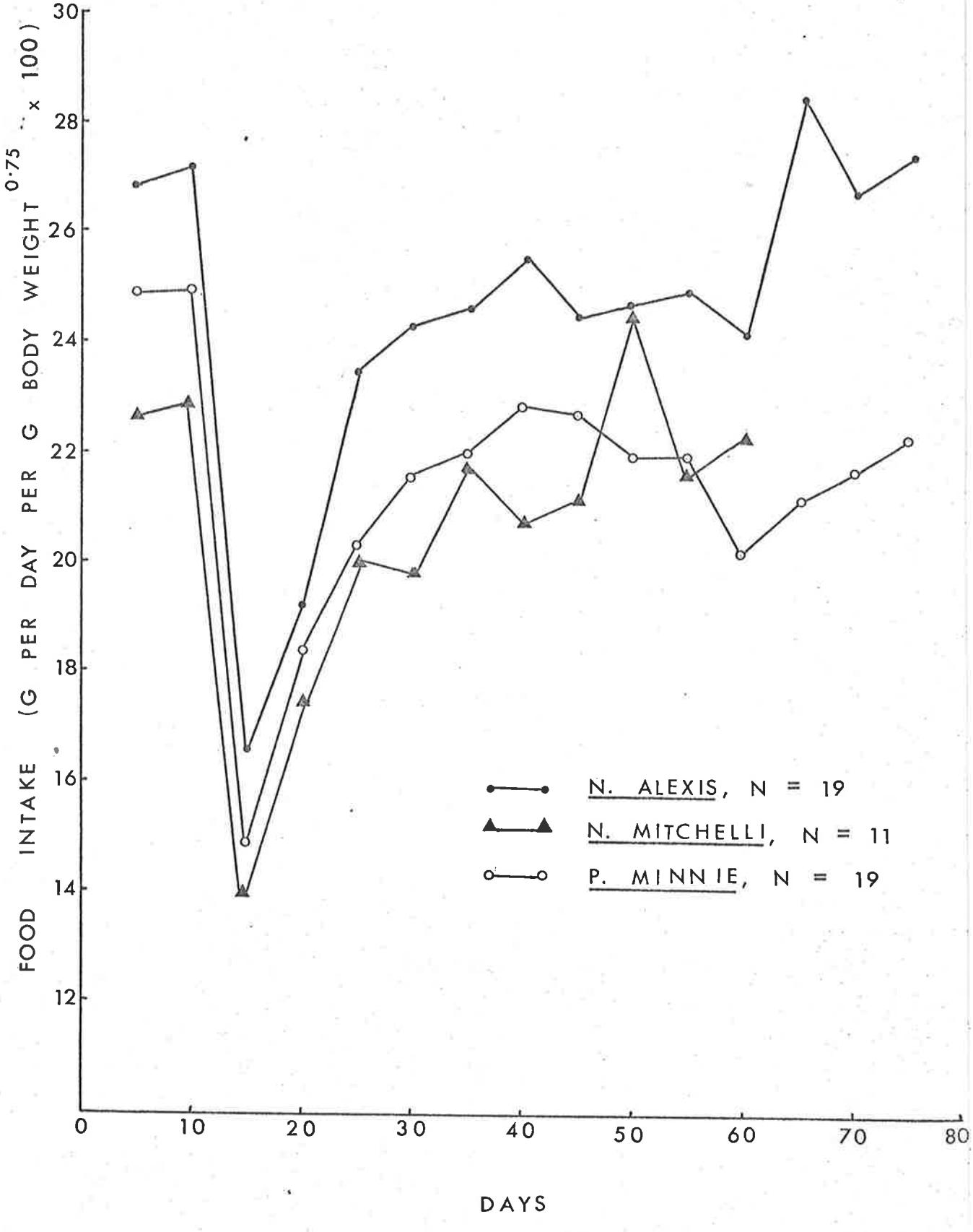

FOOD INTAKE (G PER DAY PER G BODY WEIGHT $^{0.75}$ x 100)
30
28
26
24
22
20
18
16
14
12
0
10
20
30
40
50
60
70
80
DAYS
N. ALEXIS, N = 19
N. MITCHELLI, N = 11
P. MINNIE, N = 19

TABLE 7

Changes in food intake of mice denied water.
All values are expressed in g food/day/$g^{0.75}$.

Species	Sample Size	Given Water	Denied Water		Given Water	
			5 days	50days[a]	5 days	15 days
N. alexis	21	0.271	0.166***	0.242**	0.287	0.265
N.mitchelli	10	0.251	0.149***	0.211**	0.247	0.222
P. minnie	19	0.228	0.139***	0.204	0.213	0.225

a. 30 days for N. mitchelli

Asterisks indicate values differing significantly from the initial food intake.
(***, $P < 0.001$; **, $P < 0.01$)

6.2.4. Water content of hulled oats.

The water content of the hulled oats was determined each time the food bin was refilled. The results in table 8 show very little variation throughout the experiment.

TABLE 8

Water content of hulled oats

Sample	Percent water content of oats			
	1	2	3	4
1	9.76	10.11	9.28	10.16
2	10.34	10.23	9.32	10.37
Average	10.05	10.17	9.30	10.27

In future calculations, I have used a value of 10 percent for the water content of the food.

6.2.5 Water of oxidation and free water in the food.

Crocker and Barton (1953) estimated the amount of protein, carbohydrate and fat in hulled oats. Using their values, and allowing a water content of 10 percent, I calculated the total composition of the food (see table 9).

To obtain the amount of water formed when the various constituents of the food are oxidised, it is necessary to allow for the different digestibilities of the foodstuffs.

Drozdz(1968) determined the digestibility of oats in three species of rodents, Microtus arvalis, Clethrionomys glareolus and Apodemus agrarius. The digestion coefficienus were 80 percent for protein, 84 percent for fat, and 94 percent for carbohydrates, with very little variation between species. Since the error in applying his values to my data is likely to be less than if digestibility is not allowed for, I have used his values to calculate the amount of foodstuff digested per gram of hulled oats eaten (table 9). However, this does not allow for any difference in the digestion of food which there may be between mice given water and those denied it.

TABLE 9

Water obtained when 1 g of hulled oats is eaten

Constituent	g constituent/ g hulled oats	g digested/ g hulled oats	g water/ g constit-uent	g water/ g hulled oats
Protein	0.159	0.127	0.40	0.051
Carbohydrate	0.641	0.603	0.56	0.338
Fat	0.063	0.053	1.07	0.057
Free water	0.100			0.100
Total	0.963			0.546

From the amount of water formed when the various foodstuffs were oxidised (Peters, 1935), I then obtained the water of oxidation gained from the food. Each gram of hulled oats eaten yielded 0.446 g of water of oxidation and 0.100 g of free water (table 9).

Now it is possible to calculate the amount of water obtained from the food per day by mice given water and those denied it for 5 days (table 10).

TABLE 10

Water obtained from the food per day

Species	Food intake (g/day)	Average body weight (g)	Water intake (percent body wt/day)			
			Free water	Oxidation water	Water drunk	Total
Given water						
N. alexis	3.62	32.0	1.13	5.05	7.94	14.12
N.mitchelli	3.68	35.9	1.03	4.57	13.71	19.31
P. minnie	3.89	45.3	0.86	3.83	7.34	12.03
Denied water						
N. alexis	2.04	27.9	0.73	3.26	-	3.99
N.mitchelli	1.92	32.2	0.60	2.66	-	3.26
P. minnie	2.08	38.3	0.54	2.42	-	2.96

6.3 DISCUSSION.

It is commonly observed that mammals on a restricted water intake voluntarily reduce their food intake. Although the Australian mice initially reduced their food intake when denied water, they increased it again after 5 days, and returned almost to normal after 30 days, instead of maintaining it at the lower level, or reducing it further like most other mammals. This ability to maintain a normal food intake when water intake is restricted is associated with the animal's ability to maintain its normal water balance on the reduced water intake. The two species of desert rodents, P. penicillatus and D. merriami, which lose very little water and can obtain all the water they need from oxidation, do not reduce their food intake when on a dry seed diet. However, white mice and rats, dogs, and cattle need much more water. Even when their water intake is only moderately reduced, they can only just maintain a water balance. Since their evaporative and excretory losses are high, by reducing their food intake, and therefore reducing these losses, they can gain a little water. If food intake is reduced sufficiently, water intake and water loss can be balanced. However, there is obviously a limit to the amount food intake can be reduced. since too great a reduction will result in starvation and malnutrition.

The response of N. alexis, N. mitchelli, and P. minnie to water deprivation resembles that of P. penicillatus and D. merriami rather than other mammals. The initial marked decrease in food intake indicates a period during which the mice are adapting to the new reduced water intake and the mechanisms for conserving water are coming into full operation. Once water losses are reduced to a minimum, then food intake can safely increase again without causing any additional water stress, and so reduce the likelihood of starvation.

However, while the functional value of an initial reduction and a subsequent increase in food intake of mice denied water is fairly obvious, the mechanisms which control this integration of eating and drinking are not so clear.

6.3.1 Relationship between eating and drinking.

Such an integration has usually been explained in terms of the stimulation of osmotic receptors in the central nervous system (CNS). These centres controlling feeding and drinking are located close together in the lateral hypothalamus (Grossman, 1962). Carefully placed lesions will alter either drinking or feeding, and so change their quantitative relationship (Smith and McCann, 1962). Most authors consider that food and water intakes stimulate

these osmotic receptors through changes in the volume of extra-cellular water (ECW) of the body, and much evidence has implicated the state of hydration as an important factor in regulating these intakes. For example, dogs and rats, after eating dry food, usually immediately drink (Gregerson, 1932; Kissileff, 1969). These authors suggest that this drinking is due to the animals becoming dehydrated through secreting large amounts of digestive juices. Also animals given watery food eat more than animals given salty food (Cizek, 1959).

Other factors also affect both food and water intake. Distension of the stomach, protein ingestion, increased ambient temperatures and increased calorie intake all produce thirst and food satiation (Jacobs, 1964). In addition, recent evidence suggests that the classical concept of the CNS receptor system of control may also be incomplete. The results of Jacobs (1964) suggest that peripheral receptors in the mouth and gut also transmit information through nerves to the hypothalamus to control the intake of glucose solutions and dry diets. Fitzsimons and Le Magnen (1969) showed that chemoreceptors in the mouths of rats also stimulate thirst after eating. Thus the theory behind the mechanism of control of eating and drinking is becoming much more complex.

However, often short-term satiation of hunger can still be most simply and easily explained in terms of dehydration and the classical osmotic receptors in the brain. The argument is that eating food dehydrates an animal, and that this dehydration is monitored by the continual sampling of the blood by the osmotic receptors in the hypothalamus, which responds by decreasing the hunger drive. Thus a thirsty animal reduces its food intake. Conversely, if the animal drinks or becomes hydrated again by restoring water balance, then it becomes hungry and so eats more.

There is some evidence that such a mechanism as proposed above could explain the changes in food intake of the Australian mice denied water. During the first day without water, N. alexis lost an average of 1.4 g body weight (figure 6A). This loss was partly due to the decreased food intake of 0.8 g (figure 6B), and partly due to a loss of water and body tissue which could not be replaced. Since it is unlikely that all the additional loss was due to the loss of body tissue (Kleiber, 1961), the mice were apparently dehydrated by a loss of water of up to 2 per cent of their body weight. By the third day, however, the mice had lost only 3.7 g body weight for a total food deficit of 4.1 g. While this situation is complicated by changes in the food requirement due to

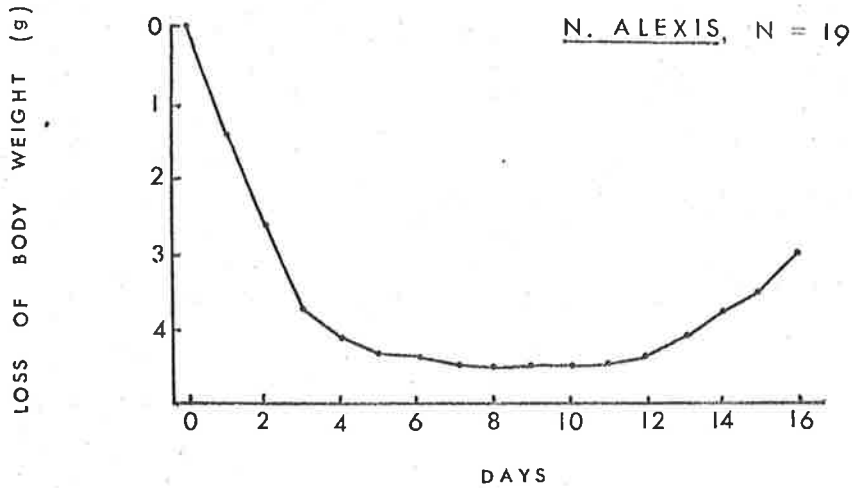
FIGURE 6.

A. Daily change in body weight of N. alexis denied water. N represents the sample size.

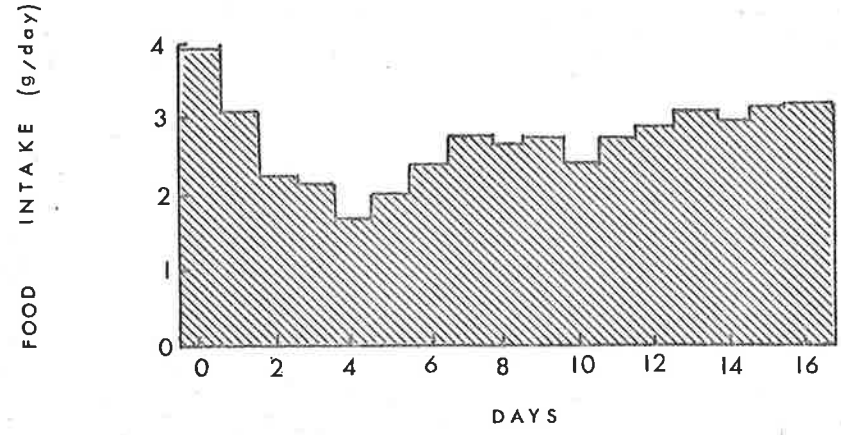
B. Daily change in the food intake of N. alexis denied water. The food was hulled oats.

C. Changes in weight from the previous day minus the changes in food intake from the previous day during the first 16 days N. alexis were denied water.

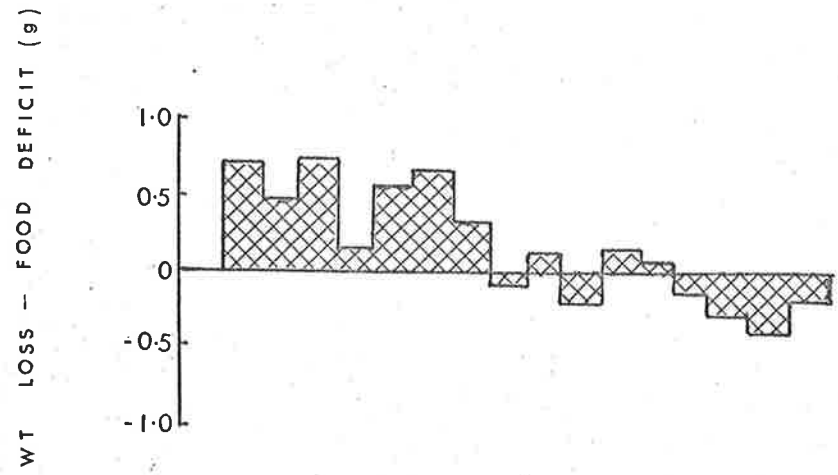
A.


LOSS OF BODY WEIGHT (g)
N. ALEXIS, N = 19
0
1
2
3
4
0 2 4 6 8 10 12 14 16
DAYS

B.


FOOD INTAKE (g/day)
4
3
2
1
0
0 2 4 6 8 10 12 14 16
DAYS

C.


WT LOSS – FOOD DEFICIT (g)
1·0
0·5
0
-0·5
-1·0

changes in metabolism and body weight, the effective food deficit is still likely to be greater than the weight loss. (The food requirement due to the lower body weight alone was only 0.2 g less).

These results suggest that during the first two days the mice were without water, they were losing water, but that during the next two days they made up these losses, and on the 5th day, when food intake increased, they had returned to their original state of hydration. The inference is that water is lost from the body initially before the mechanisms conserving water reduce the losses to a minimum. A study of the mechanisms in later sections supports this explanation further.

The different response shown by most other mammals to water restriction is possibly because they cannot conserve sufficient water to maintain a water balance if food intake again increases. However, those mice highly adapted to the desert life can conserve sufficient water even when food intake remains normal.

It is clear from the literature that the mechanisms controlling the relationship between food and water intake are still not fully clarified. Previous work has been confined solely to those mammals which continue to show a reduced food intake when water intake is restricted. A

study of mice such as those in my study, which regain or partly regain their appetite after an initial decrease, may offer additional opportunities for elucidating the mechanisms further.

6.3.2 Changes in body weight and food intake

Figure 6A and 6B show how closely the changes in food intake were reflected by changes in body weight in N. alexis. During the first four days, the initial drop in food intake was accomplanied by a sudden drop in body weight. In the following days, as food intake increased, body weight remained constant until the 12th day, but increased thereafter.

Figure 6C shows the difference between the change in weight and change in food intake from the previous day. During the first 7 days, the weight loss was greater than that due to the food deficit alone. Between the 8th and 12th days, the total weight change was about equal to the changes in food intake, while after the 13th day, the weight gain was always greater than the food gain. Thus the mice were losing body substance until the 7th day, but were making up their losses after the 13th.

Figure 7A, 7B and 7C show the results for N. mitchelli. They differ in several respects from those of N. alexis. N. mitchelli lost considerably more weight than N. alexis, and their body weight was still decreasing on the 16th day,

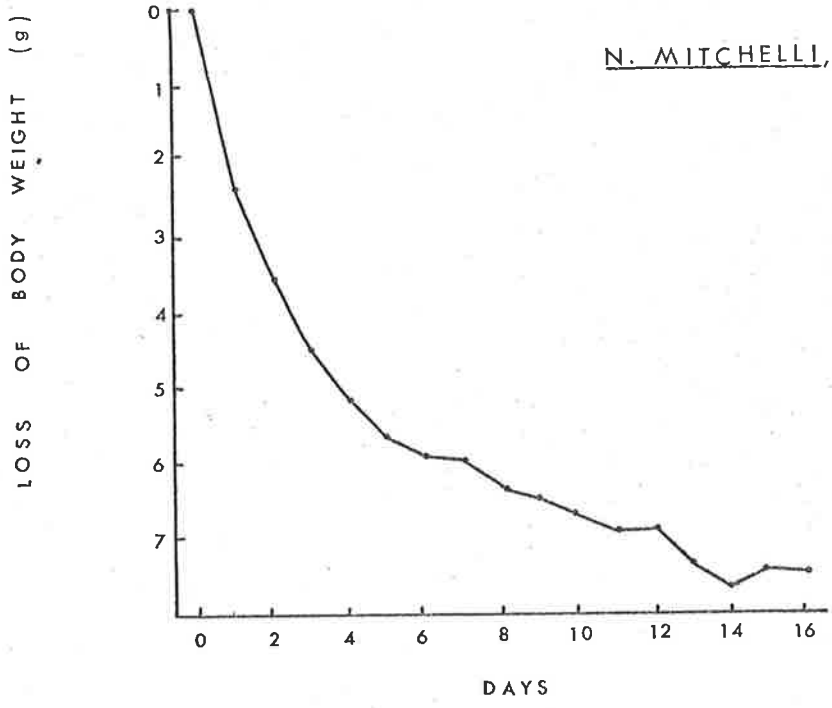
FIGURE 7.

A. Daily change in body weight of N. mitchelli denied water. N. represents the sample size.

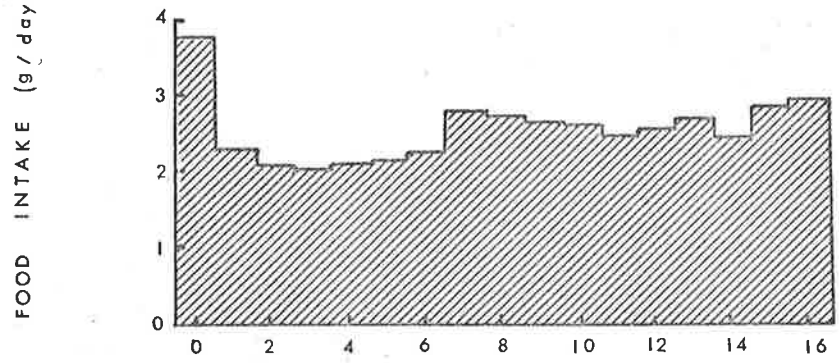
B. Daily change in food intake of N. mitchelli. denied water. The food was hulled oats.

C. Changes in body weight from the previous day minus the changes in food intake from the previous day during the first 16 days N. mitchelli were without water.

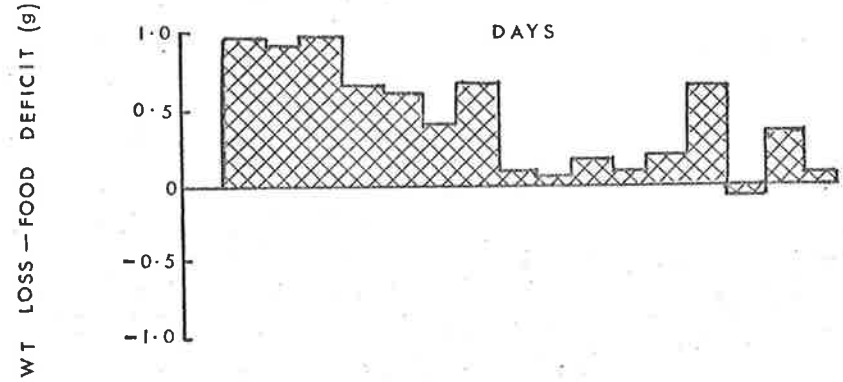
A.


N. MITCHELLI, N = 11
LOSS OF BODY WEIGHT (g)
0
1
2
3
4
5
6
7
0
2
4
6
8
10
12
14
16
DAYS

B.


FOOD INTAKE (g/day)
4
3
2
1
0
0
2
4
6
8
10
12
14
16
DAYS

C.


WT LOSS — FOOD DEFICIT (g)
1·0
0·5
0
-0·5
-1·0

while N. alexis maintained weight from the 6th day. N. mitchelli also ate much less food on the first day without w ater than N. alexis, and food intake increased more slowly after the 3rd day. Throughout the 16 days, the weight change exceeded the change in food intake except on the 14th and 16th days when they were very nearly equal. Thus the N. mitchelli were not making up their initial losses during the latter days as were N. alexis. However, the losses did become proportionately less.

These results show that the changes in food intake were largely responsible for the changes in body weight. However, other losses were also affecting body weight to some extent, particularly during the first 7 days.

6.3.3 Partitioning of total water intake.

The partitioning of the water intake of mice given water and those denied it for 5 days in table 10 (p. 40) shows that water deprivation decreased the total water intake on the average by 77 percent, of which 63 percent was due to the mice not being allowed to drink, and 14 percent due to the reduced food intake. As deprivation continued and food intake increased, however, the total decrease would become closer to 63 percent. Reducing water intake to this extent is obviously quite severe, since to maintain a water balance water loss must be reduced by a

corresponding amount. This indicates further the great ability of these rodents to conserve water.

The importance of oxidation water to the mice can be seen in that it makes up 30 percent of the total water intake for mice drinking water, and 82 percent for mice denied water. Thus N. alexis and P. minnie can gain most, and possibly all, of the water they require from the oxidation of the food. Such an ability is only equalled by a few other desert rodents, for example, Dipodomys spp., Perognathus penicillatus, Jaculus jaculus and Meriones unguiculatus. N. mitchelli on the other hand, cannot obtain all the water they require from oxidation alone, but need additional water either from drinking or from eating food with a relatively high water content.

7. URINARY WATER LOSS.

7. URINARY WATER LOSS.

The kidney, besides excreting the waste products of metabolism and controlling the solute content of the body, regulates the amount of water lost from the body. If water intake is excessive, the kidney produces a relatively dilute urine, so ridding the body of the surplus water. If water intake is scant, the kidney increases the concentration of the urine, so as to eliminate the waste products in as little water as possible and thereby conserve water. Therefore, for desert rodents with little or no water available for drinking reducing water loss by concentrating the urine is exceedingly important in maintaining their water balance.

Schmidt-Nielsen *et al.*, (1948a) were the first to examine in detail the role the kidneys play in conserving water in a desert rodent. They found that the kangaroo rat, *Dipodomys merriami*, could produce a highly concentrated urine, far higher than previously observed in any other mammal. These rodents were therefore able to excrete their waste products in a very small volume of urine which reduced their water loss considerably. This ability was largely responsible for their survival on a diet of dry seed alone.

Other desert rodents can also produce very concentrated urines. *Perognathus baileyi* and *Liomys salvani*, two other American rodents which need very little water, both produce

urine as concentrated as D. merriami (Schmidt-Nielsen, 1964; Hudson and Rummel, 1966). Wild house mice living in salt marshes of western America also produce urine equally as concentrated (Fertig and Edmonds, 1969). Even higher urine concentrations have been observed in Jaculus jaculus, Gerbillus gerbillus, and Psammomys obesus, rodents from Old World deserts (Haggag and El-Husseini, 1966). The ability to produce a highly concentrated urine is, therefore, fairly widespread among small rodents living where water is scarce.

MacMillen and Lee (1967, 1969) have already investigated the concentrating ability of the kidneys of some Australian desert rodents. Their N. alexis produced a urine even more concentrated than the Old World rodents, and was possibly the most concentrated measured for any mammal. The urine from Leggadina hermannsburgensis and N. cervinus was also highly concentrated. To further these studies on Australian rodents, and to determine the role the kidneys play in conserving water, I have measured changes in concentration and volume of urine from N. alexis, N. mitchelli and P. minnie when they were denied water. A study of kidney function may also explain the difference in the ability of N. alexis and P. minnie, and N.mitchelli to tolerate a dry seed diet.

The concentrating ability of the kidney depends on its structure. Sperber (1944), in his extensive survey of the structure of the kidneys from 139 species of mammals, correlated the thickness of the medulla and the length of the papilla with the aridity of the habitat in which the animals live. The seven species of desert rodents he examined had relatively thick medullae and long papillae, features which, according to the current concept of kidney function, are important in forming a highly concentrated urine (Ullrick et al., 1961). I have also examined these two aspects of kidney structure in the Australian desert rodents.

7.1 Methods.

7.1.1 Collection of urine.

To collect urine, the mice were housed individually in cylindrical metal cages, which were 12 cm high x 15 cm in diameter and fitted with wire mesh floors. To accustom the mice to living in these cages, they were put in them 4 days before the first collection. All collections were made at night and the mice were not allowed to eat during the 16-hour collecting period. During the first night in which urine was collected, the mice were allowed to drink, but thereafter they were denied water. Initially the mice were fed hulled oats, but later they were fed sunflower

seed to increase their nitrogen load.

When samples of urine were required to determine urine concentrations, the cages were suspended over large petri dishes containing 1 cm of vitrea oil. Each morning, urine not contaminated with faeces was pipetted into 2 ml plastic vials, and either analysed immediately or frozen at -5°C.

To measure urine volumes, the cages sat on top of large plastic funnels which had 5 ml graduated pipettes fitted to their stems. Each funnel and pipette was filled with vitrea oil. Halfway down the funnel an inverted watch glass separated the urine and faeces which fell into the oil. The urine rolled to the edge of the watch glass and slid down the side of the funnel into the pipette, while the faeces remained where they fell on the watch glass. The urine volume was then read directly in the pipette or run out and measured with micro-pipettes. Preliminary tests showed that the error in determining urine volumes in this way was less than 2 percent for volumes greater than 1.0 ml, and about 10 percent for a volume of 0.2 ml.

7.1.2 Collection of plasma.

The mice were bled twice during the experiments, once while they were allowed water, and then again after they had been denied water for a week. Blood was collected by cardiac puncture while the mice were lightly anaesthetised

with ether. The syringes used to bleed the mice were modified 1 ml plastic "Jintan" disposable syringes. A small piece of glass tubing drawn out at one end to hold a 24 gauge needle was fixed to the end of the syringe with plastic tubing. As soon as the needle penetrated the heart, blood was seen gushing into the glass tubing.

From the syringe, the sample of blood was fed into Dural vinyl tubing (internal diameter 1.40 mm), and the ends of the tubing sealed by heating momentarily in a flame. After centrifuging for 5 minutes at 5000 R.P.M., the end containing the blood cells was cut off and discarded; the other end containing the plasma was resealed and stored under vitrea oil at -5°C until needed.

7.1.3 Analysis of urine and plasma.

Osmotic concentrations of urine and plasma were determined by the freezing point method using a Fiske Osmometer. Whenever possible, undiluted samples were used, but often because of the small volume of the sample and the high concentrations, the urine was diluted as much as 1 in 6 and the plasma 1 in 2.

The concentration of urea in the urine was measured once while the mice were drinking and again after they had been denied water for 3 days. The urea concentration was determined by the method of Conway (1962), using buffered

urease solution prepared from Dunning urease tablets (Wu and Wu, 1951). Aliquots of 0.1 ml of suitably diluted samples were used in duplicate estimations.

7.4.1 Kidney structure.

Kidneys from freshly killed mice were fixed in 5% formalin, embedded in paraffin, then sectioned longitudinally. Sections passing through the cortex, medulla, and papilla were mounted on slides and stained with haematoxylin and eosin. Later, they were examined under a binocular microscope.

7.2 Results.

7.2.1. Urine concentrations.

While drinking water, most mice of each species produced a urine with an osmotic concentration between 200 and 1000 mOsm/l. When they were denied water, however, the concentration of the urine rapidly increased. The maximum urine concentrations were usually observed after 3 days without water. Urine samples taken on the 5th and 7th days were, in all but one experiment, slightly less concentrated than the 3 day samples (figures 8, 9 and 10).

When the mice were fed hulled oats, N. alexis produced the most concentrated urine of the three species (table 11). Both P. minnie and N. mitchelli produced urine significantly less concentrated than N. alexis, but not significantly

FIGURE 8.

Osmotic concentration of urine from N. alexis when given water and denied it. Numbers indicate sample size. Horizontal lines indicate means (M); vertical lines indicate ranges; rectangles enclose the interval $M \pm t_{0.95}S.E.$ Open rectangles indicate mice fed sunflower seed; diagonally hatched rectangles indicate mice fed hulled oats.

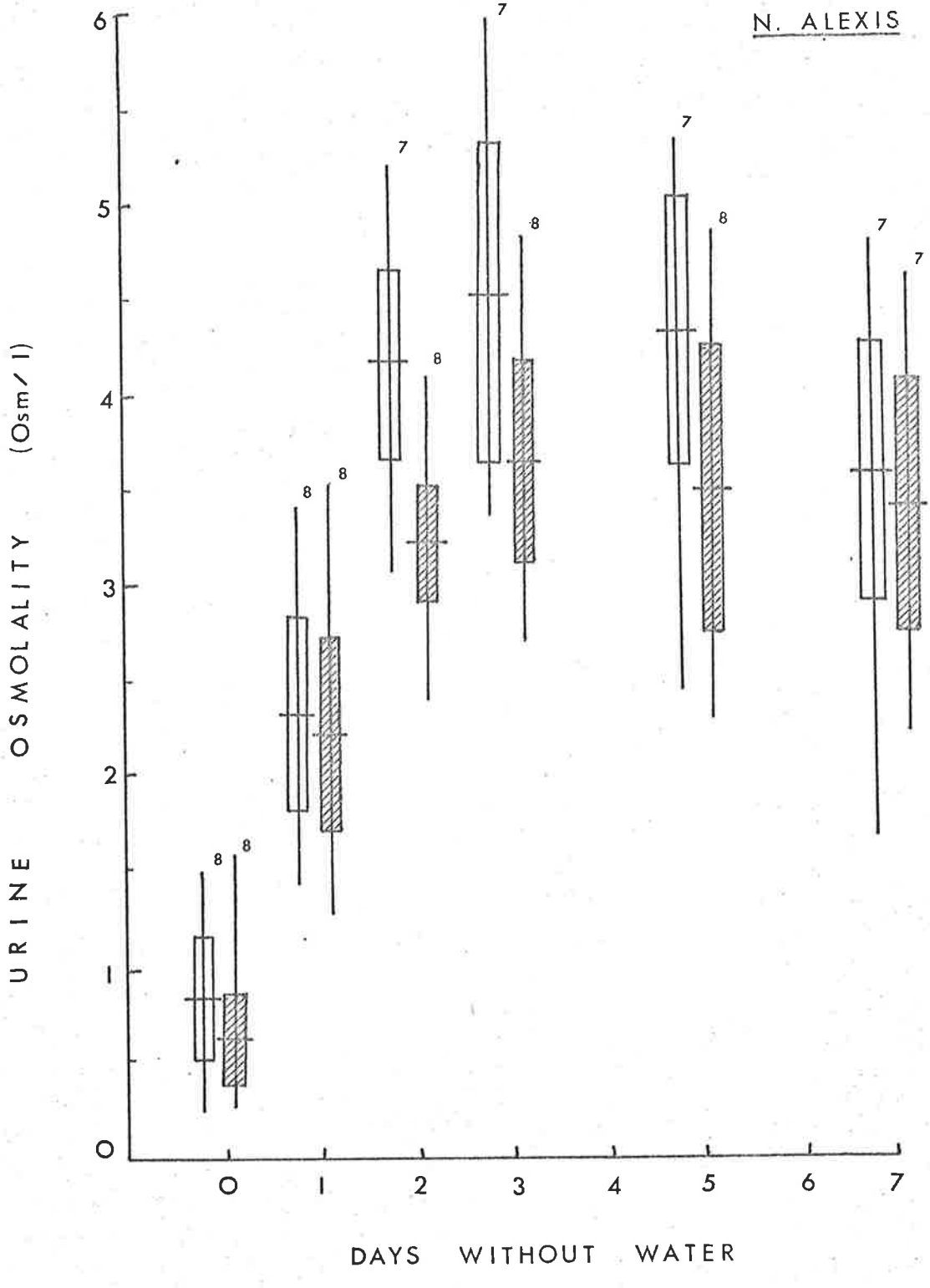

N. ALEXIS
URINE OSMOLALITY (Osm/l)
0
1
2
3
4
5
6
7
8
DAYS WITHOUT WATER

FIGURE 9.

Osmotic concentration of urine from N. mitchelli when given water and denied it. Symbols as in fig. 8.

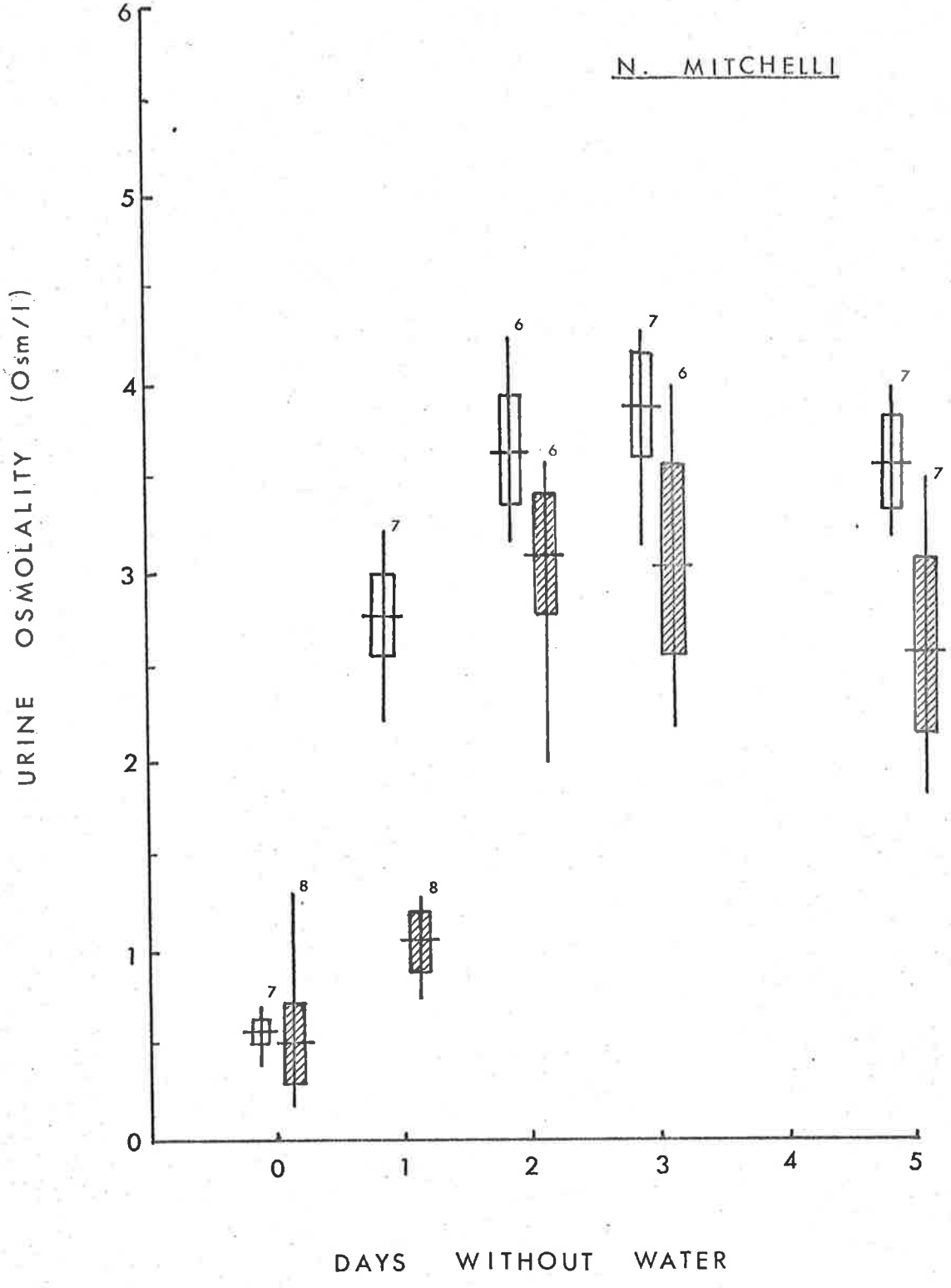
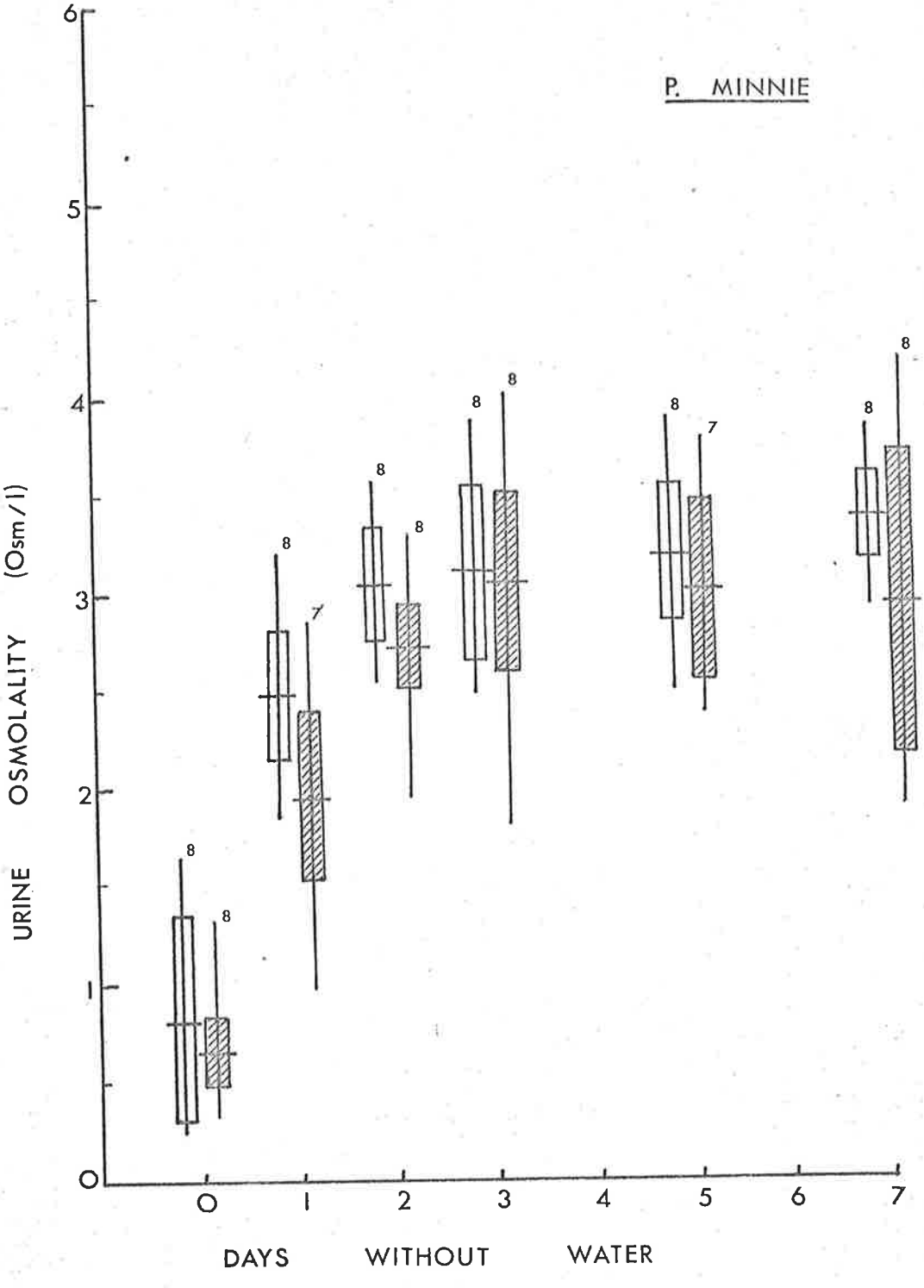

N. MITCHELLI
URINE OSMOLALITY (Osm/l)
DAYS WITHOUT WATER
0
1
2
3
4
5
6
7
8

FIGURE 10.

Osmotic concentration of urine from P. minnie when given water and denied it. Symbols as in fig. 8.


P. MINNIE
URINE OSMOLALITY (Osm/l)
6
5
4
3
2
1
0
0
1
2
3
4
5
6
7
DAYS WITHOUT WATER
8
7

different from each other. N. alexis and N. mitchelli fed sunflower seed produced urine even more concentrated than when they were fed hulled oats. However, P. minnie fed sunflower seed only slightly increased their urine concentration, so that their urine remained the least concentrated of the three species.

TABLE 11

Urine concentration of N. alexis, N. mitchelli and P. minnie three days after the mice were denied water.

Species	Hulled oats		Sunflower seed	
	Mean urine osmolality [a]	Max	Mean urine osmolality [a]	Max
N. alexis	3611 ± 576	4880	4511 ± 822	5990
N.mitchelli	3036 ± 524	4089	3860 ± 351	4256
P. minnie	3061 ± 439	3928	3177 ± 273	3876

[a]. Mean ± 2.S.E.

When the mice were denied water, the concentration of urea in the urine also increased markedly. The highest concentrations were again observed in N. alexis fed sunflower seed, and the lowest in P. minnie fed hulled oats (table 12).

TABLE 12.

Urea concentration of the urine, osmolality of the urine, and the amount of urea in the urine (expressed as a percent of osmolality) of mice given water and those denied water for 3 days.

Species	Mice fed hulled oats				Mice fed sunflower seeds			
	N	Mean Urea (mM/l)	Mean Osmolality (mOsm/l)	Urea (% osmolality)	N	Mean Urea (mM/l)	Mean Osmolality (mOsm/l)	Urea (% osmolality)
N. alexis								
Given water	8	343	670	51.2	8	634	873	72.6
Denied water	8	2355	3611	53.3	7	2985	4511	66.2
N. mitchelli								
Given water	8	284	504	56.3	7	388	612	63.4
Denied water	6	1740	3010	58.7	7	2368	3860	61.3
P. minnie								
Given water	8	564	940	60.0	8	563	813	69.2
Denied water	8	1549	3061	50.6	8	1811	3177	57.0

The amount of urea in the urine varied with the diet. When the mice were fed hulled oats, urea accounted for 50 to 60 percent of the total osmotic concentration of the urine but when they were fed sunflower seed, the urea concentrations were relatively higher and made up 57 to 72 per cent of the total concentration. This was expected since sunflower seed is 28 percent protein, whereas hulled oats is only 16 percent protein.

The ratio of urea to total osmotic concentration decreased in all but two cases when the mice were denied water. This decrease could be the result of the lower food intake of mice denied water, but it may also indicate that urea is retained by the kidney which would aid in further concentrating the urine (Chew, 1965).

7.2.2 Plasma concentrations.

The osmotic concentration of the plasma remained constant regardless of the food eaten and whether the mice were given water (fig. 11).

7.2.3 Urine volumes.

As was expected from the measurements of urine concentration, the volume of urine markedly decreased when the mice were denied water (figs. 12,13 and 14). After 5 days without water the volume of urine decreased to 5.3 percent of the volume produced when water was available in N.alexis, to 3.4 percent in N. mitchelli, and to 6.7 percent in

FIGURE 11.

Plasma osmolality of *N. alexis*, *N. mitchelli*, and *P. minnie*. Numbers indicate the sample size. Horizontal lines indicate means (M); vertical lines indicate ranges; rectangles enclose the interval $M \pm t_{0.95}$ S.E.

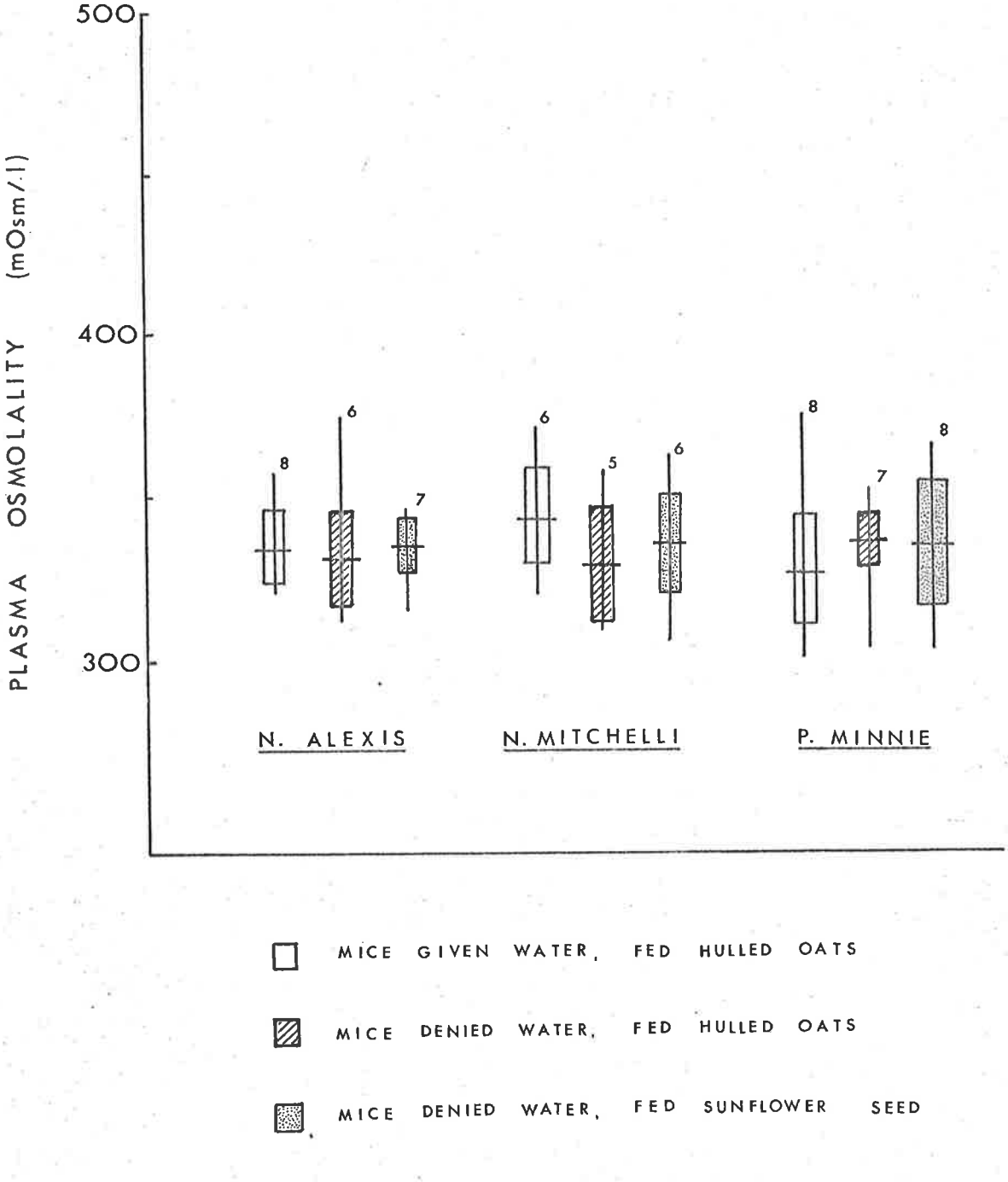

PLASMA OSMOLALITY (mOsm/.l)
500
400
300
8
6
7
6
5
6
8
7
8
N. ALEXIS
N. MITCHELLI
P. MINNIE
MICE GIVEN WATER, FED HULLED OATS
MICE DENIED WATER, FED HULLED OATS
MICE DENIED WATER, FED SUNFLOWER SEED

FIGURE 12.

Volume of urine produced by *N. alexis* when denied water. Numbers indicate sample size. Horizontal lines indicate means (M); vertical lines indicate ranges; rectangles enclose the interval $M \pm t_{0.95}$ S.E. Open rectangles indicate mice fed sunflower seed; diagonally hatched rectangles indicate mice fed hulled oats.

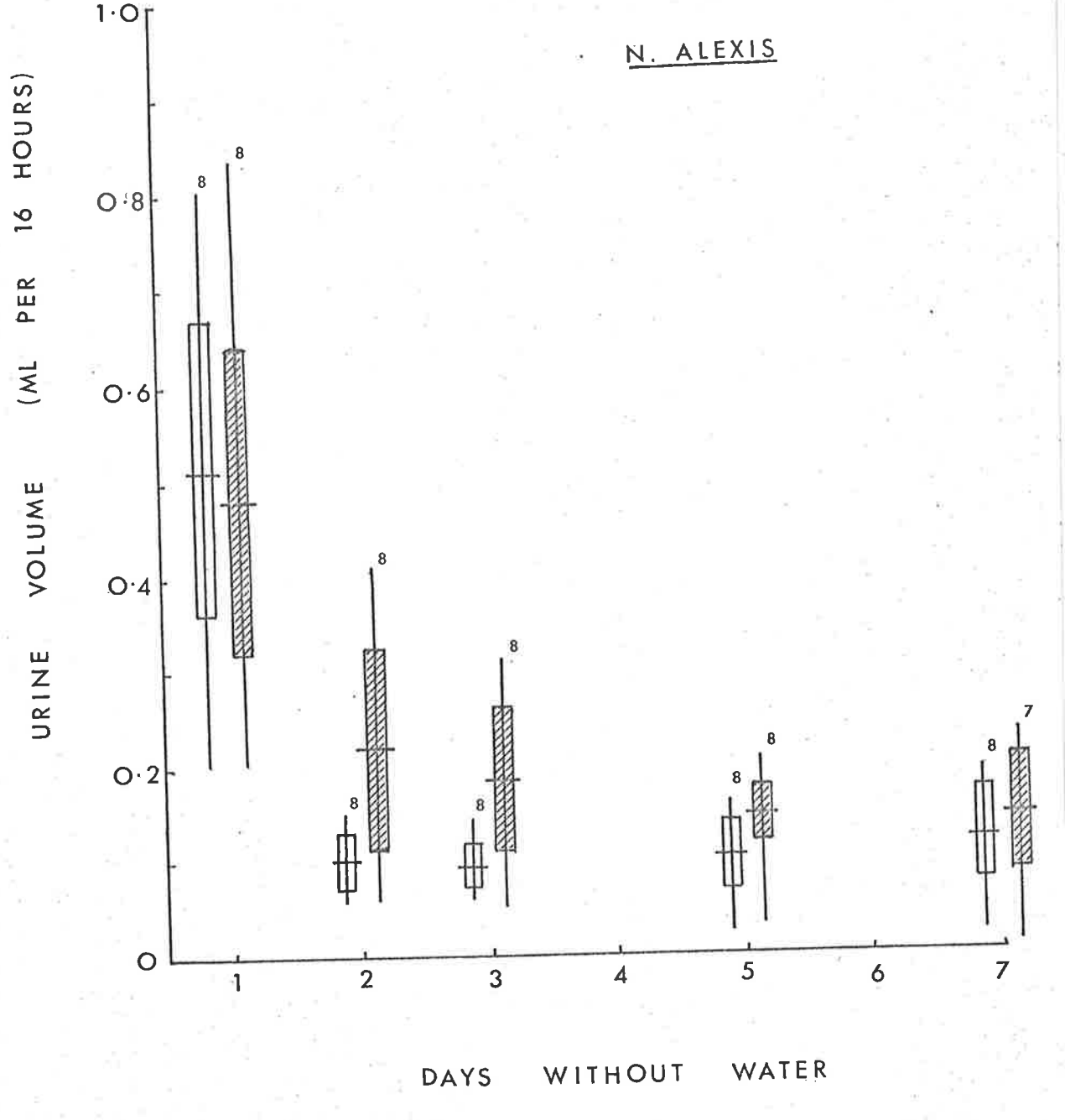

N. ALEXIS
URINE VOLUME (ML PER 16 HOURS)
1·0
0·8
0·6
0·4
0·2
0
8
8
8
8
8
8
8
8
8
8
7
1
2
3
4
5
6
7
DAYS WITHOUT WATER

FIGURE 13.

Volume of urine produced by *N. mitchelli* when denied water. Symbols as in fig. 12.

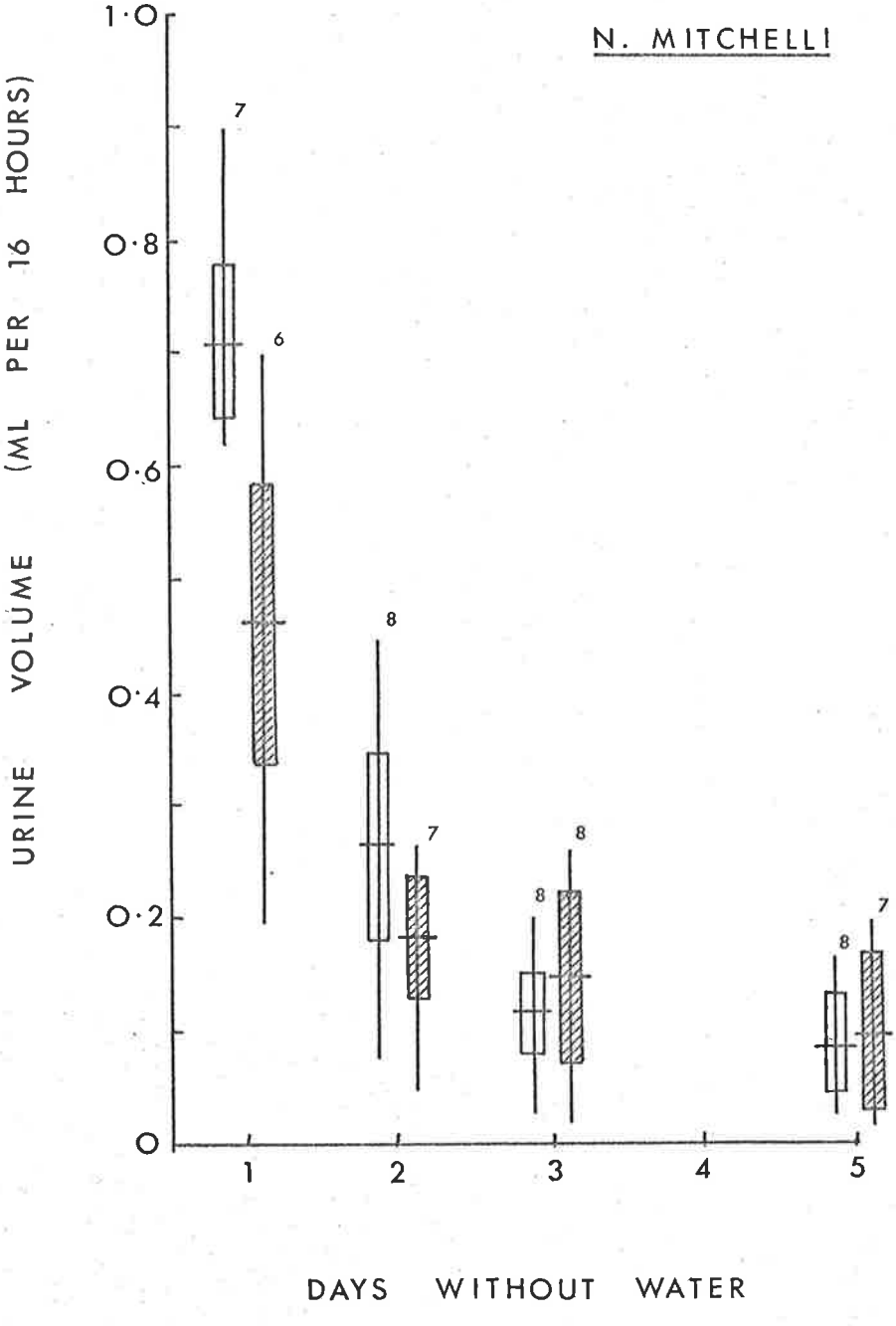
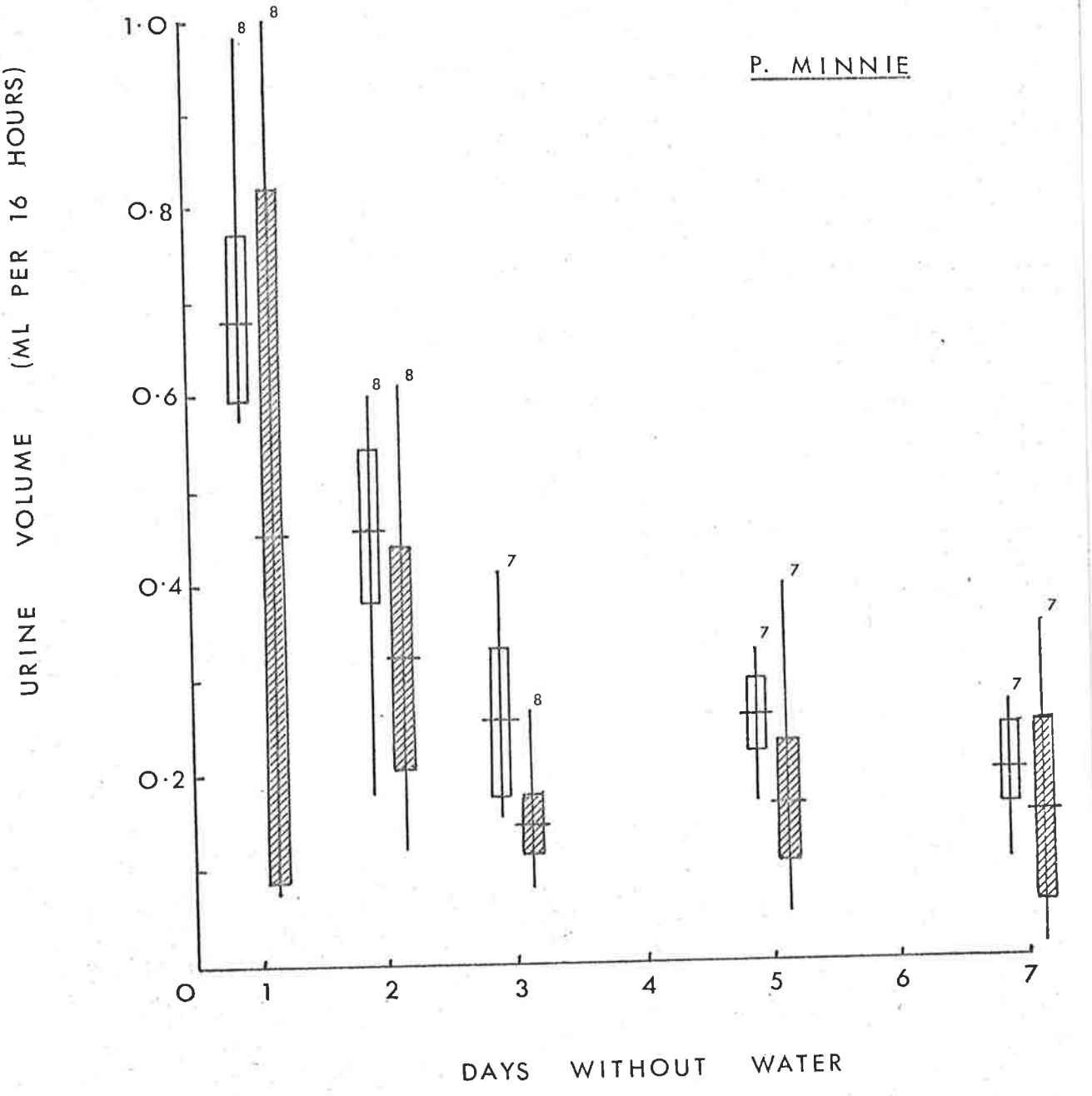

N. MITCHELLI
URINE VOLUME (ML PER 16 HOURS)
1·0
0·8
0·6
0·4
0·2
0
7
6
8
7
8
8
8
7
1
2
3
4
5
DAYS WITHOUT WATER

FIGURE 14.

Volume of urine produced by P. minnie when denied water. Symbols as in fig. 12.


P. MINNIE
URINE VOLUME (ML PER 16 HOURS)
1·0
0·8
0·6
0·4
0·2
0
1
2
3
4
5
6
7
DAYS WITHOUT WATER

P. minnie. This fall in urine volume reduced the amount of water lost by the mice by approximately 6 to 9 percent of their body weight per day (table 13).

TABLE 13

Volume of urine produced by mice given water and those denied water for 5 days

Species	Urine production	
	ml/16 hr[a]	% body weight/day
N. alexis		
Given water	2.07 ± 0.85	6.5
Denied water	0.11 ± 0.03	0.4
N. mitchelli		
Given water	3.50 ± 0.96	9.7
Denied water	0.12 ± 0.07	0.4
P. minnie		
Given water	2.82 ± 0.74	6.2
Denied water	0.19 ± 0.06	0.7

a. Mean ± 2 x S.E.

However, when expressing the urine volumes as a percent of body weight per day in table 13, I assumed that

the urine collected during the 16 hour collecting period represented the total urine excreted each day. While this is likely to be nearly true, since mice generally void little or no urine during the day, the values can only be regarded as approximate. Nevertheless, they still indicate roughly the daily loss of water through the urine.

Mice denied water reduced their urine volumes to different levels depending on the diet. N. alexis and N. mitchelli fed sunflower seed produced less urine than when fed hulled oats (figs. 12 and 13). This smaller urine volume corresponds with the higher urine concentrations of mice fed sunflower seed. However, P. minnie, which did not further concentrate their urine when fed sunflower seed, produced more urine on this diet than on a diet of hulled oats (fig. 14). Presumably, they produced more urine to excrete the additional waste products resulting from the higher protein content of sunflower seed.

7.2.4 Kidney Morphology.

The sections of the kidneys show the thick renal medullae and long papillae characteristic of mice which can produce very concentrated urines (fig. 15). The relative medullary thickness of the kidneys of each species was calculated using the formula of Sperber (1944),

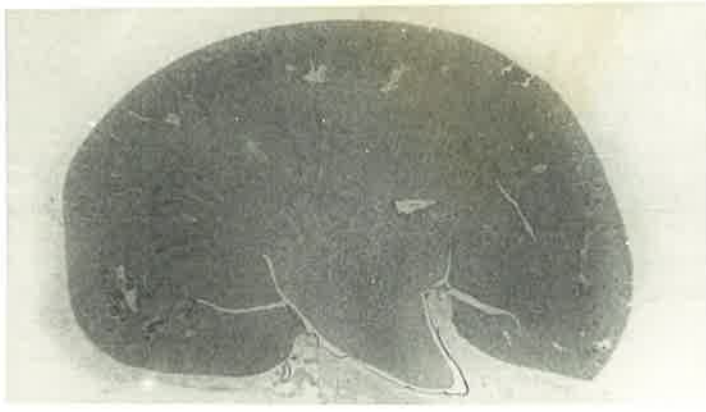
FIGURE 15.

Longitudinal sections of kidneys showing the relatively thick renal medullae and long papillae

A. N. alexis

B. N. mitchelli

C. P. minnie



relative medullary thickness

$$= \frac{\text{thickness of the medulla} \times 10}{\sqrt[3]{\text{length} \times \text{breadth} \times \text{width of kidney}}}$$

The values obtained were similar to those calculated for other desert rodents by Schmidt-Nielsen and O'Dell (1961)(table 14).

TABLE 14

Relationship between kidney structure and concentrating ability

Species	Relative medullary thickness	Max. urine conc. (mOsm/l)	Reference
Beaver	1.3	520	Schmidt-Nielsen and O'Dell, 1961
Pig	1.6	1080	Schmidt-Nielsen and O'Dell, 1961
Aplodontia rufa	2.9	820	Dolph *et al*, 1962
Rabbit	5.4	1390	Dolph *et al*, 1962
White rat	5.8	3060	Blythe *et al*, 1960
D. spectabilis	8.5	6000	Schmidt-Nielsen and O'Dell, 1961
P. minnie	8.6	3860	This study
N. mitchelli	8.9	4260	This study
Jerboa	9.3	6500	Schmidt-Nielsen and O'Dell, 1961
N. alexis	9.4	5990	This study
Psammomys obesus	10.7	5000	Schmidt-Nielsen and O'Dell, 1961

7.3 Discussion.

The Australian desert rodents *N. alexis*, *N. mitchelli* and *P. minnie* reduced their urinary water loss considerably when denied water. *N. alexis*, which were best able to survive on a dry seed diet, produced the most concentrated urine of the three species. When fed hulled oats, these rodents equalled *D. merriami* in their ability to concentrate urine (Schmidt-Nielsen *et al.*, 1948). Stressing the mice further by feeding them sunflower seed resulted in even higher urine concentrations. However, these mice did not concentrate their urine as much as the *N. alexis* studied by MacMillen and Lee (1969), who reported a mean urine osmolality of 6547 $\pm$ S.D. 1618 mOsm/l and a maximum of 9374 mOsm/l. This large discrepancy between my results and theirs is difficult to explain, though the similar amounts of urea in the urine (expressed as a percent of osmolality) found by MacMillen and Lee, (1969) and me (52.3 and 53.3% respectively) discount any errors in measuring osmolality. Therefore, either the difference is real with my *N. alexis* simply not concentrating their urine as much as those of MacMillen and Lee, or the difference reflects the different techniques used for collecting urine. Only further independent studies will finally decide just how highly *N. alexis* can concentrate their urine.

N. mitchelli, which was less independent of water than N. alexis, not unexpectedly produced a less concentrated urine. The efficiency of their kidneys in conserving water lay below that of D. merriami but exceeded that of the white laboratory rat. Surprisingly, however, P. minnie produced the least concentrated urine and lost the most water through excretion of the three species, although it survived on a dry seed diet almost as well as N. alexis. Evidently either urinary water loss was sufficiently low to enable the mice to conserve enough water or some other factor was reducing their water loss further. One avenue of water loss in which N. alexis and P. minnie may differ is the amount of water lost through evaporation. Although this loss has not been fully investigated in these mice, MacMillen and Lee (1967) reported that N. alexis lost 0.91 mg H_2O/cc O_2 consumed, while in some earlier work I found that P. minnie lost about 0.5 mg H_2O/cc O_2 (Edwards, 1967). This lower evaporative water loss of P. minnie may compensate for their higher water loss through their urine.

In most mammals, the maximum urine concentration that can be achieved on a particular diet depends on the amount of nitrogen in that diet; mice fed a high protein diet will produce a more concentrated urine than those fed on a low protein diet (Crawford, 1959; Radford, 1959).

N. alexis and *N. mitchelli* both increased their urine concentrations when fed sunflower seed indicating that they too can concentrate urea better than electrolytes. However, *P. minnie* resembles more the beaver, pig and *Psammomys obesus*, all of which do not further increase their urine concentration when fed a diet richer in protein (Schmidt-Nielsen *et al.*, 1961b). The significance of this difference between the species is not certain, but perhaps if *P. minnie* can concentrate electrolytes better than urea it can utilise halophytic plants as a water source like *P. obesus* (Schmidt-Nielsen, 1964) and possibly *N. cervinus* (MacMillen and Lee, 1969).

Most mice achieved their maximum urine concentrations after 3 days without water. It is well known that the volume of urine and its concentration is under the control of antidiuretic hormone, which is released as an animal becomes dehydrated (Chew, 1965; Schmidt-Nielsen, 1964). The delay before the maximum urine concentrations are reached is the time required for the water loss to affect the release of ADH. During the first three days without water, therefore, the mice lost more water than they gained, and hence became dehydrated. However, once the urine had reached its maximum concentration, enough water was conserved by the mice to regain their water balance. The three days

required for reducing water loss to a minimum is the same as that suggested in the previous section from the changes in food intake and body weight of mice denied water.

All three species of rodents have kidneys with long renal papillae, further supporting the proposed relationship between papilla length and concentrating ability of the kidney (Sperber, 1944). The relative medullary thicknesses of the kidneys of the Australian rodents were within the range of values calculated for other desert rodents. According to the current concept of kidney function, the thickness of the medulla indicates the length of the loops of Henle of the multiplier system which determines the maximum concentration of the urine.

Thus, in these Australian rodents, both the morphological features and the physiological abilities of the kidneys to concentrate urine indicate that the kidneys are the major sites for conserving water when intakes are scant.

8. FAECAL WATER LOSS

8. FAECAL WATER LOSS.

Faecal water loss depends on the water content of the faeces and the amount of faecal material produced. In large herbivores, which have proportionately more roughage in their diets than other mammals and relatively high faecal water contents, faecal water loss tends to be the major avenue of loss (Balch *et al*, 1953; Dukes, 1956; MacFarlane *et al*, 1963). In desert rodents, however, by far the least water lost is with the faeces since their faeces are generally much drier, and their diet of seeds contains very little fibre. The faeces of *Peromyscus leucopus* contain between 47 and 54 percent water (Chew, 1951), kangaroo rats 45 percent (Schmidt-Nielsen and Schmidt-Nielsen, 1952), and the jerboa *Jaculus orientalis* 47 percent (Kirmiz, 1962). In contrast, white rats on a diet of seeds have a faecal water content of about 61 percent (Kirmiz, 1962).

When water intake is restricted, all mammals reduce the water content of their faeces. If faecal water loss is a considerable part of the total water loss, this reduction is often an important saving of water. In waterbuck, an East African antelope, restricting water intake so that the animals just maintain 85 percent of their initial body weight, halves the faecal water loss, but has no effect on

either urinary or evaporative water loss (Taylor et al., 1969). On a dry seed diet, the water content of the faeces of J. orientalis and white rats decreases to 41.7 and 41.2 percent respectively (Kirmiz, 1962), and that of P. leucopus to 41 percent (Chew, 1951). Although the mechanisms which control the water content of faeces have not been investigated, some related work on the rate of absorption of water from the gut suggests that both osmotic and humoral factors are involved (Donnet and Garnier, 1954).

Kangaroo rats on a dry seed diet better assimilate their food, with the result that less dry matter is eliminated and, therefore, less water is lost with the faeces (Schmidt-Nielsen, 1964). This higher assimilation of food may be due to their habit of eating their faeces, and could be an extremely efficient way of minimising faecal water loss.

In this next section I have investigated this avenue of water loss in N. alexis, P. minnie and N. mitchelli to determine any changes which occur during water deprivation and the relative importance of this loss in maintaining water balance.

8.1 Methods.

8.1.1 Water Content of the Faeces.

Initially I collected the faecal pellets as they were voided by mice held in the hand so that I could determine the water content of pellets from individual animals. However, the amount of faecal material voided during each collection was so small that large errors were possible due to imprecise weighing.

In a second experiment, to overcome this problem, I pooled the faeces voided by a number of mice. Thirty N. alexis, 30 P. minnie and 10 N. mitchelli were housed in the metal cages previously described with 4 or 5 mice per cage. They were fed hulled oats, but were only allowed water to drink for the first ten days. N. alexis and P. minnie were deprived of water for 30 days, and N.mitchelli for 15 days.

Every second or third day, all the mice of the same species were put together into a large cage (55x37x24 cm), which had a wire mesh floor and was subdivided into 6 smaller compartments so that mice from each home cage could be kept separate. The strangeness of this new environment caused the mice to spontaneously defaecate, and as the pellets fell on to a stainless steel plate beneath the cage, they were placed into a weighed bottle which had a

tightly fitting lid. Collections were made between 1000 and 1200 hrs, and continued for ten minutes after the last animal was placed in the cage. Control experiments showed little or no water evaporated from the faeces during this time.

Once all the faeces were collected, the bottle was immediately reweighed and then left to dry at 105°C for 24 hours.

8.1.2 Faeces Production.

To determine the daily amount of faeces produced, 8 N. alexis and 8 P. minnie were placed in the cages used for collecting urine. The cages sat in clean petri dishes and each morning the faeces voided during the previous 24 hours were collected, dried, and weighed. Hulled oats were always available to the mice, but water was only given to them during the first five days. Food intake was measured daily, and the mice were weighed every second day. The mice were acclimatised to the cages for 4 days before the first collection.

8.2 Results.

8.2.1 Water content of faeces.

The water content of those faeces collected by hand from N. alexis and P. minnie given water are shown in table 15. The large variation in the water content of the

TABLE 15.

Water content of faeces collected from individual mice.

Species	Collection*	Sample Size	Percent water content of faeces	
			Mean	Range
N. alexis				
Group 1	A	6	53.7	43.5 - 67.4
	B	8	49.4	24.7 - 64.6
Group 2	A	8	48.1	30.5 - 55.5
	B	8	38.2	25.1 - 51.2
Group 3	A	7	36.6	25.3 - 45.7
	B	6	45.1	29.5 - 58.6
Average		43	45.2	
P. minnie				
Group 1	A	8	42.7	21.5 - 66.1
	B	8	39.2	17.9 - 59.5
Group 2	A	8	52.4	26.3 - 87.8
	B	7	61.6	42.5 - 78.3
Group 3	A	8	49.3	34.7 - 83.4
Average		39	49.0	

* Faeces were collected from each group of 8 mice on two occasions, A and B, 5 to 10 days apart.

faeces from individual mice resulted in considerable differences in the average water content for each collection, even within the same group of mice. Since this variation might mask any differences between species and between mice given water and those denied it, in the second experiment I forwent measuring variation, preferring to obtain as large a sample of faeces as was practicable.

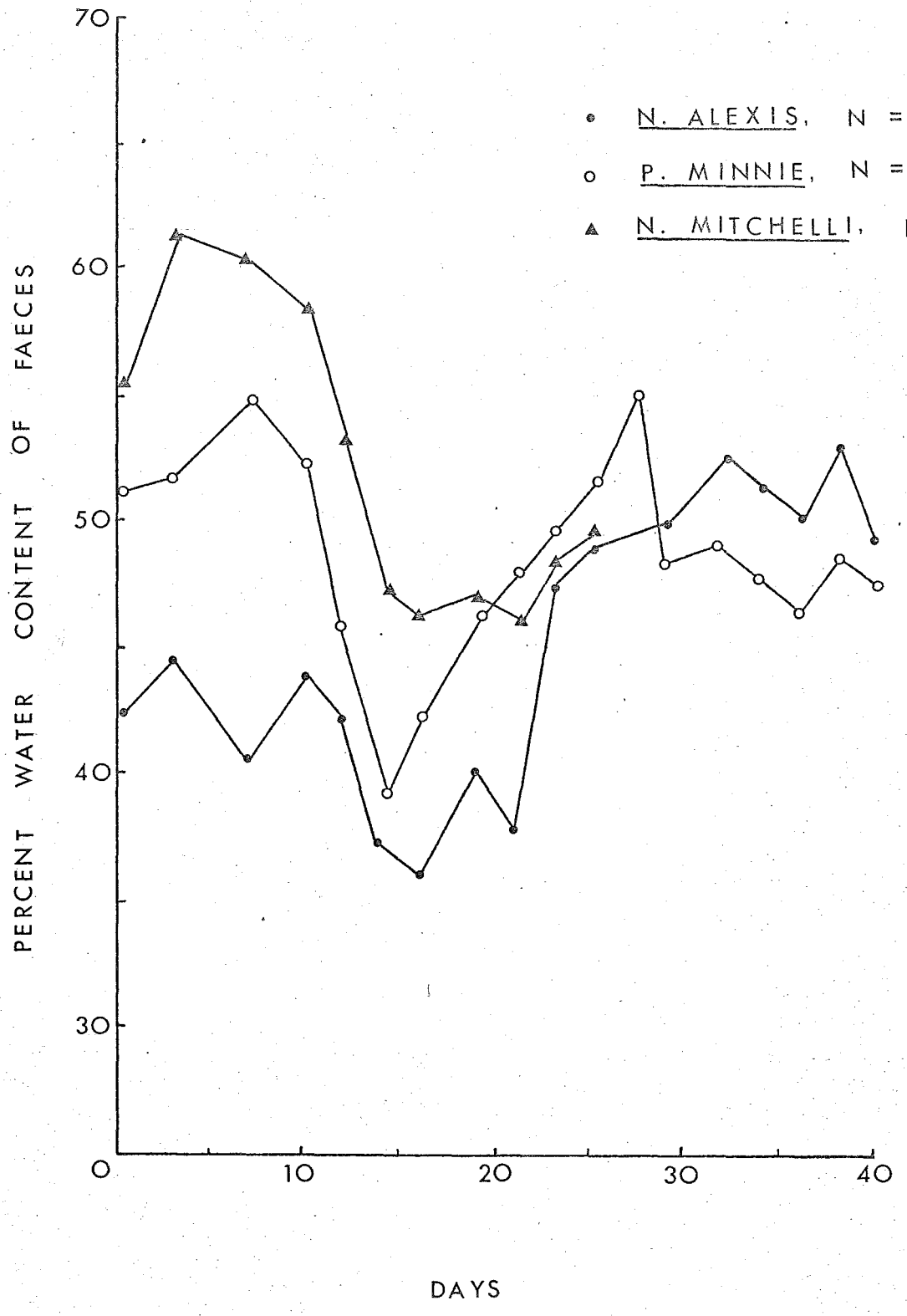
On the four occasions that faeces were collected from mice drinking water, the differences between the three species were much greater than the day to day differences within species (figure 16). The faeces of N. alexis had the lowest average water content with 42.3 percent water, P. minnie higher with 52.6 percent, and N. mitchelli the highest with 58.9 percent.

When the drinking water was removed on the 10th day, the water content of the faeces of all species decreased markedly for the next 5 days to 37.5 percent for N. alexis, 40.2 percent for P. minnie and 46.2 percent for N. mitchelli. Although the faeces of N. alexis were still the driest, they showed the smallest decrease.

As water deprivation continued, the water content of the faeces increased again, though by different amounts in the three species. The water content of the faeces of N. alexis increased quite rapidly until the 20th day

FIGURE 16.

Percent of water in the faeces of *N. alexis*, *N. mitchelli*, and *P. minnie*. All mice were denied water on day 10. N represents the sample size.


70
60
50
40
30
0
10
20
30
40
PERCENT WATER CONTENT OF FAECES
DAYS
N. ALEXIS, N = 30
P. MINNIE, N = 30
N. MITCHELLI, N = 2

without water, but thereafter remained constant at about 51 percent, a value higher than when the mice were drinking water. P. minnie showed a similar rapid increase to reach a value of 55 percent on the 17th day, but then dropped slightly to level off at 48 percent, a value lower than that of mice drinking water. The water content of the faeces of N. mitchelli remained low until the 11th day, and although there was a slight increase by the 15th day, the faeces were still much drier than they were initially.

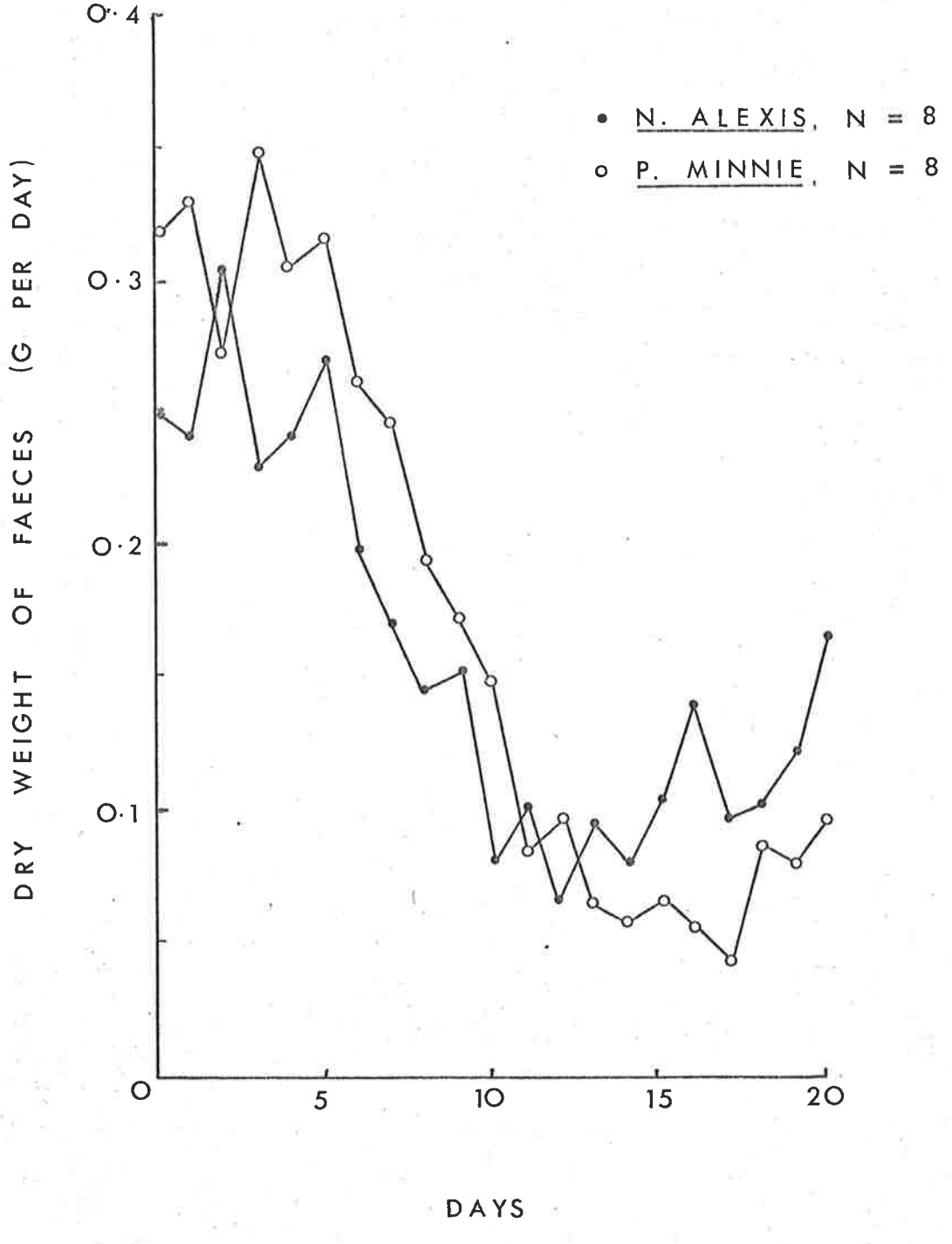
8.2.2 Faeces Production and Assimilation of food.

The average dry weight of the faeces produced by N. alexis and P. minnie dropped rapidly when the mice were denied water (figure 17). After 5 days, N. alexis voided only 29 percent of the faeces produced while drinking, and P. minnie 43 percent. However, by the 15th day without water, faecal production had again risen slightly in both species.

The apparent digestibility of the food (that is, the difference between food intake and faecal production divided by the food intake, expressed as a percent) significantly increased when water was denied the mice for 5 to 10 days ($P < 0.01$ in both cases, table 16). This increase in food assimilation could have been due to either the mice eating some of the faeces as they were voided or to more efficient

FIGURE 17.

Mean dry weight of the faeces produced by N. alexis and P. minnie. All mice were denied water on day 5. N represents the sample size.


0·4
0·3
0·2
0·1
0
5
10
15
20
DRY WEIGHT OF FAECES (G PER DAY)
DAYS
• N. ALEXIS, N = 8
o P. MINNIE, N = 8

digestion of the food in the gut, or to a combination of both these factors. I have not observed coprophagy in these mice, nor have MacMillen and Lee (1969), although it is possible that it occurs.

TABLE 16

Apparent Digestibility of the Food.

Species	Mean dry faecal weight (g/day)	Mean food intake (g/day)	Mean percent of food digested
N. alexis			
Given water	0.28 ± 0.06[a]	3.53 ± 0.18	89.9 ± 2.1
Denied water 5 to 10 days	0.09 ± 0.04	2.38 ± 0.26	96.3 ± 1.4
P. minnie			
Given water	0.32 ± 0.05	4.04 ± 0.17	91.7 ± 1.8
Denied water 5 to 10 days	0.08 ± 0.05	2.14 ± 0.19	95.6 ± 2.3

a. Mean ± 2 S.E.

Sample size (N) was 8 in each treatment.

8.2.3 Faecal Water Loss

Using the amount of faeces produced and their water content, I estimated the water loss through the faeces (table 17). The low faecal production and the low water content of faeces of mice denied water for 5 days resulted

in a 68 percent reduction in faecal water loss for N. alexis and an 80 percent reduction for P. minnie. However, the ratio of the faecal water loss to the total water loss remained unchanged at 5 percent (see fig. 19).

TABLE 17.

Faecal Water Loss

Species	Percent water content of faeces	Water lost through faeces	
		g/day	Percent body wt/day
N. alexis			
Given water	42.3	0.21	0.65
Denied water 5 days	39.0	0.06	0.21
P. minnie.			
Given water	52.6	0.36	0.82
Denied water 5 days	42.5	0.06	0.16

8.3 Discussion.

When given water, the water content of the faeces of N. alexis and P. minnie resemble the low values obtained for other desert rodents. The wetter faeces of N. mitchelli,

however, resemble more those of white rats. Although the faecal water content decreased markedly in all species when denied water, the faeces of N. mitchelli were still the wettest. Thus the two desert species, N. alexis and P. minnie lose less water through the faeces than N. mitchelli, an adaptation which will be of some benefit, even if only slight, in their more arid environment.

The changes in food intake (figure 3), and the changes in the water content of the faeces (figure 16) when the mice were denied water are very similar. Both decreased during the first 5 days, but increased again thereafter. Even the failure of N. mitchelli to return to its original food intake corresponds with the smaller increase in the water content of their faeces. This close relationship between food intake and the water content of the faeces suggests that the changes in food intake are responsible for the changes in faecal water content. The reduction in faecal water loss of animals denied water could be, therefore, a passive response to the reduced food intake rather than an active conservation of more water. However, this interaction has not been studied in further detail in any rodents.

However, work on ruminants has shown that a reduced food intake decreases the rate of passage of foodstuffs through the gut and increases the digestibility of the food

(Balch, 1961; Graham and Williams, 1962). MacFarlane et al. (1959) observed that during dehydration in camels about half the water loss came from the alimentary tract, the rest from the extracellular fluid and the cells. Dehydrated cows also decrease their food intake and decrease the water content of their faeces from 82 percent to 75 percent (Balch et al., 1953). Although it is impossible to extrapolate from ruminants to rodents because of their very different digestive systems, a study of similar variables in desert rodents could prove most interesting and offer valuable information on the mechanisms which control faecal water loss.

The decrease in faecal production when the mice were denied water was the result of both a decrease in food intake and an increase in the assimilation of the food. This latter increase could be due to more efficient digestion or to coprophagy. White rats digest their food more efficiently when food intake is restricted (Crampton and Lloyd, 1954; Quimby, 1948), and coprophagy is essential to normal digestion in white rats and rabbits (Geyer et al., 1947; Thacker and Brandt, 1955). But once again no one has investigated how the assimilation of the food of desert rodents increases when food intake decreases. This subject clearly deserves further study.

Since faecal water loss is quantitatively by far the smallest avenue of water loss in desert rodents, any decrease in faecal water content is likely to be of only small benefit. Nevertheless, their faeces are the driest found in any mammal, and therefore there must be some selective advantage in reducing faecal water loss to a minimum.

9. ACTIVITY.

9. ACTIVITY.

Activity is some form of behaviour involving movement, usually locomotion. Its effect on metabolic rate and water loss makes it important when considering an animal's water balance; any increase in activity indicates a greater metabolic rate and a greater water loss. One of the simplest methods of measuring the activity of rodents is to record the daily running of individuals in activity wheels. Mice generally learn to run in wheels in a few days and use the wheels for most activity other than that involved in feeding and grooming.

A review of the literature reveals that a deprivation or deficiency of any kind almost always causes rodents to increase their activity in running wheels (Campbell and Cicala, 1962). In particular, white rats deprived of food or water (Wald et al., 1944; Campbell, 1964), and Peromyscus maniculatus (Rawson, 1960) and P. leucopus (Kavanau, 1962) deprived of food all increase their running in wheels. Clearly, activity, in these rodents at least, is not adjusted to aid their water balance, since the greater activity merely increases their water loss.

Kangaroo rats fed dry grain also run more in activity wheels than when given succulents in their diet (Schmidt-Nielsen and Schmidt-Nielsen, 1952). However, they differ

from the previous rodents in that they maintain a positive water balance and survive indefinitely on the dry diet. The Schmidt-Nielsens suggested that these rats increase their activity to gain more water of oxidation, which results for them in a net profit of water because their concomitant water losses are so low.

Nichter (1957) further studied the running activity of kangaroo rats. He argued that if these rats do increase their activity to form more water of oxidation, then activity should cease when no water can be gained from it. This would occur if the kangaroo rats were kept at very low humidities for then they would have a negative water balance due to the higher evaporative water losses. Nichter's rats did reduce their activity at the lower humidities. However, when confined and allowed no exercise, the same rats lost less weight than when allowed to run in wheels, indicating that these exercising animals would have benefitted more by remaining entirely inactive. Apparently, if the control of activity was related to water balance, it was not well adjusted or was easily modified by other factors.

The Australian rodents, particularly N. alexis, also learned to use running wheels very quickly, and most became ardent runners after a few days practice. A very elementary study was designed to see how their activity changed when

they were denied water, and to attempt to related these changes to the water-balance picture. Already the initial decrease in food intake of mice denied water indicates a decreased metabolic rate. A corresponding decrease in activity might also be expected if activity is at all related to the water balance of these rodents.

9.1 Methods.

Only the activity of adult male N. alexis was measured; females might be unsatisfactory because of the cyclic changes in activity associated with oestrous (Slonaker, 1924). Each animal was housed individually in a metal cage containing a wooden nest box and activity wheel. The cages were kept in the constant temperature room which was lit by natural light.

The activity wheel consisted of a cylinder of expanded steel 15 cm in diameter and 9 cm wide supported on a metal frame. A mechanical counter attached to one side of the supporting frame recorded the running of the mice. The counter was designed so that turning the wheel in either direction operated it. To enable the wheel to rotate easily, powdered graphite was sprinkled between the wheel's axle and the supporting frame.

Each morning at 0900 the counters were read to determine the number of revolutions run by the mice during the previous

24 hours. Otherwise, apart from routine feeding, the mice were left undisturbed.

The mice were allowed a week to become accustomed to using the wheels. Activity was then recorded for the next 10 days while the mice were given water to drink. This was followed by 32 days during which the mice were denied water. Then the mice were again given water, and their activity recorded for a further 8 days.

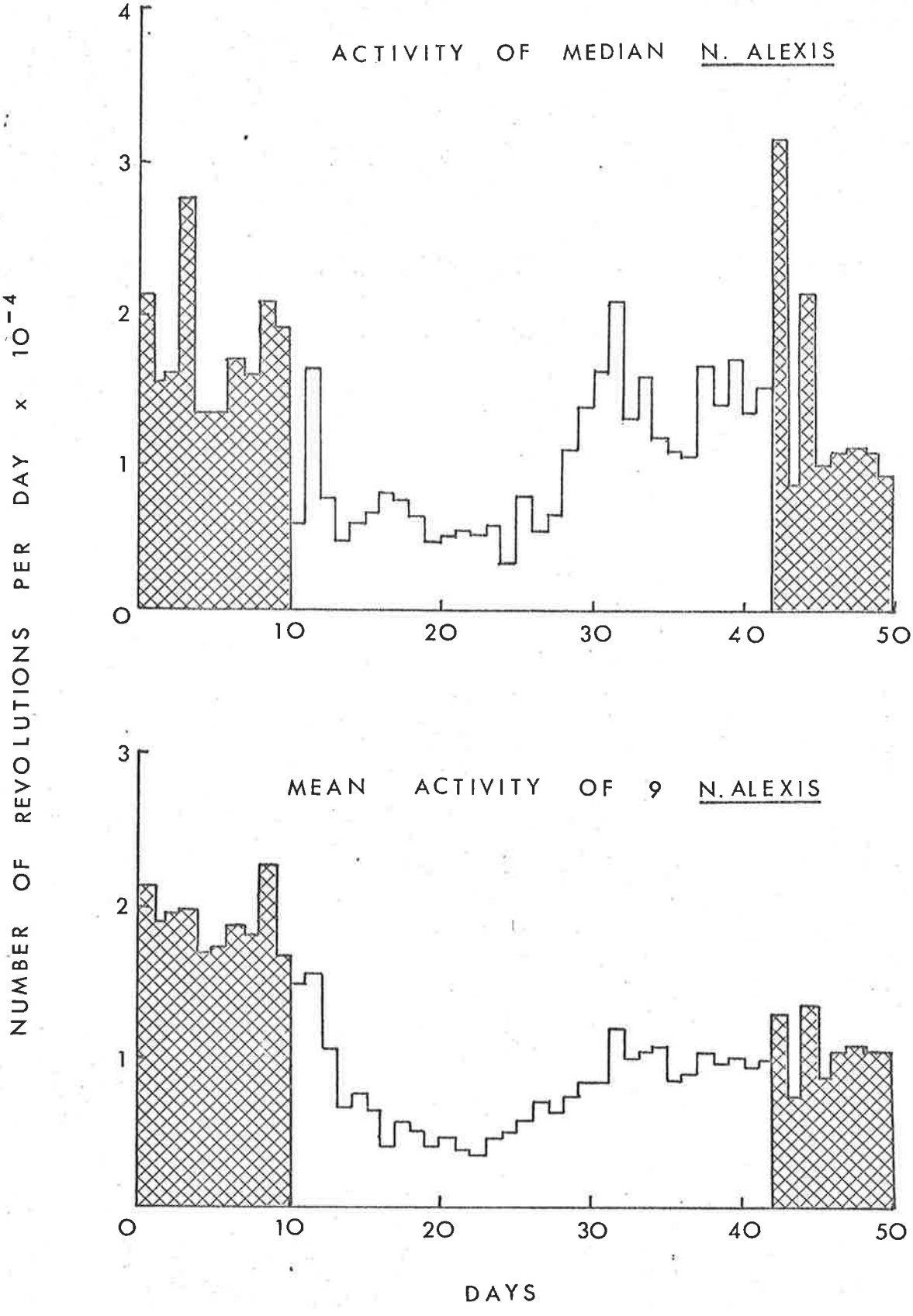
9.2 Results.

The activity of the mice in the running wheels varied considerably between individuals and from day to day. The least active animal ran an average of 9,950 revolutions per day (range 119 to 19,115) during the first 10 days; the most active animal ran an average of 35,604 revolutions per day (range 27,669 to 45,217). Since in actual distance, 3,419 revolutions is equivalent to running one mile, these mice often ran more than 5 miles a day, and even up to 13 miles, quite a distance for any animal to travel. However, these distances cannot be equated with distances run on a flat surface, since the amount of energy expended in each case will be different.

Figure 18 shows the activity of the median individual and the mean daily activity of the 9 mice. When denied water, all the mice decreased their activity markedly.

FIGURE 18.

Activity of N. alexis running in wheels. Cross hatched areas indicate when the mice were given water, open areas when the mice were denied water.


ACTIVITY OF MEDIAN N. ALEXIS
MEAN ACTIVITY OF 9 N. ALEXIS
NUMBER OF REVOLUTIONS PER DAY x 10^{-4}
DAYS
0
1
2
3
4
10
20
30
40
50

After 10 days without water, the mice were on the average 78 percent less active than when they were drinking. However, thereafter the mice became more and more active so that by the 20th day without water activity was 50 percent of what it was initially. For the remainder of the time the mice were without water, activity stayed fairly constant at this new level.

When the mice were again given water, their activity became very erratic with much running on the first day, but very little on the next. However, during the last 5 days on which activity was measured, activity again became constant at a level not significantly different from that during the 10 days before the mice were given water, and still 50 percent less than the initial activity.

9.3 Discussion.

The decreased activity of N. alexis when denied water is the opposite to what has been observed for other rodents, including the kangaroo rat. However, this initial decrease in activity does correspond with the sudden fall in food intake. Since the amount of energy expended by the mice is reduced, this decreased activity compensates, at least to some extent, for the decrease in energy available due to their lower food intake. The reduced activity also decreases the metabolic rate, since less energy is used by

the mice. This will, in turn, reduce water loss, and therefore be of further benefit during this transition stage in the animal's water balance.

The increase in activity after 10 days without water again corresponds with the rise in food intake. However, activity did not return to its initial level, indicating that some other factor may have been also modifying activity. This is further indicated by the relatively unchanged activity when the mice were again given water. This lower activity of all mice at the end of the experiment suggests that either the 10 days with water was not sufficient time for activity to recover to its initial level, or that some factor had altered the level of activity during the experiment. This may have been due to an external factor such as a change in day length, since the room was lit by natural light, or to some internal factor within the mice themselves. Unfortunately, not enough running wheels were available during the experiment to run control animals at the same time to distinguish between these possibilities.

Nevertheless, there was obviously no attempt by the mice to increase their activity so as to increase their metabolism to gain more water of oxidation as has been suggested for the kangaroo rat. The initial decrease in activity presumably reduced water loss at a critical time

in their water balance when urine volumes were declining to a minimum. This reduced activity may be a direct response to water deprivation, or indirectly related, such as through the drop in food intake. Nevertheless, it appears that the activity of these mice was in some way adjusted to their need for water.

10. DISCUSSION.

10. DISCUSSION.

The Pseudomyine rodents have been very successful in colonising the dry interior of Australia; no fewer than 10 of the 13 genera, including the Notomys and Pseudomys, have representatives living in the desert (Tate, 1951). Like the majority of other desert rodents, the Notomys and Pseudomys are nocturnal and fossorial. Their burrows are designed to lessen the burden of the daytime heat. They are dug deep, sometimes as much as one metre below the surface. At this depth the soil is relatively moist and cool in comparison to that at the surface, even during the hottest months of the year. Consequently, the humidity in the burrow is high, and the temperature moderate. Although the microclimate of burrows of Australian desert rodents has not been studied extensively, Vorhies (1945) has measured the temperature in the burrows of a number of rodents living in the desert of Arizona throughout a whole year. He found that the maximum temperatures were around 30°C and never exceeded 34°C, confirming the accepted opinion that burrow temperatures never reach levels where the rodents have to use water for temperature regulation.

However, though desert rodents apparently overcome the problem of keeping cool, they are still faced with problems arising from the comparative dryness of their environment. Avoiding the use of water to regulate body temperature

lessens the severity of these problems but does not cancel them out completely. Since free water is rarely, if ever, available for drinking in the desert, rodents must obtain most of their water from the food they eat. Yet the water content of their food can vary greatly with the coincident dryness of the environment. In central Australia where droughts are prevalent, water may become so scarce that intakes are severely restricted. Nevertheless, the Australian rodents survive under such rigorous conditions. How they survive, and some of the physiological and behavioural responses to extreme lack of water have been studied in this thesis.

The two desert species of Pseudomyine rodents, N.alexis and P. minnie, need very little water to survive. Although they drank readily when given water, they survived in the laboratory for more than 60 days when fed only hulled oats (10 percent water by weight) and kept at a temperature of 21°C and relative humidities between 30 and 60 percent, indicating their almost complete independence from exogenous water. Denying these rodents water decreased their total water intake on the average by 77 percent, but increased the contribution of metabolic water to the total water intake from 30 to 82 percent (table 10). Thus N. alexis and P. minnie can gain most, if not all, of the water they need from the oxidation of their food alone. In this respect,

they are similar to several other desert rodents, notably the desert kangaroo rat, Dipodomys merriami (Schmidt-Nielsen, 1964).

N. mitchelli, a species from less arid regions than N. alexis and P. minnie, did not survive as well as the desert species when kept under the same conditions. After 30 days without water, nearly half of the N. mitchelli had died, and those still alive were continuing to lose weight and no doubt would have died had the experiment not been terminated. Nevertheless, on the average they survived as long as, and in some cases longer than, several other rodents from semi-arid and even arid regions maintained on similar diets; D. agilis can survive an average of 27.5 days without water (MacMillen, 1964a), Microtus californicus 5.6 (Church, 1966), Neotoma lepida lepida 5.0 (Lee, 1963) and Citellus leucurus 20.0 (Hudson, 1962).

The changes in body weight when the rodents were denied water were similar to those reported by other authors (Lindeborg, 1951; MacMillen, 1964b; MacMillen and Lee, 1967, 1969; and Koford, 1969). Initially body weight decreased rapidly, but after about 5 days the daily weight loss became less and less so that by the 10th day without water body weight was remaining fairly constant. Up until this time, the changes in body weight of the three species were relatively similar. But by the 20th day without water,

N. alexis and P. minnie were gaining weight while N.mitchelli again continued to lose it. By the 30th day without water, this difference between the desert species and the semi-desert species had become even greater (figure 3).

The initial rapid loss of weight shown by all mice denied water was partly due to a loss of water and body tissue which could not be replaced and partly due to a decrease in food intake (figures 6 and 7). Food intake may have decreased as an involuntary response to thirst brought about by dehydration which in turn resulted from the delay before water losses could be reduced to a minimum. Studies on the urinary water loss which showed that urine volumes did not reach their minima until the 3rd or 4th day after water deprivation, support this explanation (figures 12, 13 and 14).

Once urinary water losses had declined to a minimum, the daily weight loss became less and the mice regained their appetites. It appears that the mice were now able to conserve sufficient water to at least partly re-establish their water balance. It is uncertain whether food intake increased because of this return to equilibrium or because of an increasing and overpowering hunger drive, although the behaviour of N. mitchelli indicate that both may be involved to some extent.

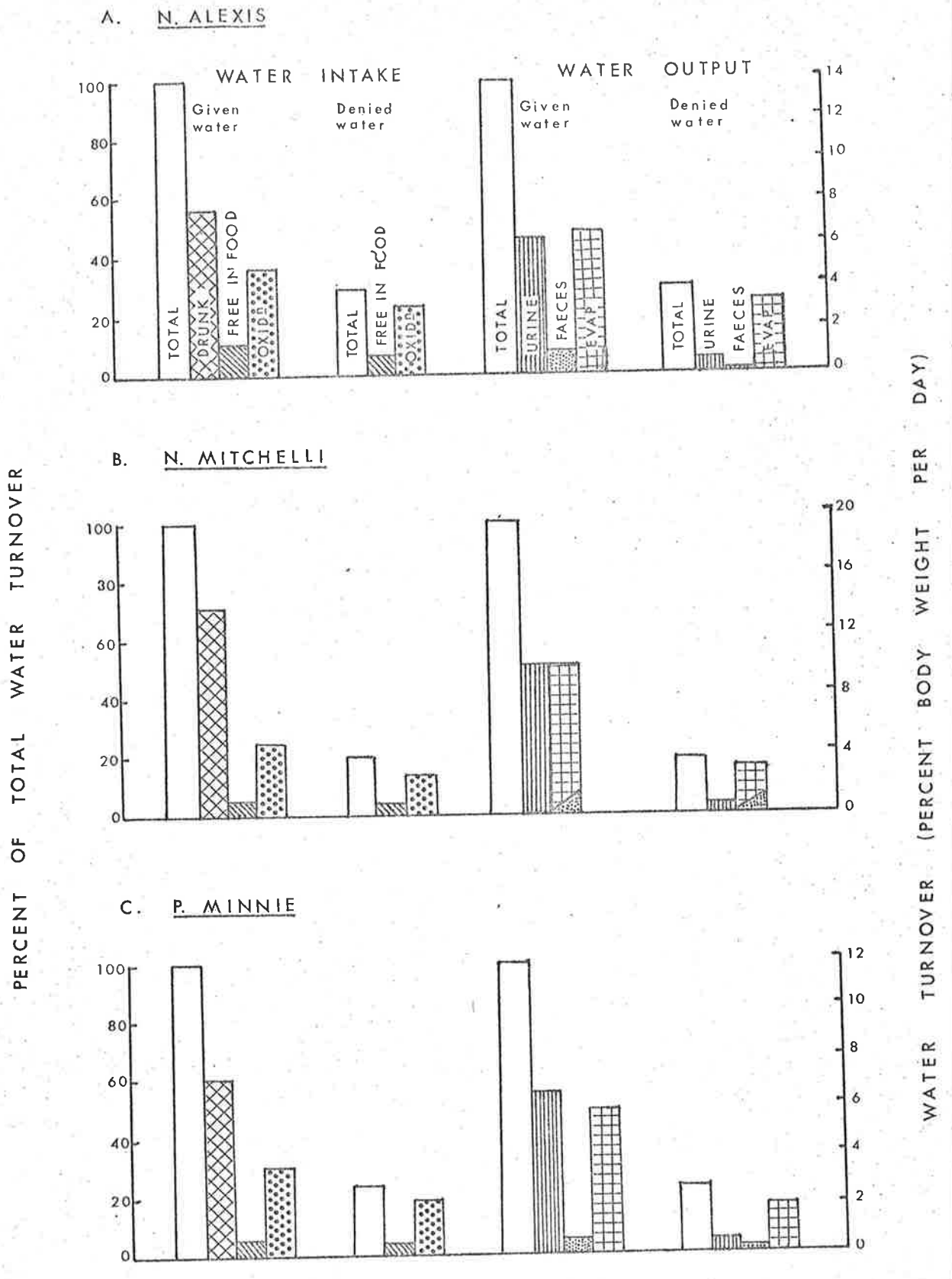
Although this argument explaining the sequence of changes which occurred when the rodents were denied water is necessarily simplified, I feel that it encompasses the most likely explanations in view of the evidence available. Thus, in summary, the changes in weight appear to be partly due to changes in food intake, which are in turn, a result of temporary disturbances in the water balance during the adjustment of the mice to the new, greatly reduced water rations.

Faecal water loss is relatively unimportant in the water balance of these desert rodents, since it accounts for only about 5 percent of the total water turnover (figure 19). Nevertheless, there must be some selective advantage in minimising this loss, since the faeces of desert rodents are consistently drier than those of other rodents. The Australian rodents are no exception, with the two desert species losing less water through their faeces than the semi-desert N. mitchelli (figure 16).

When the mice were denied water, the water content of the faeces from all species initially decreased, but increased again 4 to 6 days later. These changes in faecal water content so closely followed the changes in food intake that it appears that there is some interaction between the two. Possibly, the reduced food intake slows down the rate of passage of the food, as occurs in ruminants (Balch et al.,

FIGURE 19.

Summary of water balance. Each block represents the mean value for all mice used in each experiment. The percent of total water turnover was expressed relative to the total water turnover of animals given water. The evaporative water loss was calculated theoretically by assuming total water intake equals total water output and subtracting the other losses from the total water turnover. The ambient temperature was 21°C and the relative humidity was between 30 and 60 percent. The mice were fed hulled oats.


A. N. ALEXIS
WATER INTAKE
WATER OUTPUT
Given water
Denied water
Given water
Denied water
TOTAL
DRUNK
FREE IN FOOD
OXID.
TOTAL
FREE IN FOOD
OXID.
TOTAL
URINE
FAECES
EVAP.
TOTAL
URINE
FAECES
EVAP.
B. N. MITCHELLI
C. P. MINNIE
PERCENT OF TOTAL WATER TURNOVER
WATER TURNOVER (PERCENT BODY WEIGHT PER DAY)

1961), allowing greater water absorption from the gut. Or perhaps the changes are due to an independent but common factor, itself resulting from the water deprivation. Further investigation into the control of both food intake and water absorption from the gut would clarify this point further.

Another subject in need of further study is how the assimilation of the food increased when the rodents were denied water. If the rodents were coprophagic, an increase in the amount of faeces eaten when they were denied water would better assimilate the food. Or perhaps these rodents simply digested their food more efficiently during water deprivation.

As already found with other desert rodents which can exist on a dry diet, the most important mechanism enabling the Australian rodents to survive on such small quantities of water was their ability to highly concentrate their urine. The most concentrated urine measured in this study came from N. alexis fed sunflower seed, 3 days after they were denied water, the average osmotic and urea concentrations being 4511 mOsm/l and 2985 mM/l respectively.

Although P. minnie and N. mitchelli did not produce urine as highly concentrated as N. alexis, the osmotic concentration of their urine did on several occasions exceed

3000 mOsm/l, which is far in excess of the concentrations reached by man or the white laboratory rat (Kirmiz, 1962).

Unlike the Notomys, P. minnie could not concentrate its urine further when the diet was changed from hulled oats to sunflower seeds. This inability to increase urine urea concentrations when fed a high protein diet indicates that although N. alexis could survive in the desert quite easily on a waterless diet, P. minnie may require succulent plants to supply water. However, as many of these plants are halophytic, P. minnie would have to produce urine with high salt concentrations to benefit from them. But as yet the ability of P. minnie to handle solutions of high salt concentration has not been investigated.

When denied water, the urine concentrations of N. mitchelli were, in general, 10 to 20 percent less than those of N. alexis. This lower ability to concentrate their urine is probably why N. mitchelli were less tolerant to water deprivation than N. alexis. The osmotic concentration of the plasma of both rodents given water and those denied it, differ very little, indicating the remarkable osmotic control of the body in maintaining a satisfactory equilibrium.

As expected from the high urine concentrations, the volume of urine produced by rodents denied water was exceedingly small. Figure 19 shows that for each species this decrease in urine volume accounted for the greatest saving

of water. When given water, urinary and evaporative water loss both accounted for approximately 45 percent of the total water loss. Faecal water loss in all species was less than 10 percent of the total water loss. But when the rodents were denied water, urinary water loss was less than 25 percent of the evaporative water loss, and was only slightly greater than the water lost with the faeces. Thus, in all cases this reduction in urinary water loss was by far the greatest factor influencing the maintenance of water balance when water intakes were so low.

The evaporative water losses of mice denied water shown in figure 19 (calculated by subtracting the other losses from the total water turnover) were in all cases slightly less than half those of mice given water. Though this is quite a large reduction for an avenue of water loss which varies only slightly if measured directly, it is not so surprising in light of the results of the activity experiments, since activity greatly influences the amount of water lost through evaporation. A decrease of 80 percent in the running of N. alexis denied water may well result in a 50 percent decrease in evaporative water loss. Thus, by reducing activity, considerable water can be saved as a result of the concomitant reduced evaporative water loss. However, as seen in figure 19, this is only of secondary importance compared to the saving of water possible by

concentrating the urine above 3000 mOsm/l.

From the comparison of water balance between the three species of Australian rodents, N. alexis, a desert species, emerged as the best equipped for living in the extremely dry conditions of the Australian desert. It survived best on a dry seed diet, lost the least weight when denied water, was the quickest to regain this lost weight and produced the most concentrated urine. P. minnie, though it survived equally well under the same arid conditions, gained its lost weight less quickly and could not concentrate its urine as much as N. alexis. However, to counteract the greater loss through its urine, it may lose less water through evaporation than N. alexis.

The ability of N. alexis to concentrate its urine more than P. minnie may indicate that N. alexis has spent a greater length of time living in the desert environment. This would support Tate's (1951) view that the Notomys and the Pseudomys radiated early in the evolution of the Pseudomyines, with the Notomys long ago becoming well established in the northern deserts while the Pseudomys developed in the more temperate south with their intrusions northwards into the deserts being much more recent.

The inability of N. mitchelli to survive on a dry seed diet as well as N. alexis, and its lesser ability to

concentrate its urine may be the most important factors limiting its distribution to the more semi-arid areas it now occupies. An interesting parallel exists within the Dipodomines where D. agilis, a water dependent species from a semi-arid habitat, cannot concentrate its urine as much as D. merriami, a desert species which does not require free water (Carpenter, 1966).

11. BIBLIOGRAPHY

11. BIBLIOGRAPHY.

Adolph, E.H. (1943). Physiological Regulations. Cattell, Lancaster, Pennsylvania.

Adolph, E.H. (1949). Quantitative relations in the physiological constitutions of mammals. Science. 109: 579.

Balch, C.C., Balch, D.A., Johnson, V.W. and Turner, J. (1953). The effect of limited water intake on the digestibility and rate of passage of hay. Brit. J. Nutrition 7: 212.

Bartholomew, G.A. and Cade, T.J. (1957). Temperature regulation, hibernation, and aestivation in the little pocket mouse, Perognathus longimembris. J. Mammal. 38: 60.

Bartholomew, G.A. and MacMillen, R.E. (1961). Oxygen consumption, estivation and hibernation in the kangaroo mouse, Microdipodops pallidus. Physiol. Zool. 34: 177.

Bentley, P.J. (1960). Evaporative water loss and temperature regulation in the marsupial, Setonyx brachyurus. Aust. J. Biol. Med. Sci. 38: 301.

Blythe, W.B., Newton, M., Lazcano, F., and Welt, L.G. (1960). Effect of water restriction on urinary concentrating ability of potassium depleted rats. Amer. J. Physiol. 199: 912.

Burns, T.W. (1956). Endocrine factors in the water metabolism of the desert mammal, G. gerbillus. Endocrinology 58: 243.

Campbell, B.A. (1964). Theory and research on the effects of water deprivation on random activity in the rat, in Proc. International Symposium on thirst in the regulation of body water, edited by Wayner, M.J., Pergamon Press, N.Y.

Campbell, B.A. and Cicala, G.A. (1962). Studies of water deprivation in rats as a function of age. J. Comp. Physiol. Psychol. 55: 763.

Carpenter, R.E. (1966). Thermoregulation and water metabolism in kangaroo rats. Univ. Calif. Publ. Zool. 78: 1.

Chew, R.M. (1951). The water exchanges of some small mammals. Ecol. Monogr. 21: 215.

Chew, R.M. (1965). Water metabolism of mammals, pp. 43-178 in Physiological mammalogy, vol. 2, edited by Mayer, W.V. and Van Gelder, R.G., Academic Press, N.Y.

Chew, R.M. and Hinegardner, R.T. (1957). Effects of chronic insufficiency of drinking water in white mice. J. Mammal. 38: 361.

Chitty, D. (1954). Food and water requirements, pp. 195-209 in Control of rats and mice, vol. 1, edited by Chitty, D. and Southern, H.N., Oxford Univ. Press, London and New York.

Church, R.L. (1966). Water exchanges of the California vole, Microtus californicus. Physiol. Zool. 39: 326.

Church, R.L. (1969). Evaporative water loss and gross effects of water deprivation in the kangaroo rat, Dipodomys venustus. J. Mammal. 50: 514.

Cizek, L.J. (1959). Long-term observations on relationship between food and water ingestion in the dog. Amer. J. Physiol. 197: 342.

Conway, E.J. (1962). Microdiffusion analysis and volumetric error, 5th. rev. edit., Crosby Lockwood and Son, London.

Crampton, E.W. and Lloyd, L.E. (1954). Effect of water restriction on growing rats. J. Nutrition 54: 221.

Crawford, J.D. (1959). Service of urea in renal water conservation. Amer. J. Physiol. 196: 545.

Crocker, W. and Barton, L.V. (1953). Physiology of Seeds. Chronica Bontanica Co., Waltham, Mass.

Dolph, C.J., Braun, H.A. and Pfeiffer, E.W. (1962). The effect of vasopressin upon urine concentrations in Aplodontia rufa (Sewellel) and the rabbit. Physiol. Zool. 35: 263.

Donnet, V. and Garnier, L. (1954). Adsorption intestinale de l'eau et des sels. Arch. Sci. Physiol. 8: c205.

Drozdz, A. (1968). Digestibility and assimilation of natural foods in small rodents. Acta. Theriol. 13, 21:367.

Dukes, H.H. (1956). The physiology of domestic animals (7th. ed.) Ithaca, N.Y. Comstock.

Edwards, J.R. (1967). Water balance of the Australian native rodents Pseudomys sp and Leggadina hermannsburgensis. Hons. Thesis, Dept. of Zoology, Univ. of Adelaide.

Fertig, D.S. and Edmonds, V.W. (1969). The physiology of the house mouse. Sci. Amer. 221: 103.

Finlayson, H.H. (1939a). On mammals from the Lake Eyre basin. Part 4. The Monodelphia. Trans. Roy. Soc. S.A. 63: 88.

Finlayson, H.H. (1939b). Records and descriptions of Muridae from Ooldea, South Australia. Trans. Roy. Soc. S.A. 63: 354.

Finlayson, H.H. (1940). On Central Australian mammals. Part 1. The Muridae. Trans. Roy. Soc. S.A. 64: 125.

Fitzsimmons, T.J. and Le Magnen, J. (1969). Eating as a regulatory control of drinking in the rat. J. Comp. Physiol. Psych. 67: 273.

French, R.L. (1956). Eating, drinking and activity patterns in Peromyscus maniculatus sonoriensis. J. Mammal. 37: 74.

Getz, L.L. (1968) Influence of water balance and microclimate on the local distribution of the redback vole and white footed mouse. Ecology, 49: 276.

Geyer, R.P., Geyer, B.R., Derse, P.H., Zinkin, T., Elvehjem, C.A. and Hart, E.B. (1947). Growth studies with rats kept under conditions which prevent coprophagy. J. Nutrition 33: 129.

Gottschalk, C. and Mylle, M. (1959). Micropuncture study of the mammalian urinary concentrating mechanism: evidence for the counter current hypothesis. Amer. J. Physiol. 196: 927.

Graham, N. McC. and Williams, A.J. (1962). The effect of pregnancy on the passage of food through the digestive tract of sheep. Aust. J. Agric. Res. 13: 894.

Gregerson, M.I. (1932). Studies on the regulation of water intake. 2. Conditions affecting the daily water intake of dogs as registered continuously by a potometer. Amer. J. Physiol. 102: 344.

Grossman, S.P. (1962). Effects of adrenergic and cholinergic blocking agents on hypothalamic mechanisms. Amer. J. Physiol. 202: 1230.

Haggag, G. and El-Husseini, M. (1965). Concentrating mechanism of the kidney in Egyptian desert rodents and the evidence for the counter current system. Proc. Egypt. Acad. Sci. 19: 56.

Haines, H. and Schmidt-Nielsen, K. (1967). Water deprivation in wild house mice. Physiol. Zool. 40: 424.

Howell, A.B. and Gersh, I. (1935). Conservation of water by the rodent Dipodomys. J. Mammal. 16: 1.

Hudson, J.W. (1962). The role of water in the biology of the antelope ground squirrel, Citellus leucurus. Uni. Calif. Publ. Zool. 64: 1.

Hudson, J.W. and Rummel, J.A. (1966). Water metabolism and temperature regulation of the primitive heteromyids, Liomys salvani and Liomys irroratus. Ecology 47: 345.

Jacobs,H.L.(1964). The interaction of hunger and thirst: experimental separation of osmotic and oral-gastric factors in regulating caloric intake, in Proc. International Symposium on thirst in the regulation of body water, edited by Wayner, M.J., Pergamon Press, N.Y.

Kavanau, J.L. (1962). Precise monitoring of drinking behaviour in small mammals. J. Mammal. 43: 345.

Kennedy, J.A. (1969). The karyotypes of some Australian rodents (Rodentia: Muridae). Aust. J. Zool. 17: 465.

Kirmiz, J.P. (1962). Adaptation to desert environment - a study of the jerboa, rat and man. Butterworths, London.

Kissileff, H.R. (1969). Food-associated drinking in the rat. J. Comp. Physiol. Psych. 67: 284.

Kleiber, M. (1961). The fire of life : an introduction to animal energetics. Wiley, New York.

Lee, A.K. (1963). The adaptations to arid environments in wood rats of the genus Neotama. Univ. Calif. Publ. Zool. 64: 57.

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

Lindeborg, R.G. (1952). Water requirements of certain rodents from xeric and mesic habitats. Michigan Univ. Contribs. Lab. Vert. Biol. 58: 1.

Macfarlane, W.V., Morris, R.J.H., Howard, B. and Budtz-Olsen, O.E. (1959). Extracellular fluid distribution in tropical Merino sheep. Aust. J. Agric. Res. 10:269.

Macfarlane, W.V., Morris, R.J.H. and Howard, B. (1963). Turnover and distribution of water in desert camels, sheep, cattle and kangaroos. Nature 197: 270.

MacMillen, R.E. (1964a). Population ecology, water relations and social behaviour of a southern California semidesert rodent fauna. Univ. Calif. Publ. Zool. 71: 1.

MacMillen, R.E. (1964b). Water economy and salt balance in the western harvest mouse, Reithrodontomys megalotic, Physiol. Zool. 37: 45.

MacMillen, R.E. and Lee, A.K. (1967). Australian desert mice: independence of exogenous water. Science 158:383.

MacMillen, R.E. and Lee, A.K. (1969). Water metabolism of Australian hopping mice. Comp. Biochem. Physiol. 28: 493.

Nichter, R. (1957). The effect of variation in humidity and water intake on activity of Dipodomys. J. Mammal 38:502.

Odum, E.P. (1944). Water consumption of certain mice in relation to habitat selection. J. Mammal. 25: 404.

Peters, J.P. (1935). Body water - the exchange of fluids in man. Thomas, Springfield, Ill.

Quimby, F.H. (1948). Food and water economy of the young rat during chronic starvation and recovery. J. Nutrition. 36:177

Radford, E.P. (1959). Factors modifying water metabolism in rats fed dry diets. Amer. J. Physiol. 196: 1098.

Rawson, K.S. (1960). Effect of tissue temperature on mammalian activity rhythms. Cold Spring Harbor Symp. on Quant. Biol. 25: 105.

Robinson, P.F. (1959). Metabolism of the gerbil, Meriones unguiculatus. Science 130: 502.

Schmidt-Nielsen, B., Schmidt-Nielsen, K., Brokaw, A. and Schneiderman, H. (1948a). Water conservation in desert rodents. J. Cell Comp. Physiol. 32: 331.

Schmidt-Nielsen, K., Schmidt-Nielsen, B. and Brokaw, A. (1948b) Urea excretion in desert rodents exposed to high protein diets. J. Cell Comp. Physiol. 32: 361.

Schmidt-Nielsen, B. and Schmidt-Nielsen, K. (1950a). Do kangaroo rats thrive when drinking sea water? Amer. J. Physiol. 160: 291.

Schmidt-Nielsen, B. and Schmidt-Nielsen K. (1950b). Pulmonary water loss in desert rodents. Amer. J. Physiol. 162: 31.

Schmidt-Nielsen, B. and Schmidt-Nielsen, K. (1951). A complete account of the water metabolism in kangaroo rats and an experimental varification. J. Cell Comp. Physiol. 38: 165.

Schmidt-Nielsen, K. and Schmidt-Nielsen, B. (1952). Water metabolism of desert mammals. Physiol. Reviews 32: 135.

Schmidt-Nielsen, B., Schmidt-Nielsen, K., Houpt, T.R. and Jarnum, S.A. (1956). Water balance of the camel. Amer. J. Physiol. 185: 185.

Schmidt-Nielsen, B. and O'Dell, R. (1961). Structure and concentrating mechanism in the mammalian kidney. Amer. J. Physiol. 200: 1119.

Schmidt-Nielsen, K. (1964). Desert animals. Oxford, London.

Shkolnik, A. and A. Borut. (1969). Temperature and water relations in two species of spiny mice (Acomys) J. Mammal. 50: 245.

Simpson, G.G. (1961). Historical zoogeography of Australian mammals. Evolution 15: 431.

Slonaker, J.R. (1924). The effect of pubescence, oestration and menopause on voluntary activity in the albino rat. Amer. J. Physiol. 68: 294.

Smith, R.W. and McCann, S.M. (1962). Alterations in food and water intake after hypothalamic lesions in the rat. Amer. J. Physiol. 203: 366.

Sperber, I. (1944) Studies on the mammalian kidney. Zool. Bidrag. Uppsala. 22: 249.

Tate, G.H.H. (1951). The rodents of Australia and New Guinea. Bull. Amer. Mus. Nat. Hist. 97: 183.

Taylor, C.R., Spinage, C.A., and Lyman, C.P. (1969). Water relations of the waterbuck, an East African antelope. Amer. J. Physiol. 217: 630.

Thacker, E.J. and Brandt, C.S. (1955). Copophagy in the rabbit. J. Nutrition 55: 375.

Ullrich, K.J., Kramer, K. and Boylan, J.W. (1961). Present knowledge of the counter current system in the mammalian kidney. Progr. Cardiovascular Diseases 3: 395.

Vorhies, C.T. (1945). Water requirements of desert animals in the Southwest. Univ. Arizona, Agric, Exp, Sta., Tech. Bull. No. 49: 471.

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

Watts, C.H.S. (1970) The foods eaten by Australian desert rodents. South Aust. Nat. 44: 71.

Winkelman, J.R. and Getz, L.L. (1962). Water balance in the Mongolian gerbil. J. Mammal. 43: 150.

Wu, D.Y. and Wu, H. (1951). Determination of urea in saliva. Proc. Soc. Exp. Biol. Med. 76: 130.