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DOCTOR OF PHILOSOPHY

of

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B.A., St. Olaf College, 1961

M.A., University of North Dakota, 1963

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ADAPTATIONS TO ARID ENVIRONMENTS IN PEROGNATHUS PARVUS (PEALE)

ABSTRACT

In the upper Sonoran and transition zone areas of southern British Columbia populations of Perognathus parvus living in different habitats exist within a few miles of each other. The area was deglaciated about 10,000 years ago setting a maximum time for occupancy by small mammals. This study was initiated to compare the adaptations of individuals of these populations to the different habitats and, if possible, comment on their evolution and distribution. Animals from an environmental gradient were examined in the field and laboratory. One end of the environmental continum (low area) was characterized by low rainfall, high temperatures and a long summer. The other (high area) by high rainfall, low temperatures and a long winter.

Specimens from kill trapping indicated that the subspecies under consideration was morphologically variable with characteristics distributed in a checkerboard pattern. Analysis of stomach contents indicated that food during the summer was about equally divided between seeds, green vegetation and animal material. Seeds were the major item stored for winter food. Low area animals ate comparatively more green vegetation, possibly in response to greater water loss. Intensive live trapping and dissection of specimens indicated that high area females came into reproductive condition earlier in the spring and ceased reproducing earlier in the summer, producing fewer litters than the low area females. Young-of-year females in the low area reproduced while those in the high area did not. Average litter sizes (4.85) were the same. There was no postpartum estrus. Home ranges sizes of males (895 m^2) in the high and low areas were the same. The ranges of the females (656 m^2) were smaller. Burrows and home range centers were apparently randomly distributed and ranges of both sexes overlapped. Density was highest in the low area and decreased with altitude. Long term survival rates were high in all groups except low area young animals. Short term survival rates were highest in the winter, lowest in the spring and intermediate in the summer and fall. High area animals entered torpor

earlier in the fall than did low area animals. Adults apparently entered torpor before young animals. In the laboratory animals tended to enter torpor during the dark period and leave torpor during the light period after 3-168 ($\bar{X}$ = 46) hours in torpor. Percent of time spent in torpor increased with time at 5 C and levelled off at about 60%. When maintained at low temperatures high area animals had significantly longer torpor periods and spent a greater proportion of time in torpor than did low area animals. Subjection to water stress indicated that the low area animals were better able to conserve water by reacting more quickly to dehydration. When dehydrated low area animals were able to maintain a low plasma osmotic concentration while high area animals were not. The production of highly concentrated urine appeared to be the main reaction to dehydration. Fecal and evaporative rates of water loss were similar to those found in other small desert rodents and did not consistently decrease with dehydration. Both high and low area animals maintained their weight on a dry diet at 76% humidity at 20 C but lost weight at 42% humidity. It is suggested that the northern distribution of P. parvus is limited by the short summer season available for birth and establishment of the young. Analysis of morphological characters shows that genetic differences exist between individuals of the two populations. Concrete evidence of genetic differences in physiological characteristics is lacking but a strong circumstantial case for the existence of such differences can be built. It is suggested that high selection pressures have been more responsible for the differentiation of the populations than has restricted gene flow.

GRADUATE STUDIES

Invertebrate Zoology	P. A. Dehnel
Vertebrate Physiology	N. Holmes
Ecology	D. H. Chitty
Comparative Physiology	W. S. Hoar

PUBLICATIONS

Iverson, S.L. and R. W. Seabloom. 1963. A rapid method for cleaning small mammal skulls. Proc. N. Dak. Acad. Sci. 17: 101-103.

Hnatiuk, J. and S.L. Iverson. 1965. Habitat distribution and morphological variation of the deer mouse (Peromyscus) complex of Northwestern Minnesota and Northeastern North Dakota. Proc. N. Dak. Acad. Sci. 19:147-148.

Iverson, S.L., R.W. Seabloom and J. Hnatiuk. In Press. Small mammal distributions across the prairie-forest transition of Minnesota and North Dakota. Amer. Midl. Natur.

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A THESIS SUBMITTED IN PARTIAL FULFILMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

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We accept this thesis as conforming to the

required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April, 1967

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Department of Zoology

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Date 10 May 1967

ABSTRACT

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ACKNOWLEDGMENTS

I wish to thank my supervisor, Dr. H. D. Fisher, whose consistent support and encouragement made this study possible. The original plan of research was evolved in discussions with Dr. J. F. Eisenberg. Dr. I. Mct. Cowan, Dr. D. Chitty and Dr. P. A. Dehnel provided extremely helpful criticism. G. M. McKay helped with field work during the summer of 1965. I am grateful to all of these people, and to my fellow students, for stimulating discussions, helpful suggestions and critical comments throughout the course of this study. I am also very grateful to my wife, Alice.

INTRODUCTION

Studies of adaptations to arid environments in heteromyid rodents have been conducted along several lines, one of the most productive of which has been the work on water balance. The Schmidt-Nielsens (1951) examined kangaroo rats, Dipodomys, in great detail and found that these animals can survive without access to free water. Several adaptations make this possible. They possess a kidney which is capable of producing a highly concentrated urine, and a proposed nasal counter-current heat exchanger which makes possible low pulmonary water loss. They produce feces with low water content, and utilize behavioral means, rather than evaporation of water, to control body temperature except as a last resort. Many of these adaptations are probably also present in members of the genus Perognathus, although a complete examination has not been made. Tucker (1965a) suggests that Perognathus californicus does not conserve evaporative water to a greater extent than laboratory rats and mice. Chew and Dammann (1961) present data which indicate that Perognathus baileyi and Perognathus intermedius (pooled) lose less evaporative water than Mus musculus but more than Dipodomys merriami, although the differences may not be significant. Lindeborg (1952) showed that Perognathus penicillatus eremicus could survive on a diet of air-dried food and (1955) lost significantly less evaporative water per day than Peromyscus leucopus tornillo. Schmidt-Nielsen (1964) observed low evaporative water loss and high urine concentrations in "Perognathus sp.".

Another productive line of research has been the investigations of temperature regulation and torpor in Perognathus. Scheffer (1938) described a condition of "dormancy" in Perognathus parvus when exposed to low temperatures. Bartholomew and Cade (1957), working with Perognathus longimembris, were the first to measure the body temperatures of pocket mice

in torpor, record warming and cooling curves of torpid animals and describe the behavior associated with torpor. They have also observed torpor in several other species of Perognathus. They concluded that in P. longimembris hibernation and aestivation were the same physiological phenomenon and used the word torpor to describe both. Tucker (1962) described a daily cycle of torpor in Perognathus californicus and later (Tucker, 1965a,b) examined oxygen consumption, thermal conduction and heat exchange in P. californicus.

Scheffer (1938) investigated the ecology of P. parvus in Washington and Oregon in relation to agriculture. He found that in the dry areas of the above states the pocket mice far outnumbered other species and subsisted primarily on seeds and green vegetation, which they stored in their deep burrows. He found that each burrow was occupied by a single animal, except for females with litters during the summer breeding season. He states that the average litter size was about 5 and that the gestation period was from 21 to 28 days. Other major ecological investigations of pocket mice include those of Reynolds and Haskell (1949) on Perognathus penicillatus and Perognathus baileyi in Arizona, Hibbard and Beer (1960) on Perognathus flavescens in Minnesota and Dixon (1958) on the home ranges of Perognathus nelsoni in Texas. Eisenberg (1963) describes the behavior of many of the heteromyidae and outlines the evolution of behavior within the family. Benson (1933) examined the relationship between pelage and substrate coloration in several species of Perognathus.

Although these studies have illuminated much of the physiology and life history of members of the genus Perognathus, none of them has integrated laboratory and field approaches to several aspects of the adaptive repertory at once, nor have they compared populations of animals living in different environments. An integrative, comparative approach, however, has been taken to investigate aspects of adaptation in several small mammals.

Murie (1961) examined the metabolic characteristics of mountain, coastal and desert populations of Peromyscus maniculatus and Peromyscus eremicus. He found pelage insulation and deep body temperatures were the same in all

groups, but that the lowland P. maniculatus had a higher metabolic rate than the animals from the high altitudes. He attributed this higher metabolic rate to a more nervous temperament, which he hypothesizes is adaptive in chaparral habitat. P. eremicus had a consistently lower metabolic rate than P. maniculatus and resorted less readily to saliva-spreading as a method of evaporative cooling at high temperatures. He correlates these characteristics with the desert habitat of P. eremicus.

Nevo and Amir (1964) compared reproductive and hibernation patterns in forest dormice (Dryomys nitedula) at the extreme southern edge of their range, in Israel, with the patterns shown by Eurasian populations. They found that the dormice were active throughout the year and bore two to three litters per year between May and August in Israel, but the dormice in the northern areas were only active half a year and bore one to two litters per year. They suggest, on the basis of preliminary observations, that these differences might be genetically determined.

Fisler (1965) examined aspects of morphology, physiology and ecology in Reithrodontomys megalotis, Reithrodontomys raviventris raviventris and R. r. halicoetes in and around the salt marshes of San Francisco Bay. He suggests that raviventris and halicoetes arose from Megalotis through isolation in marshes on islands sometime during the last 25,000 years. He found many differences between the groups, some of which were correlated with environment. The marsh forms, raviventris and halicoetes, have developed a partly diurnal activity period and placid temperaments and so are limited to the heavy ground cover of the marshes. They have also developed an ability to tolerate salty drinking solutions with raviventris, which lives in the marshes with high salinity, able to tolerate water containing more salt. R. r. raviventris and R. r. halicoetes are presently isolated from each other by a series of high hills and are apparently evolving toward specific status.

The only isolating factor operating between them now is incomplete mate preference.

Perognathus parvus in the southern Okanagan Valley of British Columbia presents a unique opportunity to apply the integrative, comparative approach to an investigation of adaptation to desert environments by Perognathus. The animals are distributed throughout the valley floor, which is a northward extension of the Sonoran desert, and into the surrounding hills, which are grassland grading into forest. The population of P. Parvus at 4,500 feet altitude probably represents the furthest penetration of this species into a cool moist habitat. Populations at this altitude are located only a few miles from the valley floors. The area has been available for habitation by P. parvus for about 10,000 years and even though the climate has fluctuated during that period of time, the valley floor has probably always been warmer and drier than the higher altitude areas. This situation permits examination of the results of a maximum of 10,000 years of selection on individuals of a species living in two different environments with no apparent barriers to interbreeding.

Two possible explanations for differences between the populations which may occur are: the populations have the same range of tolerance to a specific environmental factor and are simply operating in a different part of this range, or the ranges of tolerance of the two populations have become different. Because of the lack of knowledge of this species, much of the field work in this study was descriptive and only shows the effect of environment on populations which may or may not be genetically different. The laboratory work was designed to test the capabilities of individuals of the two populations to respond to environmental conditions and so determine the ranges of tolerance of the two populations.

The working hypothesis may be stated as follows. Populations

geologically recent and geographically close, but subjected to different environments, will evolve different ranges of tolerance and modes of reaction to important environmental variables. The purposes of this study have been to test the above hypothesis and gain a better understanding of the natural history and physiology of *P. parvus*.

MATERIALS AND METHODS

The Study Area

The Okanagan Valley is a generally north-south trending valley in south-central British Columbia between the Cascade and Monashee mountain ranges. The valley is quite narrow and steep-sided and contains the Okanagan River, which forms several large lakes. In most locations along the valley there are wide benches composed of sandy alluvium, which have developed a highly arid-adapted fauna and flora.

GLACIAL GEOLOGY

The Okanagan Valley, and the rest of British Columbia, was covered by the Cordilleran Ice Sheet during the Wisconsin glaciation in the late Pleistocene. Richmond et al. (1965) state that during the middle stage of the Pinedale glaciation (about 16,000 years B.P.) the Okanagan lobe of the ice sheet extended as far south as the present location of Chelan, Washington. The recession of the ice sheet started soon after, and by 12,000 ± 310 B.P. ice was absent from the vicinity of the Columbia Plateau of Washington. After the recession of the glacier the climate continued to ameliorate, reaching a peak of maximum warmth and dryness between 6,500 and 4,500 years B.P. This latter fact was shown by Heusser (1965) in a palynological analysis of the sediments of Liberty Lake near Spokane, Washington. He found Pinus contorta (Lodgepole pine) to be the dominant species shortly after the recession of the ice. During the amelioration of climate this species was replaced by the more drought-resistant grasses. As the climate became cooler and moister again Pinus ponderosa (Yellow pine) became the dominant species.

In terms of the present study this means that probably around 10,000

years B.P. the southern Okanagan of British Columbia became marginal habitat for Perognathus. The vegetation at the time consisted of P. contorta, Pseudosuga menziezi (Douglas fir), Populus tremuloids (aspen) and associated herbs and grasses. Habitat similar to that of pine or bunch grass associations and suitable for Perognathus species continued to expand northward and upward altitudinally, reaching its greatest area between 6,500 and 4,500 years B.P. At that time areas that will not now support pocket mice were able to do so, present marginal habitats were well within the range of the animal and the now warmest and driest areas were even warmer and drier. Since 6,500 to 4,500 B.P. the climate has become cooler and wetter and areas near the northern and altitudinal range of the species have become marginal or submarginal, shifting to P. menziezi or P. ponderosa, while the entire area has become less favorable for a desert-adapted animal.

HISTORY

The history of man in the Okanagan Valley can be divided into four phases. Prior to 1811 the valley was occupied soley by Indians who, engaging in little agriculture, had little effect on the ecological balance. Between 1811 and the 1860's the valley was explored, passed through on fur trading expeditions and, toward the end of that period, prospected for gold. In the late 1860's the valley became more settled and large herds of cattle were grazed in the area. The effect of 100 years of grazing can be seen by comparing the grazed areas with the ungrazed areas on the Indian reserve. In the grazed areas the palatable bunch grasses and Purshina tridentata have been greatly reduced and the less desirable Artemsia spp. have greatly increased. Ranching in the bottom of the valley ended in 1927 with the arrival of the South Okanagan Land Project (S.O.L.P.) irrigation canal. This project made water available for irrigating most of the benchland on the west side of the Okanagan

River south of Oliver. This land is now planted to orchards, as is much of the land on the east side of the river. The only extensive tract of land in the southern Okanagan Valley that is still in its original state is the Indian reserve land on the east side of Lake Osoyoos.

CLIMATE

Kendrew and Kerr (1955) state that because of the dissected nature of the land, and the lack of weather stations, only a very general summary of the climate of the South Okanagan and surrounding hills can be made. They describe the climate as being mild continental with low precipitation and humidity. Winter is cold with snow in at least December and January, spring and fall are warm and dry, and June is the month with most rain and clouds.

There are no high altitude meteorlogical stations in the area of interest; the only ones which would be in the least comparable are those at Carmi and Princeton. The Princeton station is at the proper altitude but is on a valley floor and so is not as comparable as desired. Carmi is located at some distance from the area of interest and is at a rather high altitude. Therefore the high altitude stations will be used only to infer the direction of change in climatological parameters, and to a limited extent their values. Plant associations will also be used as indicators of environmental conditions.

PLANT ECOLOGY

If Merriam's life zone concept is applied, the extreme southern ends of the Okanagan and Similkameen are included in the upper Sonoran zone, while the surrounding grasslands are classified as transition zone. The biotic areas of Cowan and Guiguet (1956) make a division, in this case similar to Merriam's, by placing the southern valley bottoms in the Osoyoos arid, and the surrounding areas in the dry forest biotic area. More valuable

for our purposes is the bioclimatic zone classification of Krajina (1959, 1963).

According to Krajina the most arid areas compose the Ponderosa pine-bunchgrass zone of the Cordilleran cold steppe and savanna forest region, which is replaced by the interior Douglas fir zone of the Canadian Cordilleran forest in colder and wetter areas. Some of the characteristics of the zones and their subzones are shown in Figure 1, as well as the range of climatic conditions within which P. parvus is known to occur. Pocket mice are found throughout the Ponderosa pine zone and into the Douglas fir zone but climatic conditions in the extreme part of their range cannot be given because of the lack of high altitude weather stations.

Figure 2 shows the diurnal variation in mean temperature and relative humidity in July, when mean temperature and humidity reach their maximum values, at Kamloops and Carmi. The Kamloops station was selected because it was not located near a lake and so should give a better idea of variation on the benches high above lakes where the study area is located. The Carmi station is used because it is the most comparable of the highland stations.

The unconnected points show four day averages for temperature and humidity two inches above the surface of the ground in August 1966 in the high and low areas. These averages are included only to support the applicability of the long-term data used. The short-term data follow a similar cycle and maintain similar relationships when compared to the long-term curves.

During the period when the animals are active neither the humidity nor temperature are extreme. The minimum average humidity during activity is about 40%, which is determined from instruments 4 feet above the ground and so is higher than at mouse level. The highest temperature during activity is 80 F. Both sets of data show higher average humidities and lower average temperatures in the high area during periods when the animals are active.

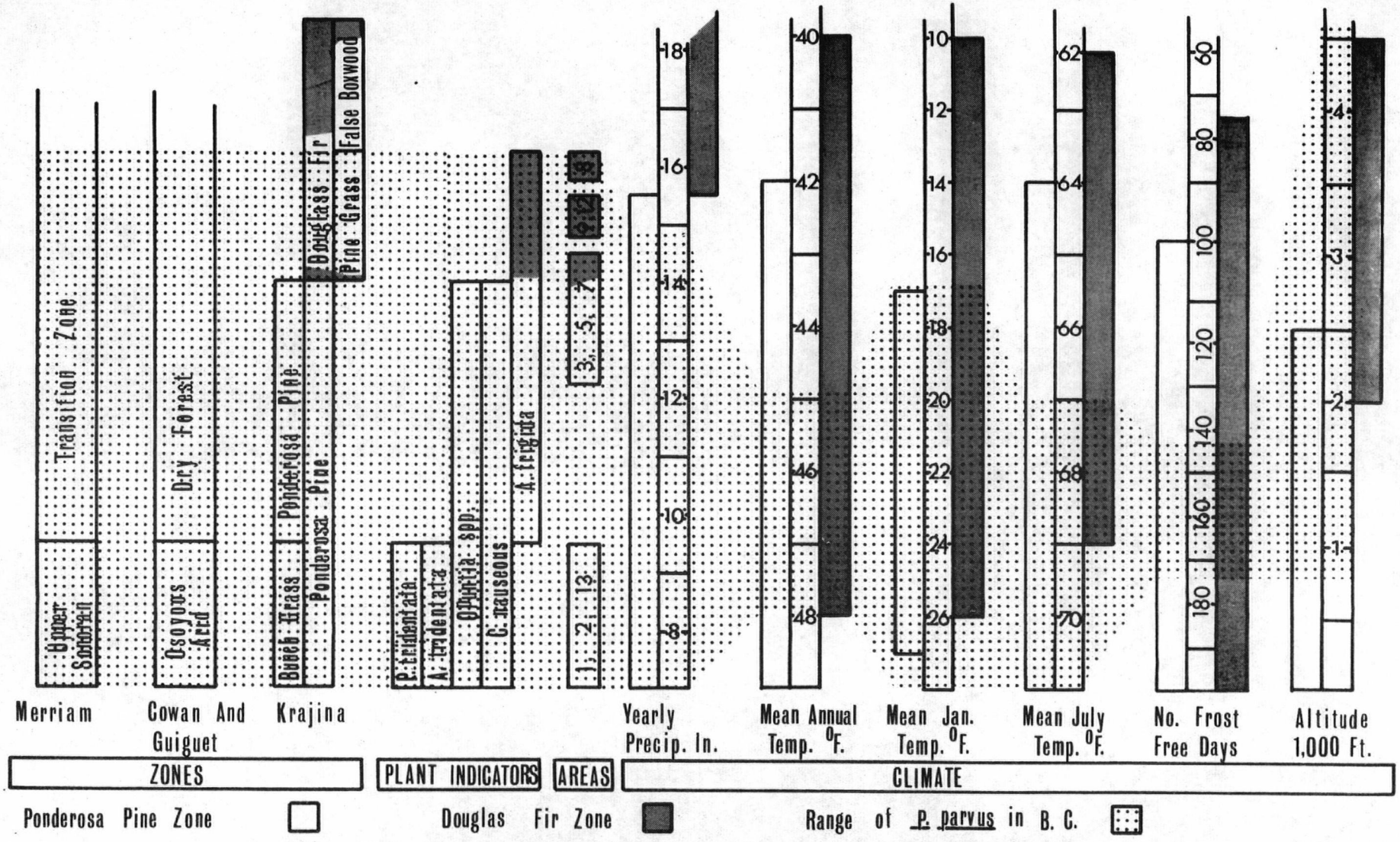


Figure 1. A summary of climate and plant associations in and near the range of P. parvus in British Columbia. Climatic extremes of the range are derived from records of weather stations inside the range of P. parvus.

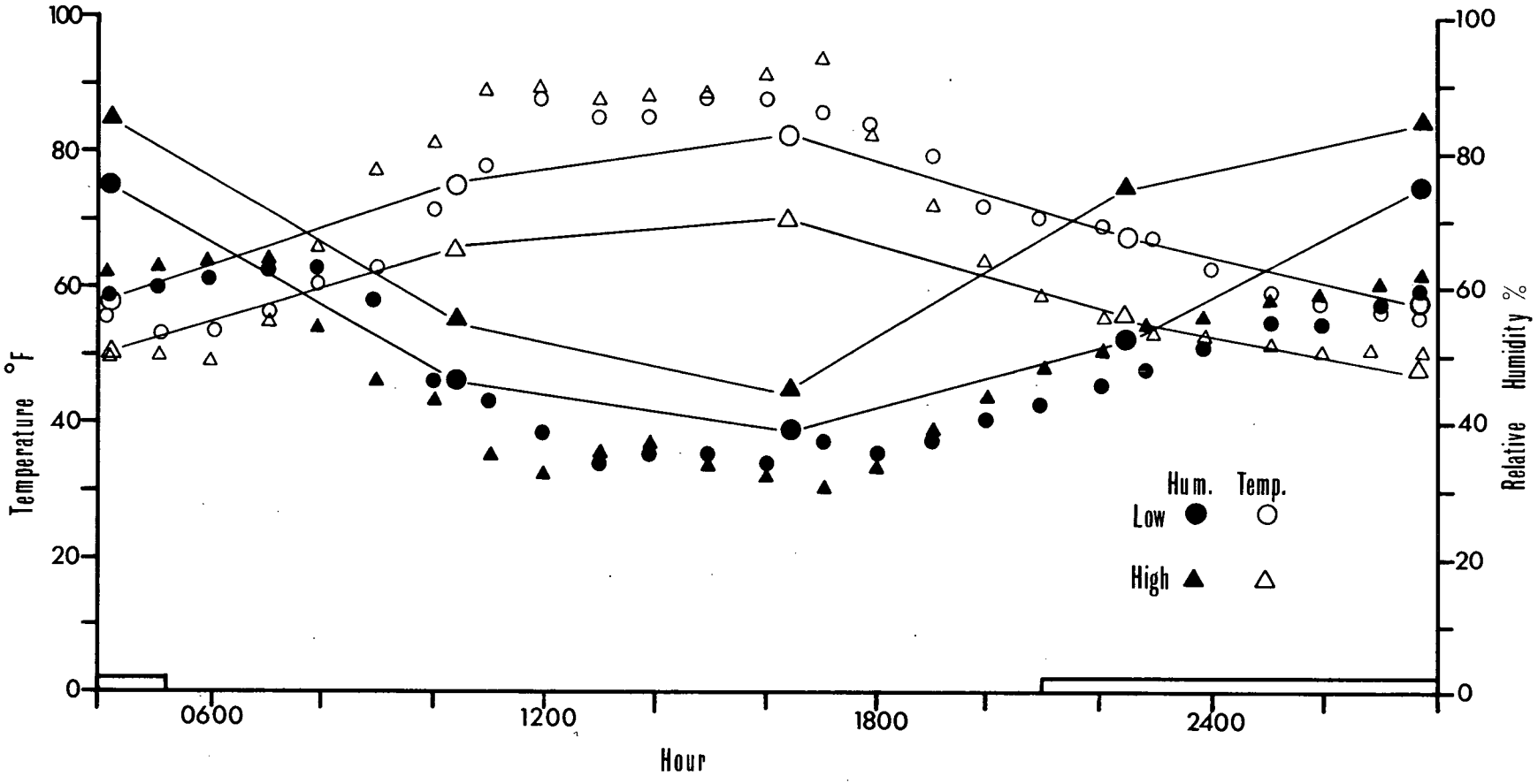


Figure 2. Diurnal variation in mean temperature and percent relative humidity in July at Kamloops and Carmi. Unconnected points show means of measurements made in the Okanagan in August.

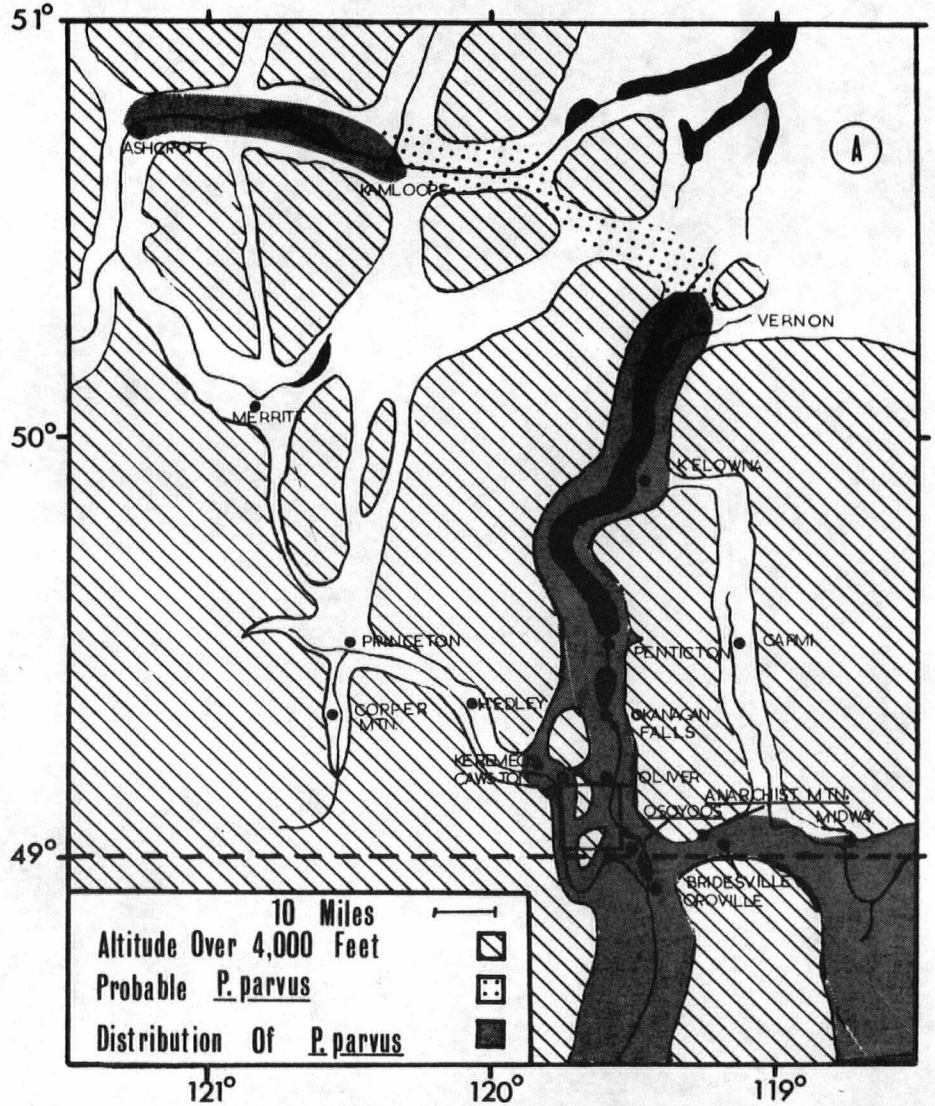
This effect can be noticed during the summer but is more apparent in the spring and fall. My records show both frost and snowfall occurred about one month earlier in the high area than in the low area in the falls of 1964 and 1965.

THE STUDY AREAS

Within the south Okanagan, areas were selected for intensive study. The locations and characteristics of these areas are shown in Figure 3 and Table I. An attempt was made to establish study areas at both ends of the ecological spectrum inhabited by P. parvus in B. C. and also between these extremes.

Areas 1, 2 and 13, established near Osoyoos in what appears to be the best development of desert-like conditions, sample one end of the spectrum. From now on this group of areas will collectively be called the "low area". Area 1 was set up in the Indian reserve and had not been subject to grazing for many years. It had a very good stand of Purshina tridentata and bunchgrasses. Area 13 was established immediately adjacent to area 1 and was similar. Area 2 was immediately across the reserve fence from areas 1 and 13 and was similar except that it had been subjected to heavy grazing and much of the P. tridentata had been destroyed.

Areas 3, 5 and 7, collectively called "high area", were located near the summit of the Richter Pass Road, B. C. highway #3. Because of the dissected nature of the land they were not adjacent to each other. They were, however, all within 200' of the same altitude and had similar soils, vegetation and land-use practices. The major difference among these areas was exposure (Table I). These areas were all within 100-200' of the local tree line, representing nearly the maximum altitudinal range of the pocket mouse in the Okanagan Valley. Because animals were scarce at the higher altitudes the major comparison in this study is between these areas and the



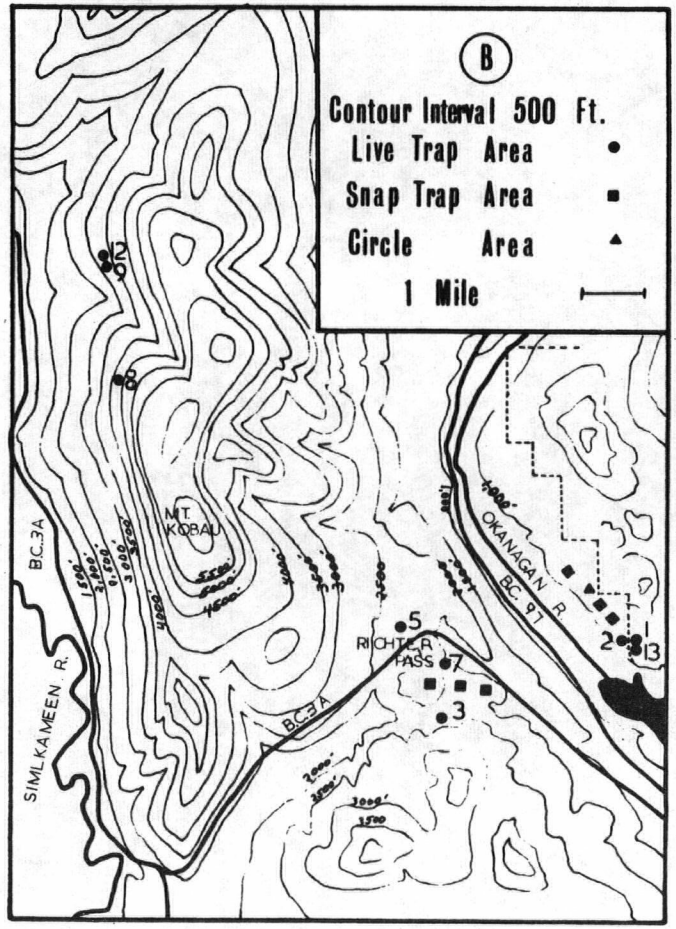


Figure 3. A. The distribution of P. parvus in British Columbia.
B. The location of the study areas.

TABLE I. A Summary of the Characteristics of the Study Areas.

Name	Identification Number	Altitude	Location	Exposure	Plant Indicators Present	Grass Type	Soil	Land Use
Low Area	Low home range 1-13	1,000'	Okanagan Valley NE Osoyoos	West-southwest 5-10° slope	P. tridentata A. tridentata C. nauseosus Opuntia sp.	Bunch grass	Azonal sandy alluvium no rocks little humus	None
	2	1,000'	Okanagan Valley NE Osoyoos	West-southwest 5-10° slope	P. tridentata A. tridentata C. nauseosus Opuntia sp.	Bunch grass	Azonal sandy alluvium no rocks little humus	heavily grazed
High Area	3	2,400'	Okanagan Valley Richter Pass NW Osoyoos	North-northeast 10-20° slope	A. frigida C. nauseosus	sod forming	brown forest clay till few rocks moderate humus	heavily grazed
	5	2,300'	Okanagan Valley Richter Pass NW Osoyoos	0 exposure 0 slope	A. frigida C. nauseosus Opuntia sp.	sod forming	brown forest clay till few rocks moderate humus	heavily grazed
	7	2,200'	Okanagan Valley Richter Pass NW Osoyoos	North-facing 10-15° slope	A. frigida C. nauseosus	sod forming	brown forest clay till few rocks moderate humus	heavily grazed
High Home Range	9-12	3,400'	Similkameen Valley SE Cawston	West 5-10° slope	A. frigida	sod forming	brown forest clay till few rocks moderate humus	lightly grazed
The Highest Area	8	4,300'	Similkameen Valley SE Cawston	West 5-20° slope	A. frigida	sod forming	brown forest clay till many rocks moderate humus	very lightly grazed

low area. All of these areas had been heavily grazed, grasses were scarce and stands of Artemesia spp. were very heavy.

Areas 9 and 12, the "high home range area", were located on a high west-facing slope of Mt. Kobau overlooking the Similkameen Valley and Cawston. The high home range area was similar to the high area except that it had not been grazed as heavily.

Area 8, the "highest area", was located at a higher altitude on the same slope as the high home range area. It was located just below treeline on the highest area of grassland that could be found. Artemesia spp. were present in low abundance, there were several rock outcroppings and P. parvus was scarce.

Methods

The prime requisite in the selection of areas was to represent the entire ecological spectrum present in British Columbia as discussed earlier. Areas were selected which were representative, accessible and undisturbed.

LIVE-TRAPPING METHODS

Once an area was selected it was measured out and a grid of traps consisting of seven rows of seven traps per row was established. The distance between the rows and between the traps in the row was 10 meters. Each trap location was marked with a permanent numbered stake. The home range areas later established consisted of nine rows of 16 traps per row. In a home range area a regular area made up traps 1-7 in rows 1-7 and a new regular size area made up traps 10-16 in rows 1-7.

Trapping was conducted with standard Longworth live-traps. A handful of oats was placed in the nestbox of each trap and a few grains were

sprinkled outside the tunnel. The traps were set during the day, checked the next day shortly after dawn, and then either collected or reset for the next night. Trap-caused mortality was very low. An area was trapped three nights the first time but the standard period of trapping was two nights.

In home range trapping 48 traps were used to cover the entire area. Traps were set at every third stake and moved forward one stake each time they were checked. In other words traps would be set at positions 1-1, 1-4, 1-7 etc. on the first night, and 1-2, 1-5, 1-8 etc. on the second night. On the fourth night the traps would be back in their original locations. Home range trapping was conducted for many nights in a row, the exact dates are given in the section on home range. The times of trapping are shown in Table II.

The animals were marked on their first capture by clipping no more than two toes per foot with a small, sharp scissors. The value of toes, from medial to lateral, was 1, 2, 4 and 7. The left hind foot indicated units, the right hind foot 10's, the left front foot 100's, and the right front foot 1000's.

On each capture the number, location, weight, age and reproductive condition of the animal were recorded. The animals were weighed to the nearest gram with a small spring scale. Reproductive condition of the males was indicated by the location of the testes. Reproductively active males had scrotal testes (TS) while non-reproductive animals had inguinal or abdominal testes (TA). Non-reproductive females had no opening to the vaginal canal (Imp.) while reproductive females had an opening (P). Middle to late pregnancy (Pg.) in females could be detected by visual observation and palpation. Milk could be expressed from the nipples of lactating (Lact.) females.

Age was recorded as either young-of-the-year (YOY) or adult (A). Because of the seasonal nature of reproduction young animals were captured

TABLE II. Periods of trapping in all areas. The X's represent two nights live trapping with 49 traps (98 trap nights), except in the home range areas where they represent continuous trapping with 48 traps. The O's represent snap trapping of specimens for dissection.

	Week	May 1234	June 1234	July 1234	Aug. 1234	Sept. 1234	Oct. 1234	Nov. 1234	April 1234	May 1234	June 1234	July 1234	Aug. 1234
	1		X X	X	X X	X	X	X	X	X XX	X X	X X	X X
	2		X X	X	X X	X	X	X		X	X X	X X	X X
Low													
	13									XX	X X	X X	X X
Area	Specimens									000	0	0	0 0
	Low HR									XX	X		
	3		XX	X	X X	X	X			X	X X	X X	X X
High	5		XX	X	X X	X	X	X	X	X X	X X	X	X X
Area	7		XX	X	X X	X	X			X X	X X	X	X X
	Specimens								0	0	0	0	0
High Home Range	9			X X	X	X	X			XXX	X X	X	X X
	HR									XXX	X		
Highest Area	8			X X	X	X	X			X	X	X	

only from late June to November. They were recognized by a number of characteristics including pelage color, weight, and color of the incisors. Young animals had greyish fine pelage, smaller size and lighter orange incisors. It was easy to recognize young animals until October, when many had molted into adult pelage and reached adult size. A few mistakes in aging during the late fall were undoubtedly made. The proportion would be low, however, because by then most of the animals had been marked.

SNAP-TRAPPING METHODS

Animals were snap-trapped for specimens for both the morphological study and the study of reproductive condition and stomach contents. Standard Victor break-back mouse traps were used, baited with whole grain oats. Traps were set about 20 meters apart in a line and left for as many nights as necessary. The number of traps per line and the exact locations of the lines were variable. Specimens for dissection were trapped near the high and low areas (Figure 3). The locations and times of trapping specimens for study skins are shown in Figure 3 and Table II.

A circle of snap traps (Table II, Figure 3) similar to that used by Calhoun (1963) was established. The basic configuration was two concentric circles cut by two diameters at right angles to each other. The diameter of the outer circle was 325 meters and the diameter of the inner circle was 162 meters. Traps were set 5 meters apart on the diameters and circles and were checked and rebaited each morning. The traps, a total of 270 were distributed in: outer circle, 205, inner circle, 40, diameters, 26.

LABORATORY METHODS

Animals used in the laboratory were trapped near the high and low study areas (Figure 3) with the methods and traps described earlier. In the laboratory they were maintained individually in glass-sided terraria 40x25 cm

with walls 20 cm high. The tops of the terraria were covered with welded wire screen. The cages were bedded with coarse sawdust about 6 cm deep. A finger-bowl filled with Okanagan soil was placed in each terrarium to allow the animal to maintain its pelage.

The animals were fed an abundance of sunflower seeds and millet weekly and lettuce twice weekly. No water bottles were used. The animal room was a windowless room used only to maintain a colony of P. parvus. The animals were maintained on a 16 hour day with the lights coming on at 0900 and going off at 0100 PST. The temperature was maintained at 20 C ± 2 C and the relative humidity fluctuated between 50 and 80%.

Under these conditions animals were maintained in the laboratory for as much as two years in very good condition. The laboratory mortality rate was low and the animals developed no gross abnormal behavior patterns. The total number of animals used in the laboratory phase of the study was 154.

RESULTS AND DISCUSSION

Morphology

Morphological variation of P. parvus in the Okanagan was examined because morphology is one of the most easily quantified and often used indicators of differences between populations. Many observed morphological changes are not of any obvious adaptive significance, but the amount of difference between populations, or the distribution of differences among populations, provide an index to possible evolutionary relationships between the populations.

METHODS

As many specimens as possible were assembled for examination. Specimens examined from British Columbia were: Osoyoos (89), Keremeos (10), Okanagan (28), Midway (1), Vaseaux Falls (1), Richter Pass (16), Vaseaux Lake (15), Vernon (44), Okanagan Landing (21), Ashcroft (14). Twelve specimens from Oroville, Washington were also examined.

Measurements used for analysis were the standard total, tail and foot lengths; the maximum width of the interparietal, minimum interorbital width and the condylobasilar length. The last three measurements were taken with a dial vernier caliper to the nearest 0.1 mm. Only those measurements taken from adult male animals were used in the statistical analysis. Animals were classified as adult or sub-adult on the basis of pelage. Those of questionable age were not included.

RESULTS AND DISCUSSION

The distribution of P. parvus in British Columbia (Figure 3) is nearly limited to the Okanagan and Thompson river valleys. The animals occur

in valley bottoms and are distributed up the valley sides in the south. The data were analyzed to permit an examination of the variation from north to south in the valley floor, and also to examine the difference between valley bottom and higher altitude mice in the south. Figure 3 shows the locations of the groups of mice analyzed.

Variations occur in morphological characters measured from Ashcroft to Oroville (Figure 4, Table III). With the exception of condylobasilar length, no smooth clines of characters are evident. In four of the five measurements animals from Osoyoos and Oroville were largest. These differences are not significant in some cases but indicate a trend for southern animals to be larger. With the exception of the cline in condylobasilar length and the tendency for Osoyoos and Oroville animals to be largest, no patterns can be seen.

Figure 5 (Table III) shows the variation across the Okanagan Valley in the Osoyoos area. The Osoyoos animals in this comparison are the largest in all measurements except for interparietal width. The high area animals in all cases, except for interparietal width, are more similar to the animals in the Vernon than the Osoyoos sample.

Interparietal width is great in Richter animals and high and variable in the Anarchist sample. When the interparietal/condylobasilar ratio is calculated highest values are once again found in the Richter animals. Most of the differences between the Richter and Anarchist animals are not significant and inspection of Figure 5 shows no consistent trends to one group of animals being larger or smaller. The same situation applies when the Vernon animals are compared to the Richter and Anarchist animals. When all comparisons are taken into account the only generalization that appear is that the Osoyoos-Oroville animals have the consistently largest total, tail, foot and condylobasilar lengths.

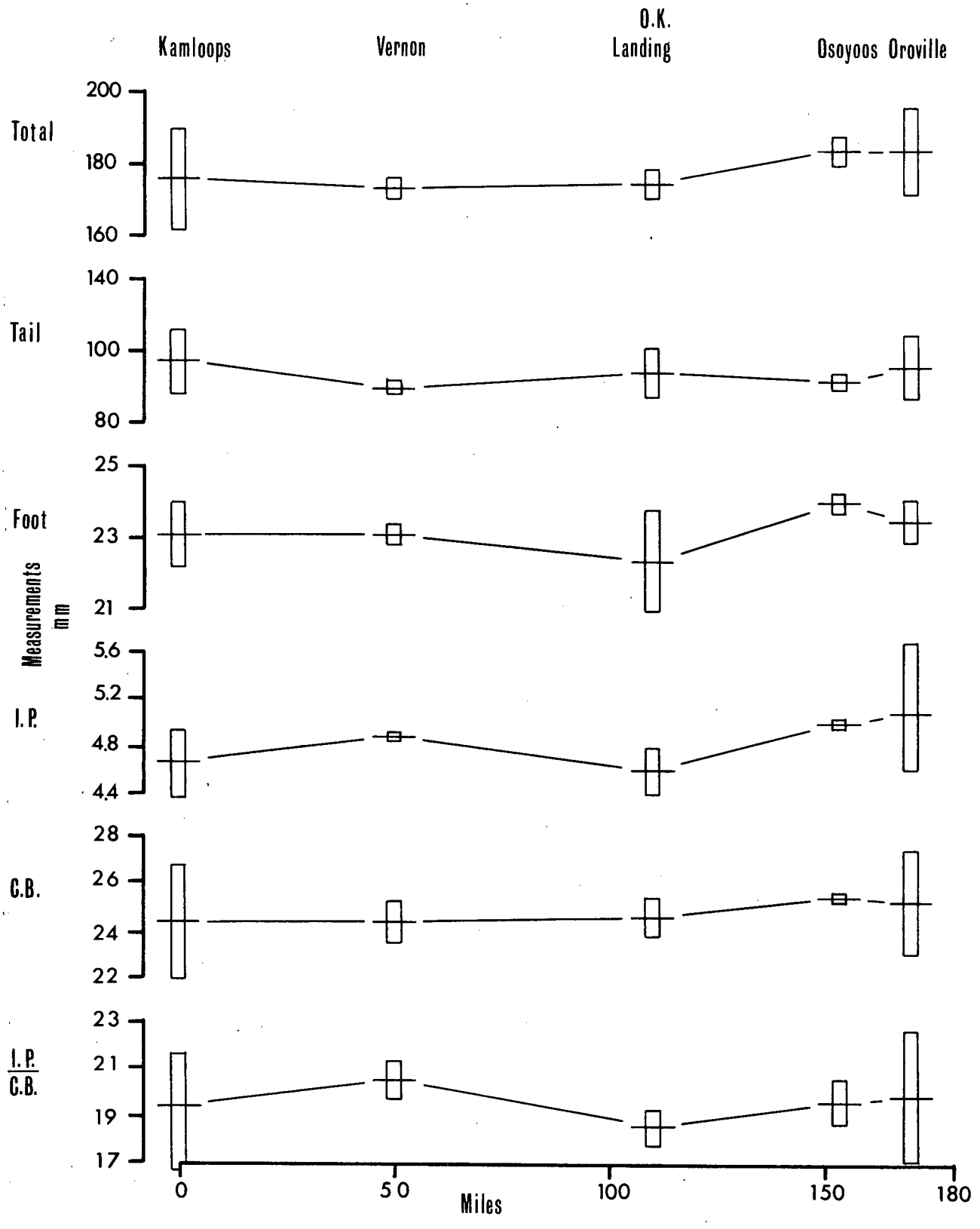


Figure 4. Clines of morphological measurements along the bottoms of the Thompson and Okanagan River Valleys. The means and 95% confidence intervals of the means are shown. Distance along the abscissa is proportional to the distance between the areas where the samples were collected.

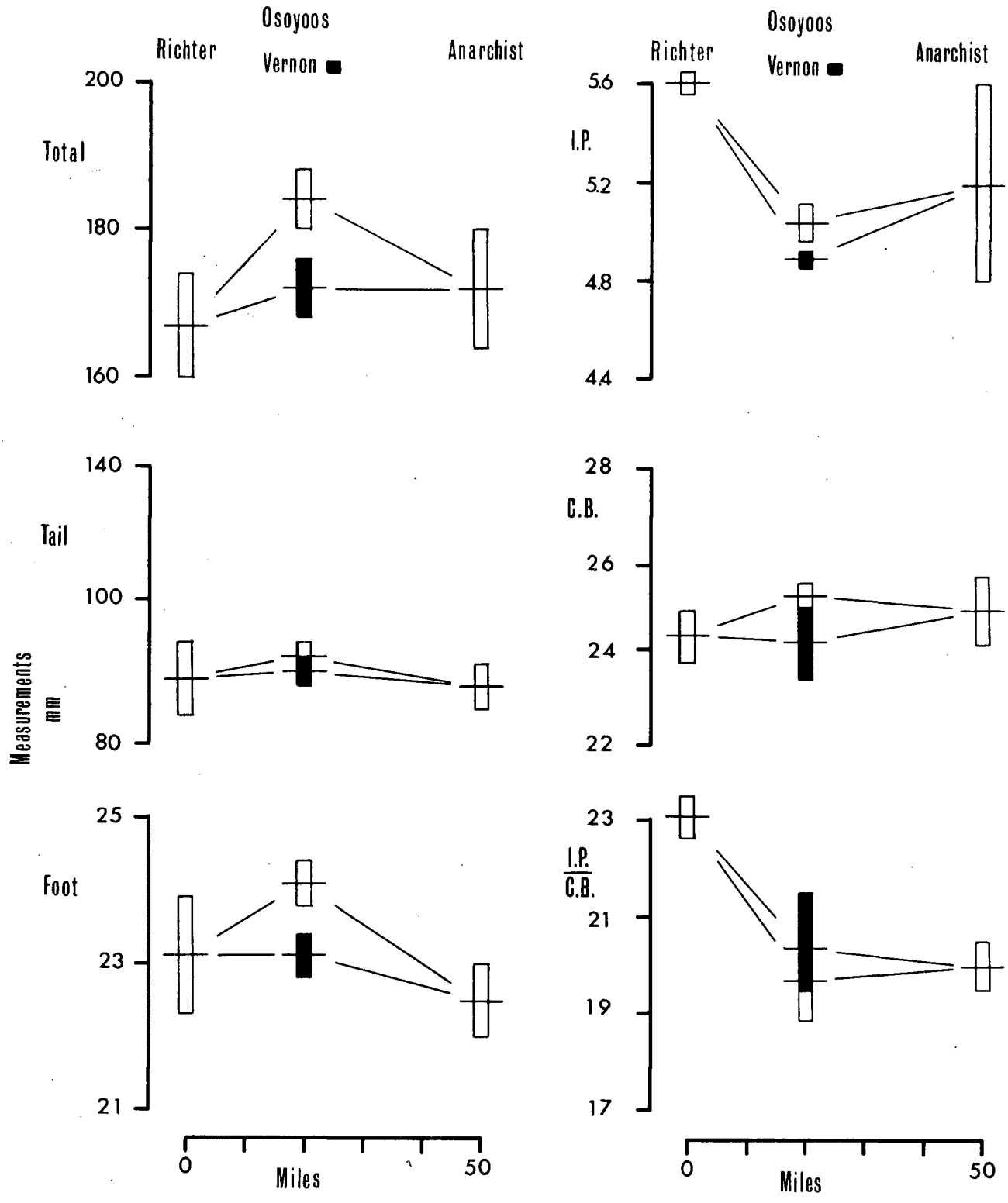


Figure 5. Clines in measurements across the southern end of the Okanagan Valley. Means and 95% confidence intervals for the means are shown. Distance along the abscissa is proportional to the east-west distance between the areas where the samples were collected.

TABLE III. Summary of measurements of adult males from different areas. Figures given are the mean, the standard error of the mean and the number in the sample.

	Total	Tail	Foot	Inter-parietal	Inter-orbital	Condylo-basilar	$\frac{IP}{CB}$
Kamloops	176.0 ± 14.7 7	97.1 ± 10.1 7	23.1 ± 0.86 7	4.7 ± 0.33 7	5.9 ± 0.15 7	24.3 ± 2.54 7	19.5 ± 2.89 7
Vernon	173.3 ± 3.6 22	90.0 ± 2.2 22	23.1 ± 0.27 22	4.9 ± 0.02 22	5.9 ± 0.04 23	24.2 ± 0.94 22	20.3 ± 0.98 22
Okanagan Landing	175.1 ± 4.2 11	94.5 ± 7.1 11	22.4 ± 1.4 11	4.6 ± 0.21 9	5.9 ± 0.12 9	24.6 ± 0.90 9	18.7 ± 0.92 9
Osoyoos	184.4 ± 4.0 30	92.3 ± 1.01 30	24.1 ± 0.28 30	5.0 ± 0.03 28	6.0 ± 0.02 27	25.4 ± 1.57 26	19.6 ± 0.93 25
Oroville	184.1 ± 11.9 7	96.1 ± 9.4 7	23.6 ± 0.53 7	5.1 ± 0.57 7	6.0 ± 0.49 7	25.2 ± 2.3 6	19.9 ± 2.98 6
Anarchist	172.0 ± 8.0 11	87.7 ± 3.2 11	22.5 ± 0.45 11	5.2 ± 0.11 9	5.9 ± 0.06 10	24.7 ± 0.62 8	20.9 ± 0.55 8
Richter Pass	166.8 ± 5.8 7	88.4 ± 5.3 7	23.1 ± 0.84 7	5.6 ± 0.4 5	5.9 ± 0.07 7	24.3 ± 0.51 6	23.1 ± 0.55 5

Bergman's rule, which states that, in a species of homeothermic animal, subspecies which exist in the cooler part of the species range tend to be larger than those living in the warmer part, appears to be generally valid for both altitudinal and latitudinal changes (summarized by Mayr, 1963). Burrowing mammals, however, almost consistently fail to obey Bergman's rule (Mayr, 1963), but react to the amount of food available in winter (Davis, 1938 for Thomomys and Stein, 1951 for Talpa). The observed body size of P. parvus in the Okanagan runs counter to Bergman's rule and may be a reaction to the amount of food available as with the animals discussed above.

Races in cool, moist areas are usually darker than those living in warm dry climates. This is known as Gloger's rule and holds true in the populations of P. parvus in the Okanagan (Cowan and Guiguet, 1956). Mayr (1963) states that this effect cannot be ascribed to substrate-adapted cryptic coloration because it is shown in nocturnal and arboreal animals. Benson (1933) however, examined the coloration of a variety of rodents living on the white gypsum sands and black lava flows of the Tularosa basin of New Mexico, and concluded that the colors observed were due to selection for cryptic coloration rather than an effect of climate. He bases his conclusion on the fact that he could find little climatic difference between the areas but that, even at night, the differences in visibility of the differently colored animals were apparent. Setzer (1949), in examining the subspecies of Dipodomys ordi, concluded that in this species the color was correlated with the color of the soil rather than the amount of moisture. It appears that in heteromyids, and possible desert rodents in general, color may more often be determined by soil color than amount of moisture. The color observed in P. parvus in the Okanagan cannot be ascribed to either cause because the color of the soil and the amount of moisture are positively correlated.

Half of the comparisons between areas are statistically significant

at the .05 level (Table IV). Significant differences are to be expected between populations, but the finding that the differences were significant in half of the comparisons made, particularly when the compared areas are close together geographically, implies a surprisingly high amount of variability. A better idea of the magnitude of the observed differences can be gained by comparing them to the usual level of difference needed to name a subspecies.

The criterion selected for comparison was the 75% rule put into numerical form by Mayr, Linsley and Usinger (1953). This rule was defined to mean 90% joint non-overlap. The point of intersection between the two curves can be calculated by dividing the difference between the means by the sum of the standard deviations. The resultant figure is called the coefficient of difference. A coefficient of difference of 1.28 equals joint non-overlap of 90% and is the conventional level of subspecific difference. A figure below 1.28 means a joint non-overlap of less than 90% and insufficient difference for naming of subspecies, while a figure above 1.28 indicates a difference great enough for subspecies to be named.

Table IV shows the calculated coefficients of difference and Student's t values for comparison between animals from Anarchist, Richter, Vernon and Osoyoos. No differences large enough to suggest the existence of two subspecies were found among the Osoyoos, Anarchist and Vernon populations. The Richter animals have a high coefficient of difference when compared to all other populations on the basis of interparietal/condylobasilar ratio and from Osoyoos and Vernon when compared on the basis of interparietal width.

Mayr (1963) points out that common and widespread species are more variable than restricted or rare ones. He goes on to say that the greater variability permits these animals to become widespread, thus allowing them to store more variability and so on in a mutually reinforcing reaction. Thus

TABLE IV. Comparisons of adult males from different areas in the South Okanagan. The upper figure is the coefficient of difference. If joint non-overlap is 90% or greater figure is underlined. Lower figure is t value. Significant ($P \leq .05$) values are indicated by ^{S}. Numbers are the same as in Table III.

	Total	Tail	Foot	Inter-parietal	Inter-orbital	Condylo-basilar	IP/CB
Anarchist x Osoyoos	.54 3.1^{S}	.62 12.3^{S}	1.09 5.9^{S}	.19 .751	1.06 5.5^{S}	.45 2.17^{S}	.72 4.20^{S}
Anarchist x Richter	.34 14.9^{S}	.07 .89	.38 1.56	.70 1.27	0 0	.30 1.10	<u>1.98</u> 13.8^{S}
Anarchist x Vernon	.06 .36	.22 3.28^{S}	.41 .74	.51 2.38^{S}	0 0	.27 1.20	.33 1.44
Vernon x Richter	.57 2.02	.14 .66	0 0	<u>8.5</u> 2.71^{S}	0 0	.06 .72	<u>1.76</u> 5.2^{S}
Vernon x Osoyoos	.58 35.5^{S}	.28 1.94	.69 4.8^{S}	.83 .55	1.01 .46	.64 5.18^{S}	.31 1.60
Richter x Osoyoos	1.26 10.1^{S}	.46 2.73^{S}	.60 3.0^{S}	<u>5.7</u> 3.08^{S}	.76 .40	.85 3.21^{S}	<u>2.19</u> 6.52^{S}

the observed variability may be part of the reason that the animal has been able to exist in the variable habitat of the south Okanagan.

The presence of many large differences, in one case large enough to be subspecific, between populations geographically close, indicates that either gene flow has been restricted or selection pressures have been high. Except for the Okanagan river, and now the irrigated orchards, no barriers are apparent. The presence of differences between areas on the same side of the river indicate that restricted gene flow alone does not explain the observed variation. The situation can possibly best be summarized by stating that the observed differences exemplify the results of high selective pressure on the members of a variable species.

CONCLUSIONS

1. Bergman's rule is not followed in the variation of specimens observed. Gloger's rule is followed, although the variation in pelage coloration may be due to the color of the substrate rather than climatic conditions per se.

2. The populations were highly variable in the characters studied. The variation was found to be distributed in a checkerboard rather than clinal pattern. On the basis of the observed variability and the distribution of the variability it is suggested that population gene frequencies are changing rapidly in response to high, local, selective pressures.

Food Habits

The investigation of food habits is important not only because of the basic ecological information it yields but also because, in this species, water taken in with food may represent the total water intake. If a popu-

lation is in an environment where water loss is great, intake of a greater proportion of food with high water content might balance the water budget with the expenditure of less energy than restricting water loss.

METHODS

The stomachs were excised, placed in water under a dissecting microscope, and opened with a cut along the midline of the greater curvature. The upper half of the stomach could then be reflected back without disturbing the food mass. The food mass was then examined and contents noted.

Possible content of the stomachs was divided into three categories: seeds, vegetative material and animal material. The seeds were normally masticated into a paste-like consistency, which, if present, formed a mass in one part of the stomach. Vegetative material could be recognized because, even though well masticated, it occurred in small pieces and retained its structure and often its green color. The animal material was least well masticated and often complete heads, legs or antennae could be recognized.

Two separate ratings were used to describe the contents of a particular stomach. One of these, "incidence", was simply a reflection of whether a class of food materials was present or absent. If the class under consideration was present a score of one was given. If it was absent a score of zero was given. The other rating was called "importance" and was an indication of the proportions of the different classes of food materials present. The food material occupying the greatest volume of the stomach was given a rating of 3, that class occupying the second greatest a rating of 2, and the class occupying the least volume a rating of 1. Any class of food materials which was absent was given a rating of 0.

Scores in each class were then summed and converted to a percentage of the greatest possible score. For example, if class x contained one stomach, the contents of which were: mostly seed, some vegetative and no animal material;

the incidence score for this class would be seed 100%, vegetative 100%, animal 0%. The importance score would be seed 100%, vegetative 66% and animal 0%.

The data were examined and it appeared that both incidence and importance were giving the same results. A correlation coefficient indicated that they were highly significantly correlated ($r = .616$, $p \leq .001$). On this basis it was decided to simplify analysis and presentation by using only the least subjective of the predictors, incidence.

Stems and leaves of representative grasses and herbs, ripe seed heads, and beetles and grasshoppers were collected from the high and low areas in August 1966, for the determination of water content. The effect of underground temperature and humidity on the moisture content of seeds was also determined. Approximately 250 g of pearled barley was placed on the surface of the soil and another sample buried at a depth of 1 meter in the high and low areas. The barley was allowed to equilibrate for eight days and then sampled for moisture determinations. All samples were weighed when collected, dried for 24 hours at 100 C and reweighed.

RESULTS AND DISCUSSIONS

Animal Material

The classical view of the diet of Perognathus is illustrated by Scheffer (1938), who states that they are "strictly vegetarian". This view was changed by Jameson (1954) who reported that of 20 specimens of P. parvus captured in California the stomachs of 14 contained animal material. The reason for this difference in opinion may lie in the fact that the earlier studies reported food habits as based on contents of cheek pouches and burrows, while Jameson reported on the contents of both pouches and stomachs. He found that the pouches of 9 of the 20 animals contained seeds, while only 1 contained animal material.

Table V shows the percentage incidence of food materials in the stomachs of different classes of animals. Animal material has an incidence between 33% and 77% in all locations and reproductive class groups. Table VI shows that animal material makes up a significant proportion of the diet. In a sample of 99 animals no animal material was found in cheek pouches (Table VII).

The type of animal food eaten appears to be exclusively arthropod and probably primarily insect. Jameson (1954) states that he found only insects and that these were mostly caterpillars. My analysis shows 12 occurrences of caterpillars, 7 of unidentifiable insect material and 2 of nearly complete mole crickets. Many of the occurrences of unidentifiable insect material consisted of heavily scleritinized appendages, which were probably from beetles. Blair (1937) states that grasshoppers, beetles, pupae and larvae make up a regular part of the diet of P. hispidus.

No significant variation was found in the amount of animal material eaten by different classes of animals or between animals in high and low areas. Animal material appears to make up a relatively constant part of the diet. It is available to and probably used by the animals during most of the time they are above ground. This is the time during which reproduction and growth takes place and animal material eaten appears to provide an important source of protein and water (Figure 6).

The impact of this high protein food on the water balance has not been investigated. Schmidt-Nielsen and Haines (1964) state the Onychomys can maintain water balance on a diet of meat alone without producing a highly concentrated urine. Since P. parvus produces a highly concentrated urine, animal matter eaten may contribute to positive water balance.

Green Vegetation

Occurrence of vegetative material in the diet of P. parvus has been reported by both Scheffer (1938) and Hall (1946). Their reports and

TABLE V. Percentage incidence of food materials in stomachs of animals in altitude, sex, and reproductive class groups. ^{s} indicates significant ($P \leq .05$) difference indicated by Chi^2 test. ^{c} indicates that Yates correction for continuity was used.

	High area	Low area	All males	All females	TA males	TS males
Vegetation	45^{s}	71	64	64	51^{s}	77
Seeds	82	83	86	79	85^{s}	88
Animal	44	48	50	48	47	53
N	100	198	181	117	89	92

	IMP females	P females	Lact. females	P females	PG females	P females
Vegetation	48^{s}	78	22^{c}	78	79	78
Seeds	66^{c}	95	55^{c}	95	81	95
Animal	33	49	77	49	42	49
N	39	41	9	41	28	41

TABLE VI. Percentage of total incidence contributed by each of the three classes of food materials. All sex and location classes are pooled.

	April	May	June	July	August	Sept.	Mean
Vegetation	41	38	28	26	28	27	31
Seeds	37	40	44	45	53	43	43
Animal	21	22	28	29	19	30	26
N	34	83	48	43	56	34	298

TABLE VII. Percentage incidence of materials in cheek pouches of a sample of mice. All sex and location classes are included. N = 99.

	Bait	Seeds	Green vegetation	Animal	Fecal
Absolute incidence	85	39	6	0	1
Percentage incidence	86	39	6	0	1

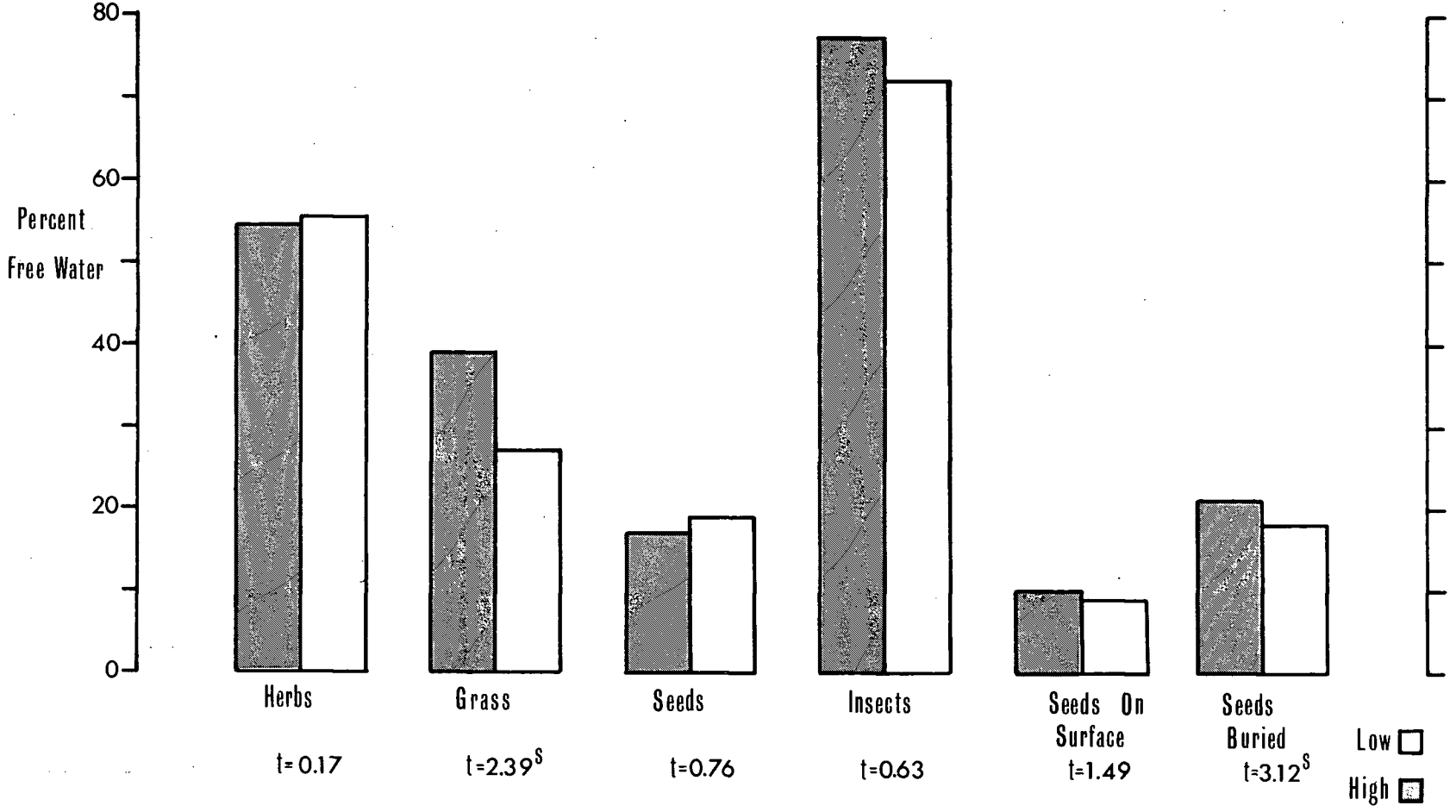


Figure 6. Percent free water in food materials collected in the high and low areas in August 1966. Significant ($P \leq .05$) differences are indicated by ^{S}. N in all groups equals 10.

the results of this study indicate that vegetative material is primarily green succulent vegetation such as grass leaves or stems.

I have observed fleshy prickly pear (Opuntia spp.) leaves which had been gnawed by mouse-sized rodents, probably P. parvus. Macerated roots were found in one stomach and lengths of rhizome have been found in live-traps. The vegetative material found in cheek pouches was mostly grass stems cut to a convenient length.

Vegetative material is similar to animal material in that it makes up a significant proportion (25 - 40%) of the summer food of the animals but is apparently not carried in pouches or stored to any great extent. Vegetative material was found in 6% of the pouches sampled and dried short stems of grass were found in one burrow.

More males with scrotal testes and perforate females have vegetative material in their stomachs than non-reproductive animals, and lactating females have higher incidences than perforate females. These same groups also have higher incidences of seeds. These differences may reflect an increase in food intake rather than a change in diet.

The incidence of vegetative material is higher in the stomachs of animals captured during April and May than in those captured from June through September. It is also higher in low area animals as compared to high area animals. The most obvious environmental correlate with high incidence of vegetative material is aridity. April and May are the two driest months in the Okanagan and the low area is much drier than the high area. Since these animals would be under some water stress, at least the stress of providing energy for the production of a highly concentrated urine, they appear to have minimized the amount of physiological work necessary by eating more succulent vegetation when in situations of greater water loss.

Vegetative material contains two to three times as much free water as seeds (Figure 6) and so provides a good source of water. Grass stems and leaves, which appear to be the main source of green vegetation eaten, contain significantly more free water in the high than in the low area (Figure 6). The amount of water available in the grasses in the low area may partially account for the greater amount of vegetative material eaten by low area animals.

Seeds

In agreement with the classical view of the diet of Perognathus, seeds are the most important food item. Seeds are present in about twice as many stomachs as any other food material and are the only food item carried in cheek pouches or stored to any extent in burrows. Because of this it is the only food available for daytime or winter feeding.

No attempt was made to identify the types of seeds found in cheek pouches or burrows or to correlate abundance of seeds collected by the mice with abundance of plants. Size of seeds utilized varied from the very small (less than 1 mm) seeds of some herbs to the large seeds of some of the grasses. Blair (1937) states that P. hispidus utilizes the most available seeds. Scheffer (1938) and Hall (1946) list species of seeds utilized by P. parvus, and Blair (1937) lists species used by P. hispidus.

Seeds were present in 39% of the pouch samples, in all 5 of the burrows which contained food, and in 83% of all stomach samples. The amount of food present in each burrow when excavated, late July, 1964, varied from 25 to 300 cc. The percentage incidence of seeds is significantly greater in reproductive animals of both sexes than in non-reproductive animals. This may reflect an increase in energy requirements of the animals or it may show a change in amount of activity.

The proportion of seeds in the diet of P. parvus increases toward

the end of the summer. This is probably due to a combination of greater availability of seeds and storage for the approaching winter.

Naturally occuring seeds contain only about 20% free water. This is less than any other class of food material (Figure 6). The water content of seeds is increased, however, by storage in burrows. After eight days buried pearl barley contained twice as much free water as that exposed on the soil surface (Figure 6). If the same relationship is true for naturally occurring seeds, stored seeds may contain nearly as much free water as fresh vegetative material. Buried seeds in the high area contained significantly more water than those in the low area.

The appearance of fecal material in one stomach, and in one pouch, and of gnawed rabbit feces in a burrow, show that these animals feed to a small extent on fecal material. Reynolds and Haskell (1949) report that fecal material of unnamed origin occurred in the cheek pouches of 6% of the Perognathus pricei but none of the Perognathus baileyi they examined. Blair (1937) reports gnawed fecal pellets of Sylvilagus floridanus alacer in 4 of the 18 burrows of Perognathus hispidus that he examined. Miller (1939), trapping near Van Horn, Texas, during the dry season, found kangaroo rat droppings in pouches of all four of the Dipodomys spectabilis baileyi which he captured. He suggests that because of food shortage it is necessary for these kangaroo rats to reassimilate fecal material.

Animals may reassimilate fecal material to salvage vitamins produced by bacterial action in the intestine. Olcese, Pearson and Schweigert (1948) showed that fecal material of rabbits is high in riboflavin. Rabbits grow well without additional riboflavin because of the amount gained by cecal absorption and reingestion of feces. In the pocket mouse reingested feces may provide both a source of vitamins and an emergency food supply.

CONCLUSIONS

1. The proportion of different materials in the stomachs of high area animals were about 1/4 vegetative material, 1/4 animal material, and 1/2 seeds. The proportions in low area animals were 1/5 animal material, 2/5 vegetative material and 2/5 seed.

2. Animal material was not carried in cheek pouches or stored in burrows, but made up a significant proportion of summer food of P. parvus.

3. Vegetative material was also not carried in cheek pouches or stored in burrows. It made up a significant proportion of the summer food and appeared to be eaten, at least partially, to provide water. It contained 25 - 55% free water.

4. Seeds were the main item in the diet of P. parvus. They had the highest incidences in stomachs and were the only item carried and stored in burrows for night and winter feeding. Buried seeds contained twice as much free water as those exposed on the soil surface.

5. Grasses and buried seeds in the high area contained significantly more water than in the low area.

6. Fecal material occurred occasionally in stomachs and burrows and may represent emergency food or a supply of vitamins, particularly riboflavin.

Reproduction

Reproduction is one of the more complex and stressful phases of an animal's life cycle and may be a limiting factor in the colonization of inclement environments. The periods of reproduction have been shown to be correlated with the more "favorable" periods of the year (Prakash, 1960 and Nevo and Amir, 1964) and so may provide a key to comparison of the severity

of different stresses acting on the population. Data on the number of offspring produced per year are important for the analysis of populations and provide a measure of the productivity of an area.

METHODS

Data presented in this section were obtained from snap-trapped and live-trapped specimens. The methods and locations of trapping were the same as described earlier.

Male snap-trapped specimens were opened with a mid-ventral incision from the abdomen to the posterior end of the scrotum. The positions of the testes were noted, the length of the right testis was measured to the nearest millimeter, and a small sample was taken from the most distal extension of the epididymis. Epididymal samples were placed in water on microscope slides, covered with cover slips, macerated, and examined at 400 magnifications. If sperm were present they could be easily seen.

Female reproductive tracts were cleared and studied following the method of Orsini (1962 a,b). The exact procedure followed was to remove the entire uterus with ovaries, cervix and part of the vagina as a single unit. It was then attached to a 1" x 3" microscope slide with a thread through the cervix and another around the tract near the ovaries. The tracts were stored in neutralized 10% formalin and then bleached, dehydrated and cleared in an automatic tissue processor. The schedule followed was: 50% alcohol + hydrogen peroxide 2 hours, 70% alcohol + hydrogen peroxide 2 hours, 80% alcohol + hydrogen peroxide 2 hours, 95% alcohol 2 hours, absolute alcohol 2 hours, absolute alcohol 2 hours, 50% absolute alcohol + 50% xylol 1½ hours, xylol 3½ hours, and finally benzyl benzoate for storage.

A few female tracts far advanced in pregnancy, or in which uterine blood vessels had been ruptured by trapping, were not sufficiently bleached

by the process outlined above. These tracts were rehydrated to 80% alcohol and hydrogen peroxide, bleached for a further 6 hours, and then dehydrated and cleared again.

The preparations were examined under a dissecting microscope with oblique light as suggested by Orsini (1962a). Condition of the tracts (post-partum, pregnant, or nulliparous) was noted, counts of embryos and placental scars were made, and presence of ovulatory follicles was noted.

For the purposes of this section live-trapping data for the summers of 1964 and 1965 were pooled. Insufficient data were present for the analysis of reproduction on a weekly basis so observations made in each two week period were pooled. The numbers were used as ratios for Chi^2 analysis and then converted to percentages for ease of understanding.

To calculate the number of litters per adult female per summer I used trapping records only for those females that had been trapped at least once every 3 weeks from the beginning of the reproductive season to the end. A period of 3 weeks was used because the best estimate of gestation period is slightly over 3 weeks (21-25 days) (Eisenberg, Pers. Comm.) and the lactation period is also probably around 3 weeks. P. californicus leave the burrow at about 22-25 days (Eisenberg, 1963). With the trapping schedule described above a reproducing animal would be captured at least once when such activity was evident, such as any time during the last week of pregnancy, or the first two weeks of lactation. Some of the trapping records indicate that pregnancy can be recognized in the field as early as 11 or 12 days and lactation may be evident for at least three weeks.

The number of litters per young female was calculated from records of animals captured both the first and fourth week of August or the fourth week of July and the third week of August. To reproduce and avoid these period a young animal would either have to be sexually mature and conceive

in the third week of June or not bear a litter until the second week of September. No evidence can be found in the trapping records that either of these possibilities occurs.

RESULTS AND DISCUSSION

Male

Figure 7a, b, c illustrates the general cycle of reproduction in male P. parvus. Unfortunately animals were not collected early enough in the spring to determine the onset of reproductive activity. Extrapolation of Figure 7b indicates that at least some males had scrotal testes early in April. By the end of May all indicators of reproductive activity in males showed that most or all of the population was reproductively capable. The males remained in reproductive condition until the end of June, when the percentage of reproductive animals in the high area began to decline, followed in about two weeks by the low animals. Early in August reproductive activity in males in the high area had ceased and by the end of August all activity in the low area was over.

High area males may have come into reproductive condition earlier than low area males but the difference was not significant (Figure 7b). The high area males did, however, go out of reproductive condition significantly earlier.

Young males of either area did not become reproductive until the next spring. In one area, however, where all adult animals in an area disappeared, the young immigrant males came into reproductive condition early in August. This indicates that social interaction may prevent sexual maturation in young males.

Female

Reproduction in females did not begin until late May, when a large

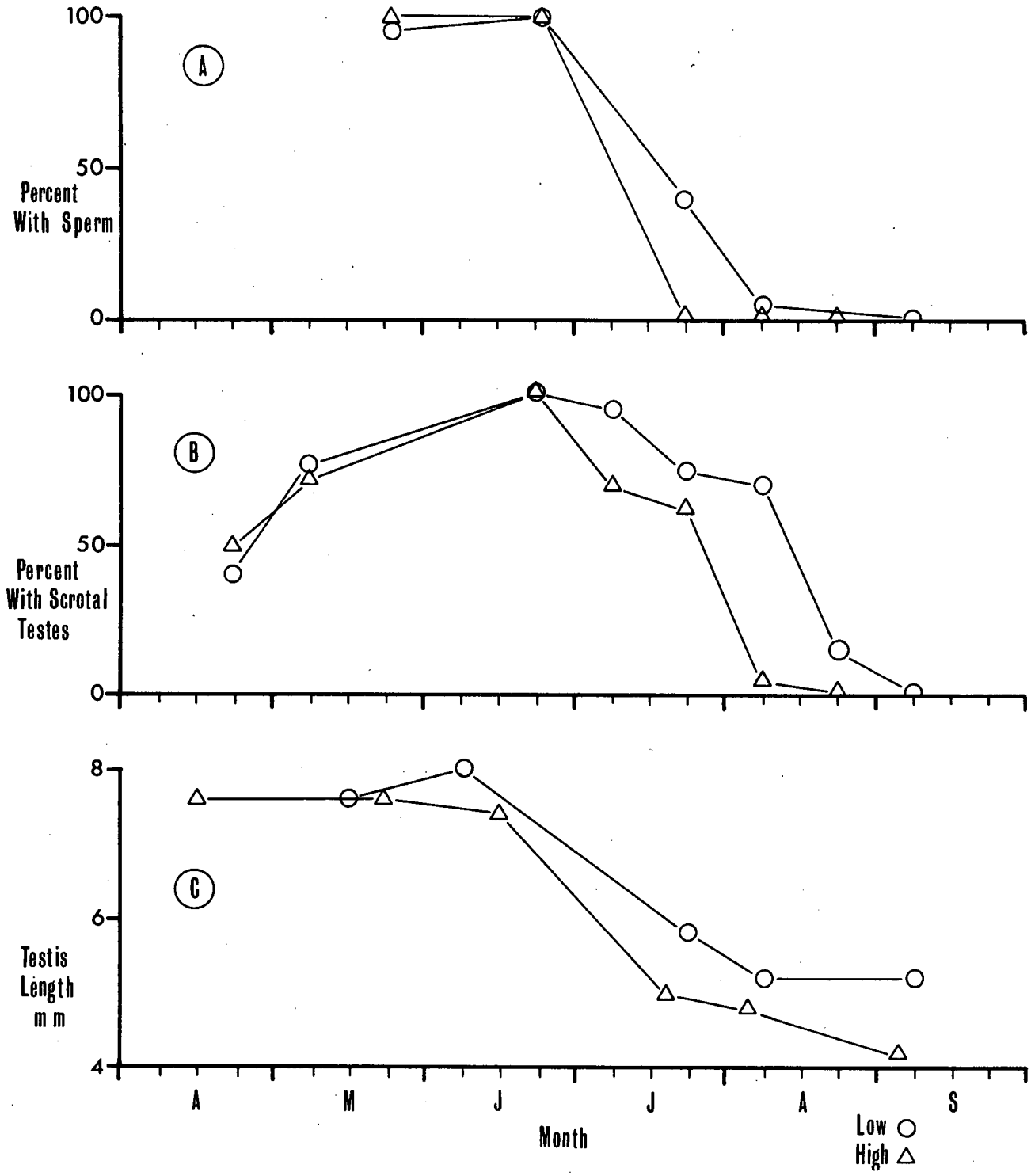


Figure 7. A. Percentages of males from the high and low areas with sperm in the distal portion of the epididymis, 1965.
B. Percentages of live-trapped males with scrotal testes, 1964 and 1965.
C. Greatest testis length of high and low area males, 1965.

percentage of the high area females were perforate and some were pregnant (Figure 8). None of the low area females became perforate or pregnant until early June. In the first part of June the differences in ratios of animals perforate and pregnant were significant.

Breeding continued at a high level in both areas until late July. By late August no reproduction was taking place in high area females, but the low area animals were still reproducing. Differences between proportions of perforate females were significant in late July and throughout August. The differences in proportions of pregnant and lactating animals were only significant in late August.

The reproductive season for high area females was earlier and shorter. This latter fact becomes apparent when the number of litters per female per summer is calculated. Table VIII shows this comparison. Low area animals had an average of over two litters per summer while high area animals produced an average of only 1.3 litters per summer. This result is similar to that found by Dunmire (1960) in an altitudinal survey of reproduction in P. maniculatus.

Another apparent effect of the shorter reproductive season in the high area is shown by Table IX. Some of the low area young reproduced while the high area animals did not. In only one high area has a young female been observed to come into reproductive condition.

Reproductive Season

It is difficult to evaluate the differences in reproductive seasons exhibited by the two populations of animals because it is not known if the two populations react to the same environmental cues the same way. Both photoperiod (Asdell, 1965) and temperature (Parks, 1960) have been reported to cause development of the gonads of seasonal breeders to a state in which reproduction is possible.

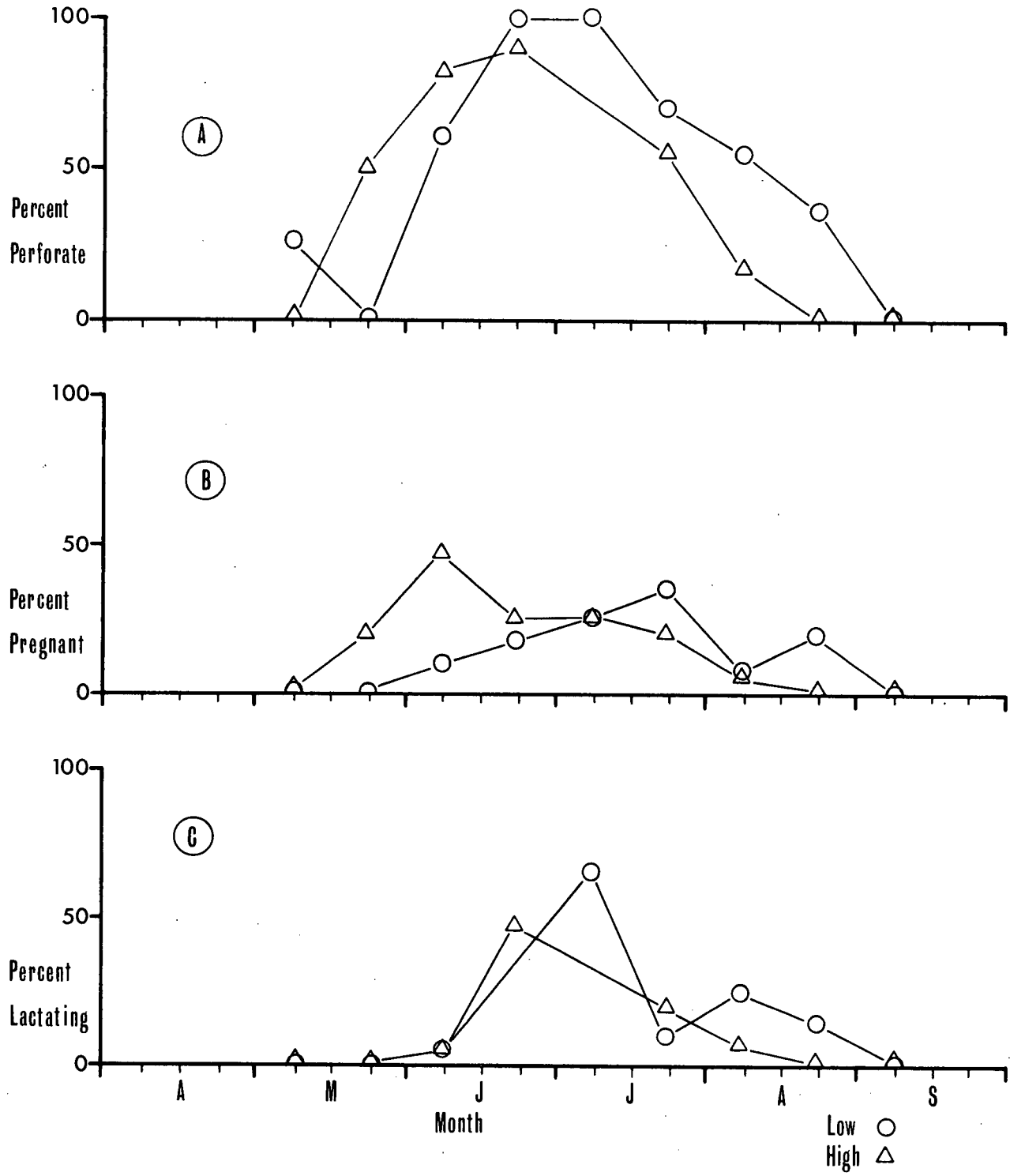


Figure 8. A. Percentages of high and low live-trapped females that were perforate,
(B). Pregnant, and
(C). Lactating, 1964 and 1965.

TABLE VIII. Numbers of litters per adult female per summer in high and low areas, 1964-1965.

	High	Low
N	20	20
$\bar{X}$	1.30	2.06
Range	0-2	1-3
S^2	0.27	0.33
T	4.85	

TABLE IX. Numbers of litters per young-of-the-year female in high and low areas, 1964-1965.

	High	Low
N	10	28
$\bar{X}$	0	0.35
Range	-	0-1
S^2	-	-
T	-	

TABLE X. Comparisons of embryo (Emb.) and placental scar (P.L.S.) counts between areas, and comparisons between embryo and placental scar counts, 1965.

	High Area		Low Area		Embryo - P.L.S.		High - Low	
	Embryos	P.L.S.	Embryos	P.L.S.	High	Low	Embryo	P.L.S.
N	3	8	20	8	11	28	23	16
$\bar{X}$	5.0	4.62	4.90	4.88	4.73	4.89		
Range	4-6	4-6	4-6	4-6	4-6	4-6	4-6	4-6
S^2	1.0	0.56	0.41	0.41	0.62	0.40		
T	.69				.68			

In view of the environmental differences between the areas a reaction to photoperiod may best explain why males on high and low areas came into reproductive condition at the same time. Photoperiod may trigger development in the females also, with the higher pregnancy rates in June in the high area being due to a greater food supply causing earlier maturation of ova (Asdell, 1965). The differences in times at which the animals go out of reproductive condition and the differences in percentages of young females that reproduce do not support the hypothesis of a photoperiod-controlled reproductive period.

Temperature as a controlling factor fits nicely with the observations at the end of the breeding season and with differences observed in reproduction in young animals. It does not agree with the observations at the beginning of the reproductive season.

With the amount of data at hand it is impossible to point to a single factor that causes the onset of reproduction. Further study would probably show that one of the above mentioned factors influences the development of gonads. Ovulation in the female and the onset of breeding will probably be found to be influenced to a large extent by local factors such as rainfall. Prakash (1960), working with 19 species of mammals in an area with a total precipitation of 8-14" per year, found that all were cyclic breeders and that most bred during the period of maximum precipitation.

The overall average number of embryos and placental scars per female was 4.85 (Table X). Counts of embryos and placental scars from high and low areas varied from this figure but were not significantly different from each other. Placental scar counts were lower, but not significantly lower than embryo counts.

Post-partum estrus has been reported in some subspecies of Peromyscus maniculatus (Svihla, 1932) and in several other rodents (Asdell,

1964) but to my knowledge has not been reported in heteromyids. No ovulatory follicles or pregnancies were found in animals with placental scars. This indicates that a post-partum estrus did not occur. Overlap is nearly 100% between lactating animals and those with placental scars. This indicates that placental scars in these animals last for about 3 weeks.

Reproductive data on P. parvus available from other areas are presented in Table XI. The sample size, particularly in the study in Utah, is small and the samples may not be comparable. There appears to be a trend for the reproductive season in the southern areas to begin and end earlier. There may be a slight lengthening of the reproductive season since young animals are born only in a three month period in British Columbia but in a four month period in the other areas.

Scheffer (1938), working in the State of Washington, found an average of 5.17 embryos per pregnant female. This figure is not significantly different from the average found in this study. The other studies do not present enough data for a statistical comparison, but there appears to be a trend to larger litters in the south.

CONCLUSIONS

1. High and low area males came into reproductive condition at the same time. Young did not normally reproduce in either area.

2. High area females came into and went out of reproductive condition significantly earlier than did low area females.

3. Young females in the low area may reproduce while those in the high area did not.

4. Embryo and placental scar counts from the high and low areas did not vary significantly. The average was 4.85.

5. Low area females had significantly more litters per summer than

TABLE XI. Summary of available reproduction data on P. parvus. Yes-no refers to whether author states that young are born that month. Question mark indicates conflicting evidence. Reported number per litter is also shown.

	March	April	May	June	July	Aug.	Sept.	N	Range	$\bar{X}$	S^2	T
British Columbia	no	no	no	yes	yes	yes	no	39	4-6	4.85	.45	1.59
Washington (Scheffer, 1938)	no	no	yes	yes	yes	yes	no	132	2-8	5.17	1.47	
Nevada (Hall, 1946)		?	yes	yes	yes	no	no			5.58		
Utah (Duke, 1957)		yes		yes	yes	no	no			5.38		

high area females

6. No post-partum estrus was observed.

Home Range and Burrows

Information on home range contributes to the understanding of population phenomena and movements of animals, gives clues about the relationships between animals and may reflect the amount of available food. The burrowing behavior of the animal is important because the burrow is the physical environment of the animal during the daylight hours and so has an effect on water loss and temperature regulation.

METHODS

Trapping was conducted as described earlier. The high home range area was trapped for 15 nights from May 12-23 and June 7-9. The low home range area was trapped from May 14-25 and June 3-6 for a total of 16 nights. The circle of snap-traps was operated for 11 nights from May 13-23.

On four occasions in each area captured animals were released and followed until they entered a burrow. The location of the burrow was noted on a map.

Home range area of animals captured more than five times was computed by the boundary strip method. Capture points were plotted, 1/2 the distance to the next trap was added, and outlying points were connected to form a polygon of the greatest possible area. Area, in square meters, could then be computed by the formula: Area =((1/2 # points on border) + (# points inside - 1)/4) x 100. Home range centers were determined by the method of Hayne (1949).

RESULTS AND DISCUSSIONS

Home Range

One indication of home range size is the distance in animal travels. This can be calculated using either distances between successive captures or between the original location of capture and all others (Hayne, 1949). Table XII presents the results of measuring the distance between original capture points and all subsequent capture points. The home range size, as indicated by trip length, is the same for high and low area males. There is, however, a significant difference in home range size between low area males and females. So few observations were made on high area females that a statistical treatment was not possible. They appear to have a home range size similar to that of the low area females. This suggests that high and low area males have home ranges of the same size, that females have ranges of the same size, but that the differences between the sexes is significant. The difference between the sexes was expected and agrees with most reports in the literature (Davis and Golley, 1963).

Blair (1943) reports that in Dipodomys merriami and D. ordii the home range of the females is smaller than that of the males in March, but by May the home ranges are the same size. He reports that in Perognathus penicillatus in the same area the home ranges of the males were significantly larger than those of the females from March through May. The possibility of the difference in home range size between males and females being an artifact of season is not ruled out but appears unlikely.

The failure to find differences within each sex between areas was surprising and disagrees with the usual generalizations about home range size. Davis and Golley (1963) state the points of disagreement: 1. "numerous studies of small rodents give different values for different ecological situations ...", 2. "Mammals in dense populations have smaller ranges than those in sparse populations".

TABLE XII. Distance between original capture point and successive capture points. Proportions shown for 20 meter intervals. Significant ($p \leq .05$) Chi^2 marked ^{s}.

Meters between first and successive captures	High Area					Low Area				
	Incidence ♀ %	N	Chi^2	Incidence ♂ %	N	Chi^2	Incidence ♂ %	N	Chi^2	Incidence ♀ %	N
0-25	33.3	4		25.0	14	0.64	30.6	49	3.61	42.2	49
26-45	16.7	2		21.4	12	0.65	26.9	43	4.4^s	38.8	45
46-65	33.3	4		30.4	17	0.0014	30.6	49	0.75	25.9	30
66-85	0	0		10.7	6	0.22	7.5	12	7.4^s	0	0
86-105	0	0		3.6	2	0.005	1.9	3	0.0034	0.9	1
106-125	16.7	2		8.9	5	2.83	2.5	4	0.30	0.9	1
Total No.		12			56			160			116
Homogeneity test Chi^2						6.35			103^s		

Table XIII shows the results of analysis of home range size by the area method. The data are too few for statistical comparison but this independent method supports the above evidence that the sizes of the home ranges of males in the high and low areas are the same. The low area females have, by this method also, a smaller home range than the males. Too few high area females were captured to allow any real home range determinations to be made. The fact that home ranges are the same size in areas of high and low population density suggests that in P. parvus competition and intra-specific aggression do not determine home range size or space out the animals.

Four types of data are at hand to bear on this hypothesis; mutual overlap of home ranges, distribution of home range centers, distribution of burrows and removal trapping. If competition does not space out animals home range centers and burrows will be randomly distributed, home ranges will overlap to a large extent and animals will not expand their home ranges when adjacent animals are removed.

Figure 9 shows the home range boundaries of animals captured more than 5 times, which represent about half of the adult resident population. It is apparent that the amount of mutual overlap is very great in all groups. Few animals were trapped on the high area but those trapped show greater overlap than would be expected if spacing mechanisms were functioning.

Table XIV shows the results of fitting the distribution of burrows to a Poisson distribution. A variance of less than unity indicates spacing, greater than unity indicates clumping, and unity indicates a random distribution (Andrewartha and Birch, 1954). The chi squared figure indicates that none of the six variances differ significantly from unity. This indicates that the burrows of males, females, and total populations in the high and low area are randomly distributed.

TABLE XIII. Home range size as determined by measurement of areas.

No. times captured		5 - 6	7 - 8	9 - 10	11 - 12	overall
Low ♂	N	10	6	4	2	22
	Range	425-1250	350-1500	800-1325	950-975	350-1500
	$\bar{X}$ meters^2	735	983	1116	962	893
Low ♀	N	10	2	4	1	17
	Range	250-1250	550-700	500-1050	575	250-1250
	$\bar{X}$ meters^2	664	625	675	575	656
High ♂	N	6	1	1	-	8
	Range	400-1688	1250	1400	-	400-1688
	$\bar{X}$ meters^2	756	1250	1400	-	898

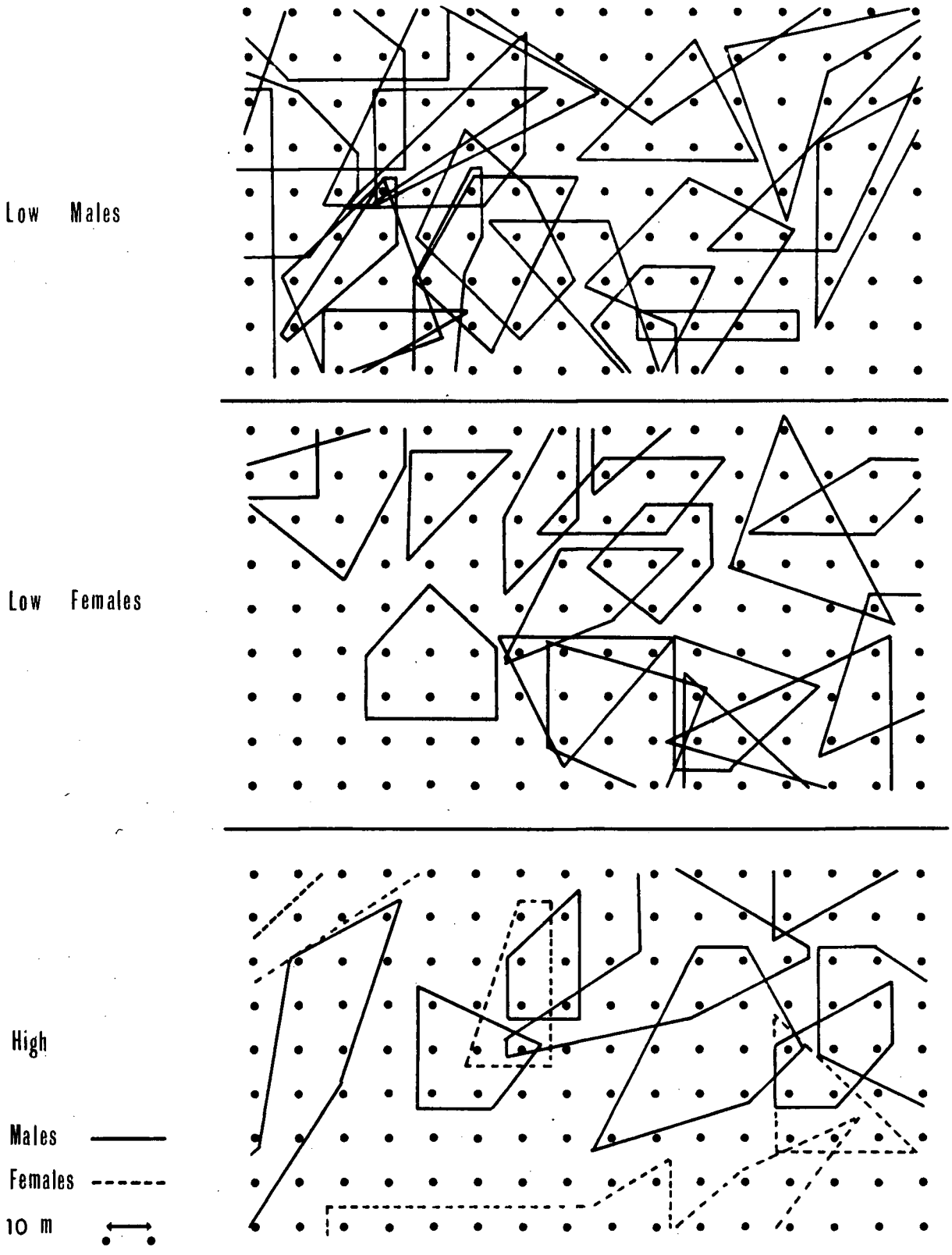


Figure 9. Home ranges of males and females in high and low areas. The minimum number of captures used to determine a home range was five. The black dots represent trap locations.

TABLE XIV. Mean, variance and Chi^2 values for fitting distribution of burrows to a Poisson distribution. None of the Chi^2 values is significant. This means that the animals' burrows are randomly distributed.

	N	$\bar{X}$	S^2	X^2
Low ♂	28	0.200	1.07	128.0
Low ♀	39	0.283	0.84	100.2
Low total	67	0.475	0.67	79.8
High ♂	16	0.117	1.03	122.7
High ♀	11	0.100	1.08	128.0
High total	27	0.225	1.08	128.8

.05 level of significance $\leq$ 130.

TABLE XV. Mean, variance and Chi^2 values for fitting distribution of home range centers to Poisson distribution. None of the values is significant.

	N	$\bar{X}$	S^2	X^2
Low ♂	22	0.230	1.01	119.7
Low ♀	17	0.192	0.81	96.9
Low total	39	0.45	1.004	119.5
High ♂	8	0.108	0.915	108.9
High total	8	0.133	0.90	106.5

Table XV shows the results of applying the same statistic to the distribution of home range centers, which also show a random distribution for both areas and all sex groups. These random distributions imply that the presence of one animal has no effect on the choice of a burrow site or on the location or configuration of the home range of another.

Calhoun (1963) predicts on the basis of social interaction that when resident animals are removed adjacent home ranges will expand to occupy the open area. If, as the evidence above indicates, home ranges of P. parvus are not affected by social interaction this expansion of home range should not occur. Table XVI summarizes the results of an experiment to test this prediction. Snap traps set in a circle were operated for 11 days before the experiment had to be terminated because of raids by magpies. Because of the short period of time involved the results may not be conclusive, but they seem to indicate that animals on the edge of the trapped area do not expand their home ranges. Number of animals captured per day drops as expected after the first few days.

It could be argued that the large number of animals captured on day 4 represents a wave of immigration. There are two lines of evidence against this. Immigration need not be hypothesized to account for the number of animals captured. The density in the area covered by the circle, assuming all 101 mice were residents and the trapped area was the diameter of the circle plus 1/2 the mean home range diameter, was 0.001 mice per square meter. A figure calculated in the same way for resident animals on the nearby home range area is 0.0032 mice per square meter.

If the animals captured on the fourth day were mostly immigrants, a higher proportion than on the first day should have been captured on the rim of the circle than inside the circle. On the first day 22 animals were captured on the rim and 7 on the inside, while on the fourth day 21 animals were

TABLE XVI. Numbers of animals captured per day in the circle trap line.

Days	*P. parvus* ♂	*P. parvus* ♀	*P. parvus* sex ?	*Peromyscus maniculatus* 0	*Peromyscus maniculatus* 0	Total *P. p.*	Total *P. m.*
1	17	10	2	2	3	29	55
2	7	5		3	2	12	5
3	7	4		0	1	11	1
4	18	7	3	2	2	28	4
5	9	5		0	0	14	0
6	1	1				2	0
7		2				2	0
8	1	2		1		3	1
9			2			2	0
10			1			1	0
11						—	—
						101	16

captured on the rim and 7 on the inside. On the basis of the above two lines of evidence we can reject the hypothesis that immigration occurs and can state that, at least up to 10 days, mice with home ranges bordering on empty territory do not expand their home ranges.

The studies on home range are difficult to compare because of the use of different methods and amounts of trapping. Most of the species appear to have home ranges similar in size to that reported here. P. penicillatus (Blair, 1943) and possibly P. merriami (York, 1949) have larger home ranges.

Home ranges of males overlap in P. penicillatus (Blair, 1943), P. nelsoni (Dixon, 1958 and in P. merriami (York, 1949). Blair reports seasonal overlap in females, Dixon reports little overlap and York reports great overlap in home ranges of females. Individuals of Perognathus spp. generally appear to have overlapping home ranges with some exceptions in reproductively active females.

Burrows

The type of burrow system constructed by pocket mice seems to depend to a large extent on the substrate. Denyes (1954) working with P. penicillatus and P. merriami in the laboratory found that in sand the animals built a simple system with two entrances. In loam the animals constructed a more complex system. When a hard crust was formed on the loam the animals constructed a system with only one entrance through the crust but a complex system below.

Scheffer (1938), working in an area where a sub-surface mineralized layer in the soil was present, found that P. parvus excavated several tunnels from the surface, which joined to penetrate the mineralized layer in a single hole. Then, with the mineralized layer as a roof for the tunnels, the system became complex again. Blair (1937) found P. hispidus constructing complex tunnels under limestone slabs. Most of these tunnels had several entrances.

He states that the burrow systems of immature animals were less complex than those of adults.

It appears that, given a choice, Perognathus spp. excavate burrows with several entrances under a structure such as a rock or mineralized layer in the soil. There is often a single nest chamber below the local frost line (Hibbard and Beer, 1960) and a storage chamber which may be located near the entrance (Scheffer, 1938). Tunnel entrances may be, but are often not plugged during the day. A mound of soil in front of the burrow entrance is often at least a temporary feature of pocket mouse burrows.

The burrows excavated in this study were in sandy soil without fragments or mineralization. Two basic types of burrows were found. The most numerous type, the "escape" burrow, was found to be simple and shallow, 20-30 cm deep, without a nest chamber or food cache but with at least two entrances. The "permanent" burrows had nest chambers, food caches, several entrances, and several tunnels penetrating to maximum depth which was usually more than 1 m. The presence of the two types of burrows helps explain why animals were observed to enter different burrows when released in different parts of their home range.

It is probable that each animal constructs or occupies a single permanent burrow system and excavates or explores several escape burrows in different parts of its home range. An animal would, therefore, have an underground refuge available near all parts of its home range. Scheffer (1938) states that only one adult animal lives in each burrow system. This was determined by trapping under cages set over burrow entrances and by excavating burrows in the winter. Other species of Perognathus (P. hispidus, Blair, 1937; P. penicillatus, Blair, 1943; P. merriami, Blair, 1953) live singly as adults. On this basis permanent burrow systems must be considered as defended territory. It is not known if escape burrows are defended and used by only

one animal or if they are utilized by several animals.

Territoriality

Scheffer (1938) and Eisenberg (1963) describe extreme aggressiveness of Perognathus when two animals are confined. Eisenberg states that Perognathus spp. will not readily tolerate conspecific physical contact and have evolved behavioral mechanisms for minimizing such contact. These behavioral mechanisms for minimizing contact tend to minimize fighting and possible physical injury in situations where retreat is possible. They act to form an inviolate zone immediately surrounding an animal that is recognized by both members of an encounter.

It appears that in P. parvus, and probably most other members of the genus, the permanent burrow and possibly the escape burrows are the only parts of the home range that are defended and can be called a territory. The size, configuration and location of the rest of the home range seem to be independent of the influence of other animals and independent of at least some ecological factors.

CONCLUSIONS

1. Males had larger home ranges than did females.

2. Males, and probably females, of high and low areas had home ranges of the same size.

3. Burrow sites and home range centers were distributed randomly for males, females, and total populations in both high and low area animals.

4. Adult animals did not appear to expand their home ranges when adjacent animals were removed.

5. Each adult animal had a complex, permanent burrow system, which was occupied singly, and defended, and several escape burrows scattered around its home range.

Populations

The date on populations provide a yearly cycle of numbers and measures of long, and short, term survival rates. These data permit a comparison of density and survival rates in the high and low areas and identification of periods with high mortality. The correlation of densities and periods of high mortality with environmental factors may provide information about factors limiting the distribution of the species.

METHODS

Areas were trapped as described earlier. Because the size of the trap-affected area is unknown, density figures are expressed in animals per trapping area. Since the sizes of home ranges of animals in the high and low areas are apparently the same this figure should be sufficient for comparative purposes. Data on the numbers of animals are counts of those captured plus those known to be alive because they were captured both before and after the trapping period. These counts are used because we cannot make the assumption, necessary for estimation of total numbers, that marked and unmarked animals are at equal risk of capture. The figures given, based on direct enumeration, are minima because animals may be present but not captured. The survival rates, calculated by the method of Chitty and Phipps (1966), are also minimum rates expressed as survival per month.

RESULTS AND DISCUSSION

Throughout most of the year the smoothed line, indicating numbers of animals per trapping area (Figure 10), averages fluctuations due to discontinuous sampling, but in the fall and spring the line departs from the observed number of animals (Table XVII). In September and October animals begin to go into torpor and are no longer trapped, so the low numbers of

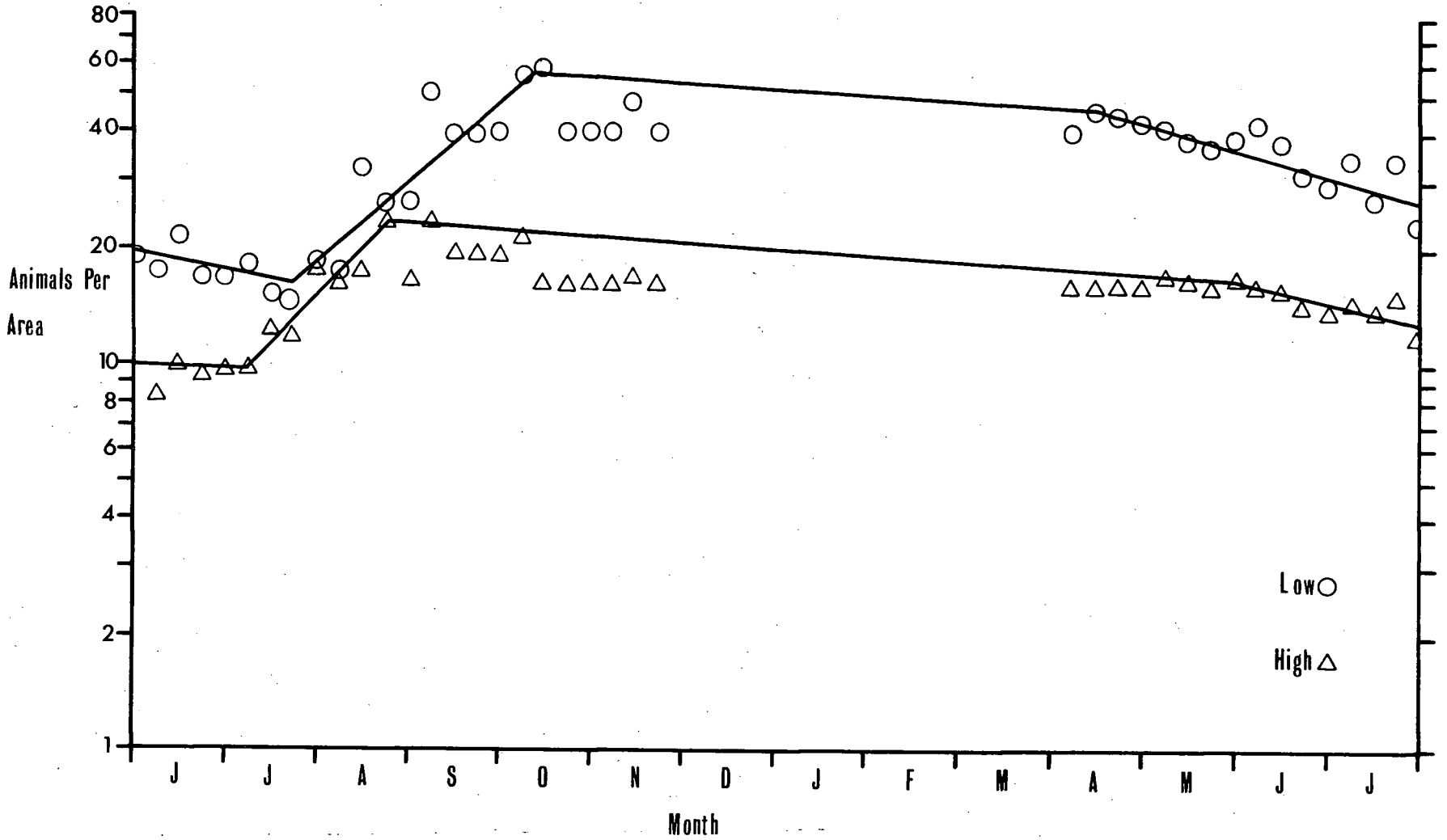


Figure 10. The numbers of animals present per area in the high and low areas from June, 1964 to July, 1965. The lines were smoothed by eye from data presented in Table XVII.

TABLE XVII. Numbers of animals present in the high and low areas from June 1964 to July 1965.

	June				July				Aug.				Sept.				Oct.				Nov.			
Low																								
Adult ♂♂	21	19	23	15	15	16	14	13	13	13	19	14	14	18	15	15	15	17	16	14	14	14	15	14
Adult ♀♀	16	14	18	17	17	17	15	15	15	13	14	11	11	17	16	16	16	18	19	16	16	16	17	14
Young ♂♂						1	0	0	2	2	16	13	13	33	23	23	23	41	44	30	30	30	37	31
Young ♀♀	1	1	1	1	1	1	1	1	7	7	16	13	13	34	24	24	24	37	36	20	20	20	24	21
Young No. 2 ♂♂																								
Young No. 2 ♀♀																								
Total	38	34	42	33	33	35	30	29	37	35	65	51	51	102	78	78	78	113	115	80	80	80	93	80
No. per area	19	17	21	16	16	18	15	14	18	18	32	26	26	51	39	39	39	56	58	40	40	40	56	40
High																								
Adult ♂♂	1	18	18	17	17	17	21	20	20	19	19	23	19	19	18	18	18	18	17	17	17	17	17	17
Adult ♀♀	1	6	11	10	11	11	14	13	14	12	12	11	10	11	9	9	9	11	9	9	9	9	9	9
Young ♂♂							3	3	13	12	12	18	16	17	13	13	13	14	9	9	9	9	9	9
Young ♀♀									8	6	6	17	13	18	17	17	17	19	13	13	13	13	14	13
Young No. 2 ♂♂																								
Young No. 2 ♀♀																								
Total	2	24	29	27	28	28	38	36	56	49	49	69	48	65	57	57	57	62	48	48	48	48	49	48
No. per area		8	10	9	9	9	13	12	19	16	16	23	16	22	19	19	19	21	16	16	16	16	16	16

TABLE XVII (cont'd)

	April				May				June				July			
Low																
Adult ♂♂	14	14	14	13	13	11	11	10	9	6	6	6	6	5	5	3
Adult ♀♀	14	14	14	14	14	11	11	11	11	10	9	9	9	8	8	6
Young ♂♂	31	38	36	36	36	31	30	33	35	29	24	22	27	22	23	13
Young ♀♀	21	22	23	22	26	24	24	23	30	30	23	22	23	19	19	16
Young No. 2 ♂♂													2	0	3	2
Young No. 2 ♀♀															9	4
Total	80	88	87	85	84	77	76	77	85	75	62	59	67	54	67	44
No. per area	40	44	44	42	42	38	38	38	42	38	31	30	34	27	34	22
High																
Adult ♂♂	17	17	17	17	17	14	14	14	14	12	10	10	9	8	8	5
Adult ♀♀	9	9	9	9	9	9	9	9	9	9	8	8	8	7	7	7
Young ♂♂	9	9	9	9	10	12	10	11	11	9	8	7	7	6	7	4
Young ♀♀	13	13	13	13	15	15	15	16	15	17	16	16	18	18	17	14
Young No. 2 ♂♂													1	0	2	1
Young No. 2 ♀♀												2	1	1	3	3
Total	48	48	48	48	51	50	48	50	49	47	42	43	44	40	44	34
No. per area	16	16	16	16	17	17	16	17	16	16	14	14	15	14	15	11

animals known to be alive in October and November reflect both mortality that has taken place and mortality that will take place some time during the winter. The low numbers of animals trapped in the early spring reflect continued torpor in some animals. Showing winter mortality as constant is more accurate than lumping it all into the late fall months, but is undoubtedly an over-simplification.

Figure 10 brings out three points. The population density in the low area is higher than that in the high area; the yearly cycle in numbers is similar to that found in other small mammals (Sadleir, 1965); numbers in both areas were higher in the spring of 1965 than in the spring of 1964.

The difference in average density between the high and low areas may indicate that the valley floor is the more favorable habitat. The trend to decreased population size with higher altitude is shown in Table XVIII. As far as could be determined, 4,500 ft. is about the maximum altitude reached by pocket mice in this area. The highest grasslands were at 4,700 ft. on a south-west facing slope. No Perognathus were trapped at this altitude in 100 snap-trap nights. Density and distribution in this area appear to be limited by some factor or factors covariant with altitude.

The length of the reproductive season, which varied with altitude, may limit the altitudinal distribution. Animals in the high area, 1,500 ft. above the low area, produced an average of 1.3 litters per summer as opposed to the low area animals which produced 2.06 litters per summer. The highest altitude populations were about 2,000 ft. above the high sample area and may have been at the maximum altitude for the production of one litter per summer.

It is also possible that P. parvus is able to occupy grasslands to the treeline, but at the higher altitudes must be present in very low density and liable to local extinction. If this occurred, repopulation would be very slow because few surplus animals are produced per year (Table XIX). Conversely,

TABLE XVIII. Number of animals known to be present, middle of August, 1964, at different altitudes.

	Low	High	High Home Range	Highest
Area	1 - 2	3-5 - 7	9	8
Altitude	1,000	2,500	3,500	4,500
No./area	22.1	17.2	13.1	2.0

TABLE XIX. Number of young animals produced per area per year in high and low areas. The number, range and variance of the reproductive data are given in Tables VIII, IX, and X.

		No. ♀♀ / area	No. litters/ summer	No./litter	Total No. young born	Grand Total
Low	Adult	7.5	2.06	4.89	75.55	84.11
	YOY	5.0	.35	4.89	8.56	
High	Adult	3.7	1.30	4.73	22.75	22.75
	YOY	3.0	0	0	0	

if populations in the valley produce more young than are needed to maintain their numbers their average losses must be greater than those at the higher altitudes.

Survival rates of males and females did not differ consistently nor did Chi square analysis show any significant differences between them. Males and females have therefore been pooled within age classes and areas. High area adults had consistently higher survival rates than did low area adults, except between August and October (Table XX). The yearly survival rate for adults (Table XXI) was also higher in the high area but not significantly so. In view of the insensitivity of the Chi square test, the data may have biological significance even though a statistical one is not shown. The rates of adult survival in the two areas may be different but it is not necessary to assume so to explain the maintained difference in density between the two areas.

The high area young survived better, on both a monthly and yearly basis, than did the low area young (Tables XX and XXI). The high area young, on the long term, survived as well as did the high area adults, but on the low area the young did not survive as well as the adults (Table XXI). The lower survival rate in the low area is necessarily associated with the higher reproductive rate and low increase in total numbers. These data merely show that the losses take place mainly in the young animals.

None of the proportions from which short term survival rates (Table XX) were derived was significantly different when confidence intervals were determined from a Clopper and Pearson chart (Steele and Torrie, 1960). In all groups, however, survival from October to April was better than it was at any other time of the year. Survival rates were consistently low in April to June, with some instances of low rates in the fall.

Because the rates calculated are minima any animals that become untrappable (because of a change in behavior or emigration from the trapping

TABLE XX. Number of animals released (N) and proportion (P) known to be alive one month later.

	June-July		July-Aug.		Aug.-Sept.		Sept.-Oct.		Oct.-April		April-May		May-June		June-July	
	P	N	P	N	P	N	P	N	P	N	P	N	P	N	P	N
Low Adults	.727	44	.750	16	.600	25	.804	21	.902	13	.563	4	.533	15	.705	17
Low Young	1.000	1	.000	1	.843	32	.745	65	.872	77	.516	32	.648	37	.677	59
High Adults	.875	32	.859	29	.422	20	.625	8	.914	7	.000	1	.583	12	.722	18
High Young			1.000	3	.660	32	.807	26	.849	16	1.000	4	.666	15	.720	25

TABLE XXI. Long-term survival expressed as the number known to be alive/the number released and the proportion surviving each month (P). Chi squares marked ^{s} are significant, those marked ^{c} were calculated using Yates correction for continuity.

Period	June - June		Sept. - July		Sept. - July		Sept. - July	
	Low Adults	High Adults	Low Young	High Young	Low Adults	Low Young	High Adults	High Young
P	.895	.934	.829	.912	.924	.829	.884	.912
Proportion alive	12/44	14/32	10/65	12/30	9/20	10/65	7/24	12/30
X^2	2.24		6.99^{s}		7.73^{s} 6.13^{c}		.69	

area) will be included in numbers estimated to be dead and will bias survival rates downwards. The possibility of a change in behavior cannot be ruled out, but the routine trapping of most of the resident population month after month suggests it did not occur. Torpor, however, removes an animal from the trappable population. If an animal entered torpor before the October sampling period and died sometime during the winter, its death would be assigned to the month in which it entered torpor. Although monthly survival rates of animals in torpor are higher than those of active animals, several months of mortality in torpid animals would be concentrated into the month when the animals became torpid. This effect may have contributed to the low survival rates in August to October.

Large amounts of emigration could also cause an erroneously low survival rate. If it is assumed that movements of animals were general phenomena, with animals both leaving and entering the study area, the amount of emigration can be evaluated by comparing the number of animals lost with the number of new animals of the same age group. Starting in July in the high area, and August in the low area, high losses of adult animals are nearly balanced by an influx of new adult animals (Table XXII). The time of this movement is correlated both with the end of the reproductive season of the males and the appearance of large numbers of young animals. The combination of the onset of torpor and an apparent movement of adult animals may combine to explain at least part of the indicated low survival of adult animals in the fall months.

The low survival rate in the spring cannot be explained by either of the two factors discussed above. It is possible that food or water may limit survival during this time of year. Even during the driest spring, however, food and water in the form of grass stems, Opuntia leaves, insects and seeds would be available. The animals captured in the spring appeared to be well fed and in good condition.

Social interaction may have limited survival during the early

TABLE XXII. The number of new adults and the number of adults that permanently disappeared during the late summer and fall of 1964 in the high and low areas.

	Low area		High area	
	new	lost	new	lost
July	1	6	8	5
August	7	6	6	6
September	12	10	1	5
October	6	4	2	2
November	2	7	No captures	
Totals	28	33	17	18

reproductive season. Sadleir (1965) has shown a correlation between onset of the reproductive season, increased aggressiveness in males and sudden decrease in population density. Healey (1966) has verified the correlation between reproductive condition in males and increased aggressiveness and has shown a negative correlation between aggressiveness and survival of juveniles. Although a large drop in total numbers was not found in the spring in this study both populations decreased in density more rapidly in the spring than over the winter.

The increase in numbers of animals in both areas from the spring of 1964 to the spring of 1965 may have been the result of study procedures. Since the system of trapping included the use of bait in a groove in front of the trap some food could have been collected and stored by the animal before it was captured. Bendell (1959) observed that an increased food supply may have increased numbers in an island population of Peromyscus. Since both populations increased in about the same proportion the cause would appear to be either food provided by trapping or a general environmental or population phenomenon.

Von Bloeker (1928 and 1932) noted high numbers of Perognathus longimembris, P. spinatus and P. baileyi while trapping for specimens. It is not known if pocket mouse populations show cyclic fluctuations or occasional very high densities as are observed in some mammals. The evidence contributed by Von Bloeker suggests, however that Perognathus populations may be locally very dense, possibly in response to rainfall.

CONCLUSIONS

1. Population density was negatively correlated with altitude.

2. High area adults and young and low area adults had similar survival rates, while low area young animals had significantly lower survival rates.

3. Overwinter survival in all groups was better than survival at any other time of year.

4. Consistently low survival rates were found in the spring in all groups and some instances of low rates were also found in the fall. The indicated low survival rates in the fall may be artifacts caused by emigration or the onset of torpor.

5. The observed increase in density in both areas may have been due to experimental methods or a general climatic or population factor.

Torpor

The examination of torpor is important because the ability to reduce metabolic rate and conserve both food and water appears to be a major adaptation to existence in cold or dry habitats. The colder environments of the high areas in this study may be expected to act as a selective pressure toward longer periods of torpor.

METHODS

Observations on activity and torpor were conducted in a modified 18 cubic foot refrigerator. A constant temperature was maintained in the refrigerator by replacing the stock control unit with a Ranco 3 F fixed differential sensor and switch. Temperature and relative humidity in the refrigerator were recorded with a spring-wound Serdex thermohumograph. Air was circulated past the cooling plate, temperature sensor, recorder, and animal chambers with a small fan. The normal interior light of the refrigerator was replaced with two twenty-five watt bulbs controlled by an Intermatic time switch. The shelves of the refrigerator were replaced with racks containing the activity cages described below. Polyethyelene film with an

armhole was taped over the opening of the refrigerator to minimize loss of cold air during feeding and observing animals.

The activity cages consisted of glass dishes 16 cm in diameter and 5 cm deep. A cage made of galvanized wire screen 10 cm high covered the top of the dish. The cages were hung from pivots 1 cm below the top of the dish. The supporting racks consisted of the pins on which the cages pivoted, a microswitch next to each pin to detect movement, and stops at the sides of the cages to prevent vertical movement of more than 1 cm. The microswitches were adjusted, and the cages balanced so that the bottom of the cage was horizontal and the microswitch tripped at the least possible movement. Observations, after final adjustments, indicated that nearly all locomotory movements by the mouse caused the switch to trip. The cages contained a layer of sawdust 1 cm deep for bedding. Movement of the sawdust to one side of the cage did not materially effect the sensitivity of the system.

The microswitches switched a 110 volt AC circuit connected to an Esterline Angus event recorder. The recorder was adjusted to run at 6 inches per hour. Microswitches on the door of the refrigerator and in the lighting circuit were also connected to the recorder.

Animals to be used in the experiments were selected randomly from available animals in the colony. They were weighed to the nearest 0.1 g and assigned randomly to cages. The animals were placed in the apparatus at about 0900 hours and the recorder was started 24 hours later. The animals were given a surplus of millet, renewed each day at 0900 hours. The animals were also observed at about 1200, 1700 and 2000 hours. Respiration rate was used as the criterion for torpor. Thermoregulating animals had a respiration rate of greater than one inspiration per second while torpid animals at 5 C had respiration rates of less than one or two inspirations per 5 seconds. A few grains of sawdust were placed on the back of each animal when it was first

found to be torpid. It was assumed that arousal had not taken place if the sawdust was still in place when the animal was next observed. At each observation the state of each animal was recorded on the activity record.

The activity records were analyzed by counting the number of two-minute periods per hour in which the animal was active. Periods of torpor were timed to the nearest hour from the beginning of the first hour in which the animal was not active until the end of the last hour in which the animal was not active. This period of inactivity was analyzed as torpor only if the animal was visually observed to have a low respiration rate during the period.

During the experiment the temperature was controlled at 5 ± 1.5 C. The humidity varied between 40% and 60% and averaged about 55%. The lights were on the same cycle as that in the animal room, coming on at 0900 PST and going off at 0100 PST. The experiment was run twice for 40 days, with the animals weighed before and after, and the body temperatures of the animals at the end of the experiment measured with an YSI telethermometer. In each experiment 6 high and 6 low animals were used.

In the experiment to determine the effect of a change in photoperiod on the times of onset and end of torpor 12 low area animals were placed in the refrigerator under the same conditions as above except the dark period was shifted to 0700 to 1500 hours and the experiment was terminated after 30 days.

RESULTS AND DISCUSSION

Torpor in the Field

Torpor, used here to include hibernation, estivation, and daily torpor, can be investigated only to a very limited extent with trapping studies. In this study trap success (number animals captured/number animals present) was calculated. Low trap success during a particular time of year

or in a particular class of animal is taken to indicate lack of surface activity. It could be argued that trap success reflects trapability rather than surface activity. This possibility cannot be ruled out, but the high trap success during summer, when food is plentiful, and low trap success in spring and fall, when food is less common, argue against it. The fact that Scheffer (1938), working in a different area with a different type of trap and bait, found similar low trap success in the early spring and late fall also supports the idea that low trap success reflects little surface activity. Low surface activity may not be correlated with torpor, but torpor in periods of low temperature and food supply appears to be adaptive, while underground activity does not have such an obvious advantage. Low trap success, however, must be used as an indicator of torpor since no other field indication was available.

Figure 11 shows trap success in both high and low areas throughout the year. The last animals were captured in the high area in the last week of October, while the low area animals were active until the end of November. The actual end of above-ground activity seems to come only when the ground is covered with snow. The low area was trapped weekly with a few traps and animals were captured each week until the second week of December when snow fell. Snow fell on the high area some time between the end of October and the third week of November, when the area was trapped. At that time the snow was only about 10 cm deep but no animals were captured and no signs of activity could be seen. Scheffer (1938) states that between late December and early March a few animals may be captured in sheltered situations. In this study the earliest spring trapping was conducted in late April. At that time both high and low area animals were active in low numbers.

Scheffer (1938), working in southern Washington, found animals appearing by the middle of March. Scheffer's data and extrapolation of

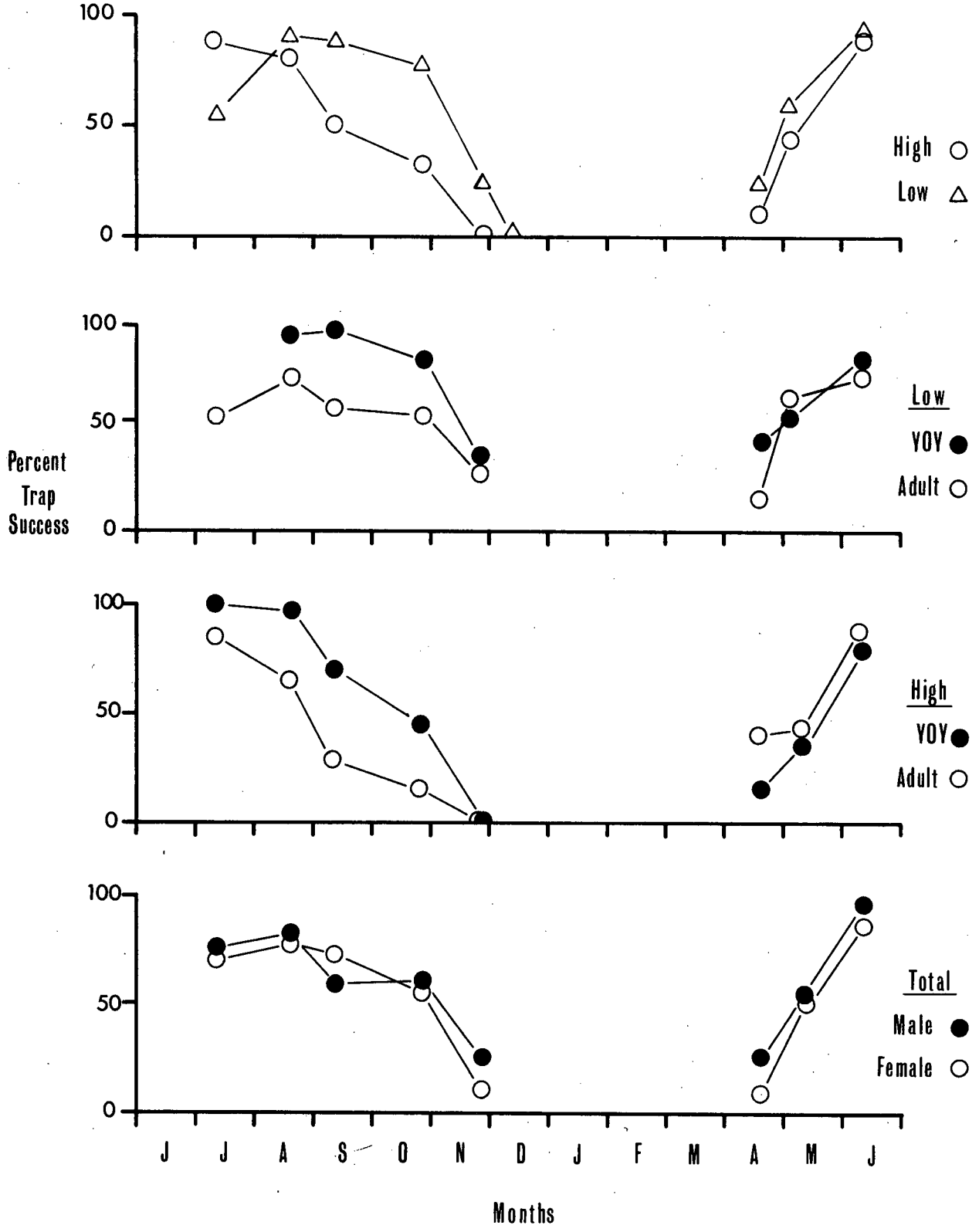


Figure 11. Percent of animals known to be alive that were captured throughout 1964 and 1965.

curves in Figure 11 suggest that time of emergence in the southern Okanagan would be late March of early April.

Figure 11c shows that in both high and low areas young animals were active in greater proportions in the late fall than were the adults. This probably once again reflects the fact that to survive the winter the young animals must excavate a burrow and store a large amount of food.

Figure 11 suggests that males may stay active longer in the fall and become active earlier in the spring than the females. The difference is not significant. Scheffer's (1938) data show a very large difference (April 1921, 67 males - 28 females, April 1924, 76 males - 4 females, March 1924, 40 males - 4 females). Hoffmeister (1964), in analyzing records of museum specimens of six species of Perognathus from the Southwest U.S., found that from January through May all six species showed sex ratios in favor of males. The percentages found varied from 100% males to 59.4% males. He suggests that females may be in torpor, rearing young, or trap-shy at this time of year. Results from this study and from Scheffer's (1938) on reproduction in P. parvus suggest that, at least in the north, the females are not yet reproductive. Consistent results in spite of the diversity of trapping methods used in these three studies make the theory of trap-shyness less likely. The early emergence of male Perognathus may be a similar phenomenon to the earlier reproductive activity in many male mammals (Asdell, 1965).

The Yearly Weight Cycle

Figure 12 shows the yearly weight cycle in different groups of P. parvus. Because of small and variable sample size and trapping of different individuals each month, it was not considered possible to analyze the data statistically. Several trends are suggested by the distribution of the means of different groups. There is a general increase in weight in all groups

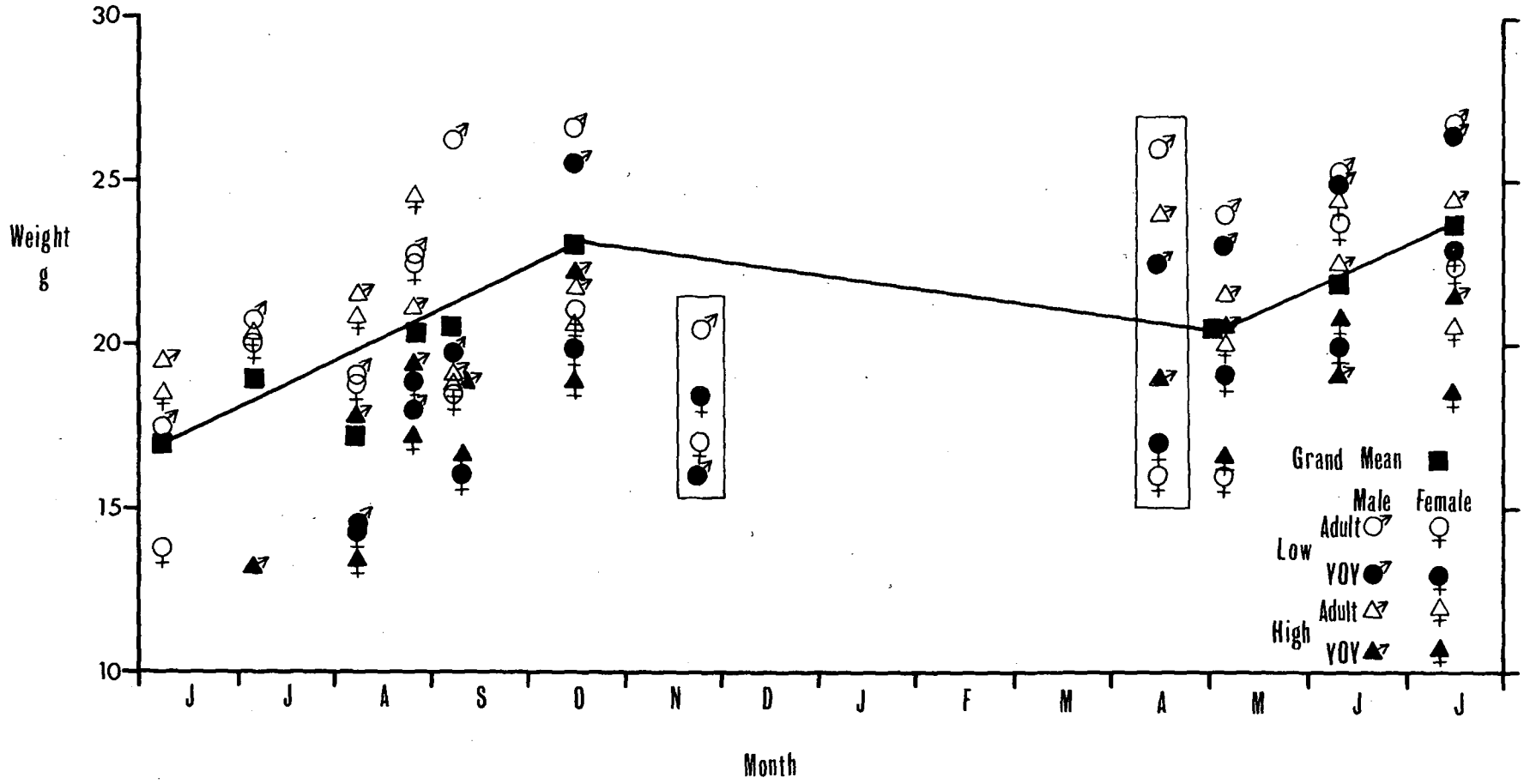


Figure 12. Mean weights of different age and sex groups of animals throughout 1964-1965. The line is fitted by eye to the mean of means. Boxes enclose data which are suspect because of low numbers.

from May to October followed by a decrease over winter. The magnitude of this decrease is difficult to determine for several reasons. The maximum weight of the animals in the fall may not have been determined. The average weights of the small samples of animals captured in November are much below the averages of the larger samples from October. This may be due to the larger and heavier animals going into torpor earlier. Wade (1930) pointed out that fat Thirteen-lined ground squirrels tended to hibernate before thin animals. The larger and heavier animals would tend to be the animals that were born earlier in the season and had had more time to store food. Lyman (1954) pointed out that hamsters prevented from storing food delay hibernation. Early entry into torpor by heavier animals may have occurred as early as October, therefore decreasing the average weight for the group. In April the samples are too small to give any valid indication of the average weight. The first valid weights are for May, when some of the animals may have been out of torpor and gaining weight for nearly a month. These objections mean that the overwinter weight loss, indicated at about 5%, should be considered the minimum. The maximum weight gain between August and October observed in an adult animal was 26%. These figures place the percent weight gain for torpor somewhere between 5 and 26%, which means that most of the energy for survival overwinter comes from stored food rather than fat.

The Characteristics of Torpor

The word "torpor" is used throughout partly because it has been applied before to Perognathus (Bartholomew and Cade, 1957) and partly because it avoids fruitless discussions of the definitions of hibernation and estivation. Torpor does not imply a different phenomenon from hibernation and estivation. If hibernation is defined as "a periodic phenomenon in which body temperature falls to a low level approximating ambient, and heart rate, metabolic rate, and other physiologic functions fall to correspondingly minimal levels", the words become synonomous.

The general characteristics of torpor in P. parvus are similar to those summarized by Cade (1964) for other species of Perognathus. P. parvus captured in live-traps have occasionally been observed to enter torpor during all months from April to November. It enters torpor spontaneously in the laboratory with food available at temperatures from 20 C to below 5 C. The lowest rectal temperature observed in a torpid animal was 2 C at an environmental temperature of 0 C, the highest, 21 C at an environmental temperature of 20 C. The normal body temperature varies between 34 and 37 C and can be maintained at this level indefinitely at 5 C if food is available. At 5 C the shortest period of torpor observed was 3 hours, the longest was 168 hours and the average length of 241 periods of torpor was 46 hours. Warming rates and behavior during arousal from torpor were similar to those observed in P. longimembris by Bartholomew and Cade (1957).

Torpor in the Laboratory

Figure 13 shows the activity cycle in high and low animals at 5 C. The peak in activity occurred shortly after the dark period started. Activity then decreased during the night and reached a minimum after the start of the light period. These data fit Scheffer's observations (1938) that P. parvus in the field are more active in the early night than toward dawn. Scheffer states that he very occasionally observed a pocket mouse above ground during the day, but I have never seen one. It appears that P. parvus is strictly a nocturnal animal with most of its activity occurring in the early part of the night.

At 5 C amount of activity decreased with time in both high and low groups. This was seen in both a shortening of the activity period and a decrease in the peak activity. This is partially due to the fact that with food available P. parvus does not have a diurnal cycle of torpidity as observed (Tucker, 1962) in P. californicus with decreased rations. During

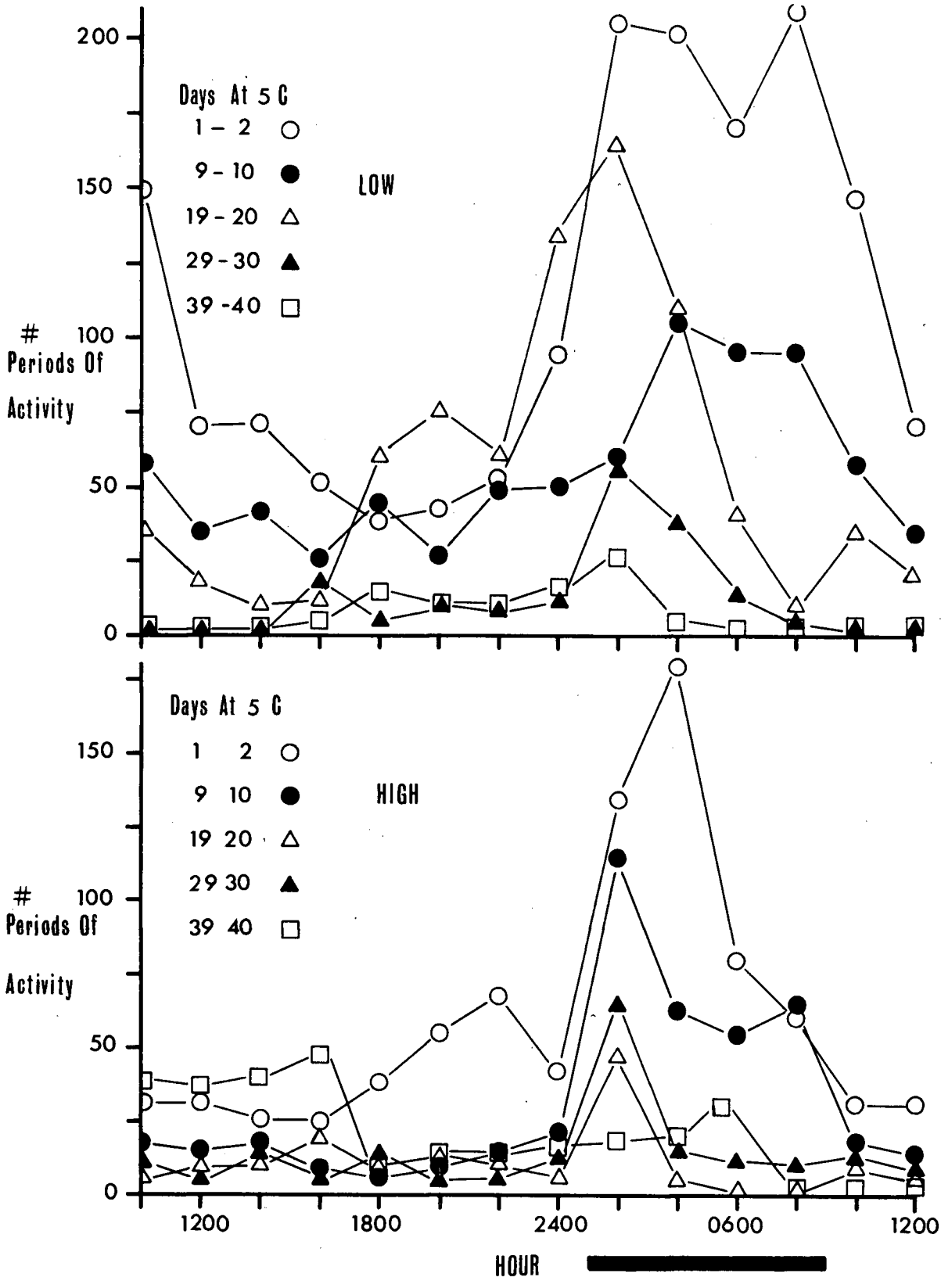


Figure 13. Number of 2 minute periods per hour in which activity took place in captive high and low area animals after different lengths of exposure to 5 C. The dark period is shown by the horizontal bar.

the later part of the experiment many of the animals were torpid through the dark period. Those that were active showed a short-lived burst of activity when the lights went off. This may represent a behavioral acclimation to low temperature, since activity uses more energy than sitting quietly.

Figure 14 shows the times of entrance into and exit from torpor in the animals observed. Both high and low animals tend to enter torpor during the dark phase of the cycle and become active during the light phase. Tucker (1962) found that his animals also entered torpor during the dark period of the cycle and were aroused from torpor during the following light phase. The same tendency is apparent in P. parvus except the animals may remain in torpor throughout one or more light phases.

When the dark period is shifted 6 hours forward the peak times of entrance into and exit from torpor are also shifted about the same amount forward (Figure 14). This demonstrates that animals are reacting to photoperiod in timing torpor periods rather than to some other stimulus, such as noise, in the laboratory. A direct effect of photoperiod in timing torpor is not necessarily indicated but the mechanism responsible for the timing of torpor can at least be modified by a change in photoperiod.

The average length of the torpor period, Table XXIII, increases from the beginning of the experiment to the end. It is also significantly greater in the high area animals for the first twenty days of the experiment. The percent of time spent in torpor (Figure 15a) also increases throughout the experiment and is greater in high area animals. Figure 15b illustrates by another method the difference in length of torpor periods between the two areas and the increase in length of torpor period with increasing time at 5 C.

The difference in length of torpor periods is the difference that was hypothesized to occur as an adaptation to the different environments. The advantage of winter torpidity is usually considered to be an adaptation to

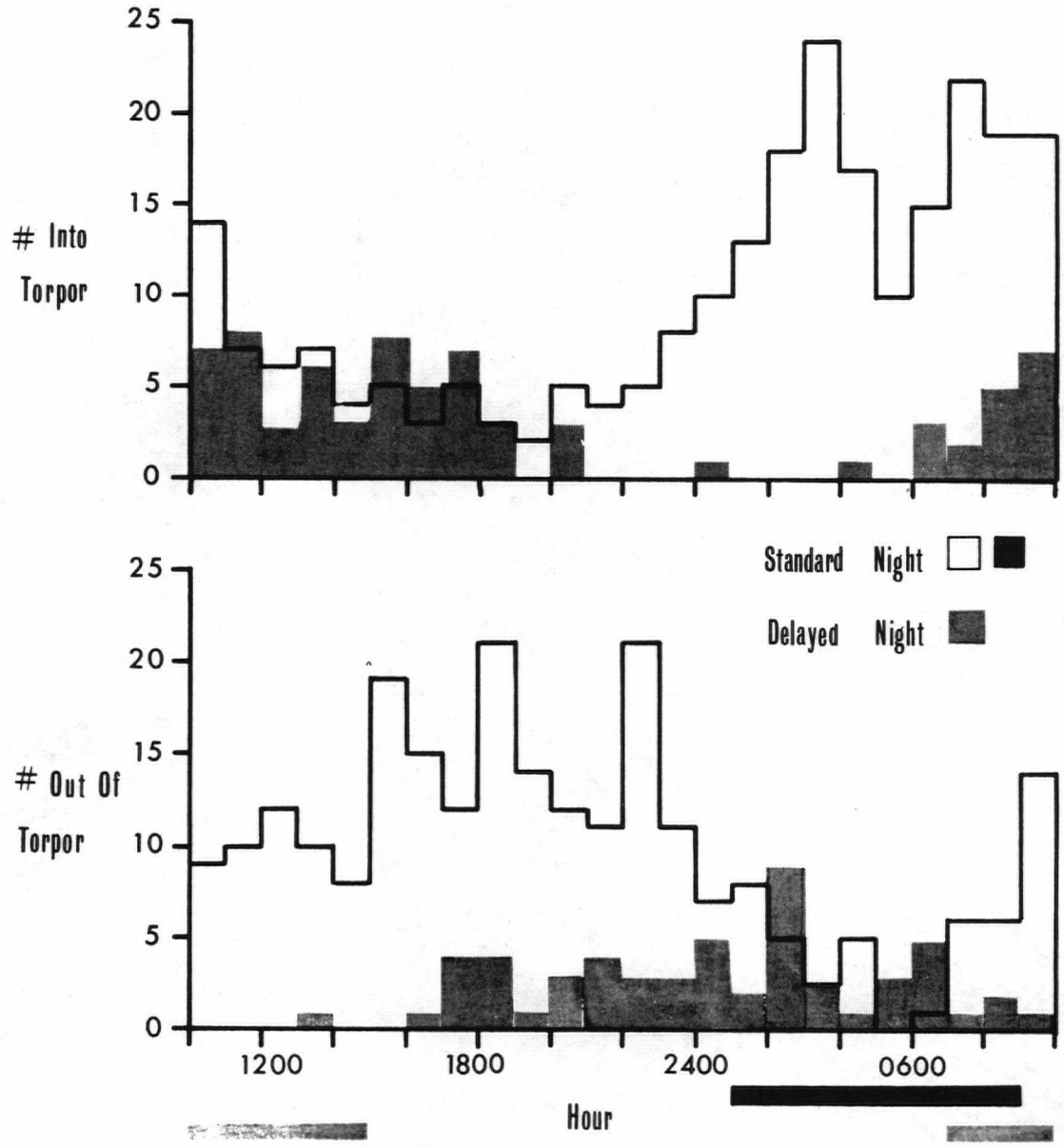


Figure 14. The total number of high and low area animals that entered and left torpor during different hours of the day during a 40 day period at 5 C. The number of animals in the normal photoperiod experiment was 24, in the delayed photoperiod experiment it was 12.

TABLE XXIII. Length of torpor periods, in hours, during different 10 day periods for high and low animals. ^{s} indicates $P \leq .05$.

Day	Low Area Number	Mean	T	High Area Mean	Number
1-9	34	31.6	4.46^{s}	36.5	34
10-19	25	44.3	10.2^{s}	59.8	32
20-29	33	51.9	0.14	52.1	28
30-39	25	47.0	1.61	49.3	30
Total	117	43.3	1.59	49.1	114

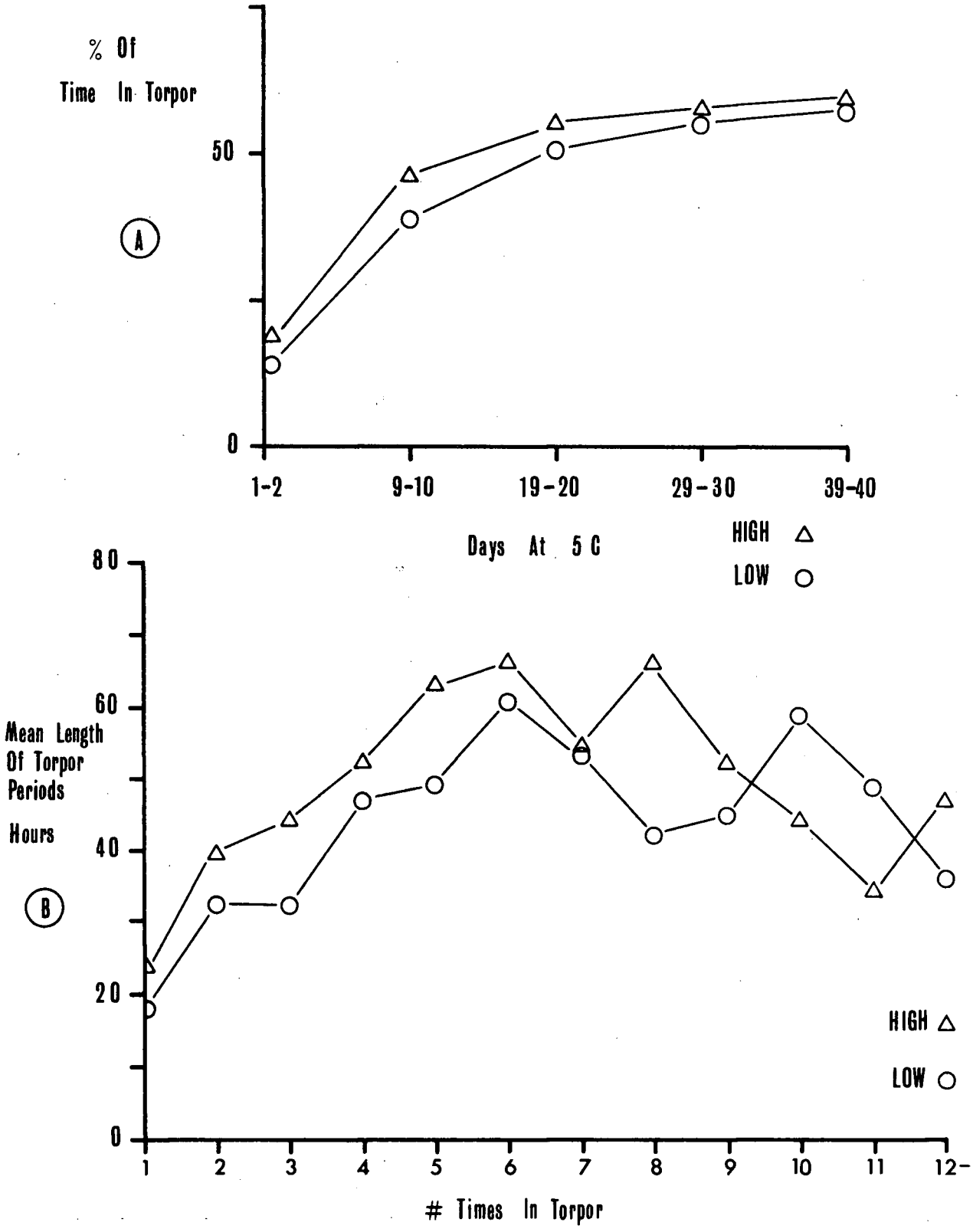


Figure 15. A. Percentage of time spend in torpor in high and low area animals after different lengths of time at 5 C. B. Mean length of torpor period in high and low area animals after different numbers of torpor periods. The low area animals entered their longest period of torpor on day 18.6 (13-31) and the high area animals entered their longest period of torpor on day 18.4 (11-33).

conserve energy during a time in which food is in short supply. The advantage of longer torpor periods is that, since a high proportion of energy spent in a torpor cycle is spent during arousal (Tucker, 1965b), a longer torpor period conserves more energy. Tucker also showed that at least in P. californicus at 15 C, a total saving of energy will result even if the animal arouses immediately upon reaching its minimum temperature. From this it can be stated that torpor is adaptive in the sense of saving energy, and that long periods of torpor save more energy. The interesting question that arises from this relationship is: what is the factor that limits the maximum length of periods of torpor to only a few days?

The increase in the average length of torpor period to a maximum in 20 to 30 days probably represents acclimation of the animal to the low temperature. Kayser (1965) has noted an increase in the length of torpor periods in ground squirrels in early winter, followed by a steady state and a decrease with the approach of spring. The variation in lengths of torpor periods after the maximum is reached may represent a steady state with individual differences becoming more apparent, or they may represent an actual decrease in the length of torpor periods for all animals. Even after the length of torpor periods has ceased to increase, and possibly decreased, the percentage of time spent in torpor continues to increase. This may represent a second phase of acclimation to low temperature in which the length of the torpor period is at its maximum and the only method left to increase the amount of time in torpor and so conserve energy is to decrease the length of the periods of activity.

CONCLUSIONS

1. High area animals went into torpor earlier in the fall than low area animals.

2. Adults in both high and low areas appeared to go into torpor earlier in the fall than young-of-the-year animals.

3. Males may have gone into torpor later and come out earlier than females.

4. Animals tended to gain weight from May to October. The average weight loss over winter appears to be about 5%.

5. Under laboratory conditions P. parvus was a strictly nocturnal animal with a peak in activity occurring shortly after dark. Activity patterns of both groups of animals were similar.

6. With continued exposure to a temperature of 5 C there was a trend to lower average activity and a shorter period of peak activity in both groups.

7. Both groups of animals tended to enter torpor during the dark period and arouse from torpor during the light period.

8. High area animals had significantly longer torpor periods during time periods day 1-9 and 10-19 than low area animals. There was no significant difference during time periods 20-29 and 30-39.

9. Percent of time in torpor increased during the course of the experiments and apparently levelled off at about 60%. High area animals consistently spent a higher percent of time in torpor.

10. The mean length of torpor periods increased from torpor periods 1-6 and then showed a decreasing trend. The maximum length of torpor period was reached on day 18. High area animals showed longer average torpor periods than low area animals.

Water Balance

Adaptations to conserve water are one of the major specializations in the Heteromyidae. They play an important role in the ability of these species to inhabit the drier areas of North America. A comparison of ability to minimize water loss through the different channels in individuals of populations from dry and moist habitats may give indications of the relative importance and susceptibility to change, of the underlying mechanisms.

METHODS

A humidity chamber of polyethylene film 1.2 m long, 0.6 m high and 0.6 m wide was constructed in the animal room. The seams were welded except for the lower front which could be rolled up for an airtight seal or opened for access to the animals. A small amount of fresh air leaked into the chamber through holes behind the fan, in some of the seams and when the animals were weighed. The chamber was not airtight but did restrict air flow enough to permit a constant humidity to be maintained. Shallow metal pans containing the humidity controlling solutions covered the bottom of the chamber. A small fan circulated air over the pans. The animals were maintained in 24 wide-mouth gallon jars laid on their sides and bedded with coarse sawdust. The jar covers were replaced with welded wire mesh. Temperature and relative humidity in the chamber were recorded with a Serdex thermohumograph.

The saturated salt solution method of humidity control was used (Winston and Bates, 1960). This method takes advantage of the fact that saturated solutions, with extra salts, of certain salts will maintain a constant relative humidity in a confined volume of air. The salts used were NaCl and $Zn(NO_3)$. At 20 C these salts maintain humidities of 76% and 42%

respectively (Winston and Bates, 1960). Throughout the course of the experiment relative humidity varied less than ± 4% from the desired level and temperature varied less than ± 2 C.

In the second set of experiments animals were maintained in 15 cm diameter cages with wire mesh bottoms to determine fecal and urinary water loss and water intake. These cages were exposed to room conditions which were 60 ± 6% relative humidity and 20 ± 2 C.

Urine samples were collected for the determination of osmotic concentration by placing a glass dish containing paraffin oil below each cage. After 24 hours uncontaminated samples of urine were collected in capillary tubes and frozen on dry ice. Osmotic concentrations were determined with a Ramsey-Brown freezing point apparatus (Ramsey and Brown, 1955).

Daily food intake, and dry weight of urine and feces were determined. A weighed quantity of food was presented to each animal and a preweighed funnel-shaped filter paper was placed below each cage. Dropped food and feces rolled down the filter paper, through a small hole in its center and into a collecting dish below. Food and fecal material were then separated and weighed. Urine was absorbed by the filter paper. Feces and filter papers were dried at 100 C for 24 hours and weighed. Dry weight was then calculated.

Water content of feces was determined by collecting fecal pellets immediately after defecation, weighing, drying for 24 hours at 100 C and reweighing them. Water content of pearl barley and lettuce was determined.

Tail blood was collected in a heparinized capillary tube, and centrifuged. The plasma was then collected and osmotic pressures were determined as for urine.

Evaporative water loss was determined in a constant pressure closed

system respirometer at 20 ± 0.1 C and a relative humidity of 0%. Air from the animal chamber was circulated through a U tube immersed in alcohol cooled by dry ice, a lithium hydroxide CO_2 absorption column, another U tube in cold alcohol, a temperature equilibration coil and finally back into the animal chamber. Animals were placed in the chamber over paraffin oil and the system was closed, placed in operation and allowed to equilibrate for one-half hour. Pre-weighed U tubes were then placed in the system and it was allowed to operate until the animal had used 50 cc of oxygen. The U tubes were weighed and water loss and metabolic rate were calculated.

All animals were fed an excess of pearl barley equilibrated to the applicable conditions. Control animals were given a small amount of lettuce daily to provide water.

Table XXIV shows the experimental groups, treatments, and numbers in the groups for both experiments. Animals were assigned randomly to treatments. All animals were weighed daily to the nearest 0.1 g. Weight change was calculated as a percent of original weight.

RESULTS AND DISCUSSION

Weight Loss

The results of the weight loss experiment are shown in Figure 16. The values for percent of original weight on the tenth day were submitted to a three-way analysis of variance. The results of this test are shown in Table XXV.

Throughout the course of the experiment all of the control groups gained a small amount of weight while all of the experimentals lost varying amounts of weight. The gross difference between the experimentals and the controls is significant at a high level (Table XXV). The gross difference between the high and low populations is also significant (Table XXV) while

TABLE XXIV. Experimental groups, treatments and numbers for both sets of experiments. The operations carried out on days 1-10 apply only to the second set of experiments. Animals in the first set were weighed daily for 14 days.

Day	1	2	3	4	5	6	7	8	9	10
Experimental groups										
High area animals experimental (no water) N = 12		Equilibration period		Urine collected in paraffin oil	Food feces and urine collected on filter paper	Wet feces collected for water content of feces		Urine collected in paraffin oil	Food feces and urine collected on filter paper	Wet feces collected. Blood collected. Evaporative water loss determined
High area animals control (given water) N = 12		All animals given water								
Low area animals experimental (no water) N = 12										
Low area animals control (given water) N = 12										

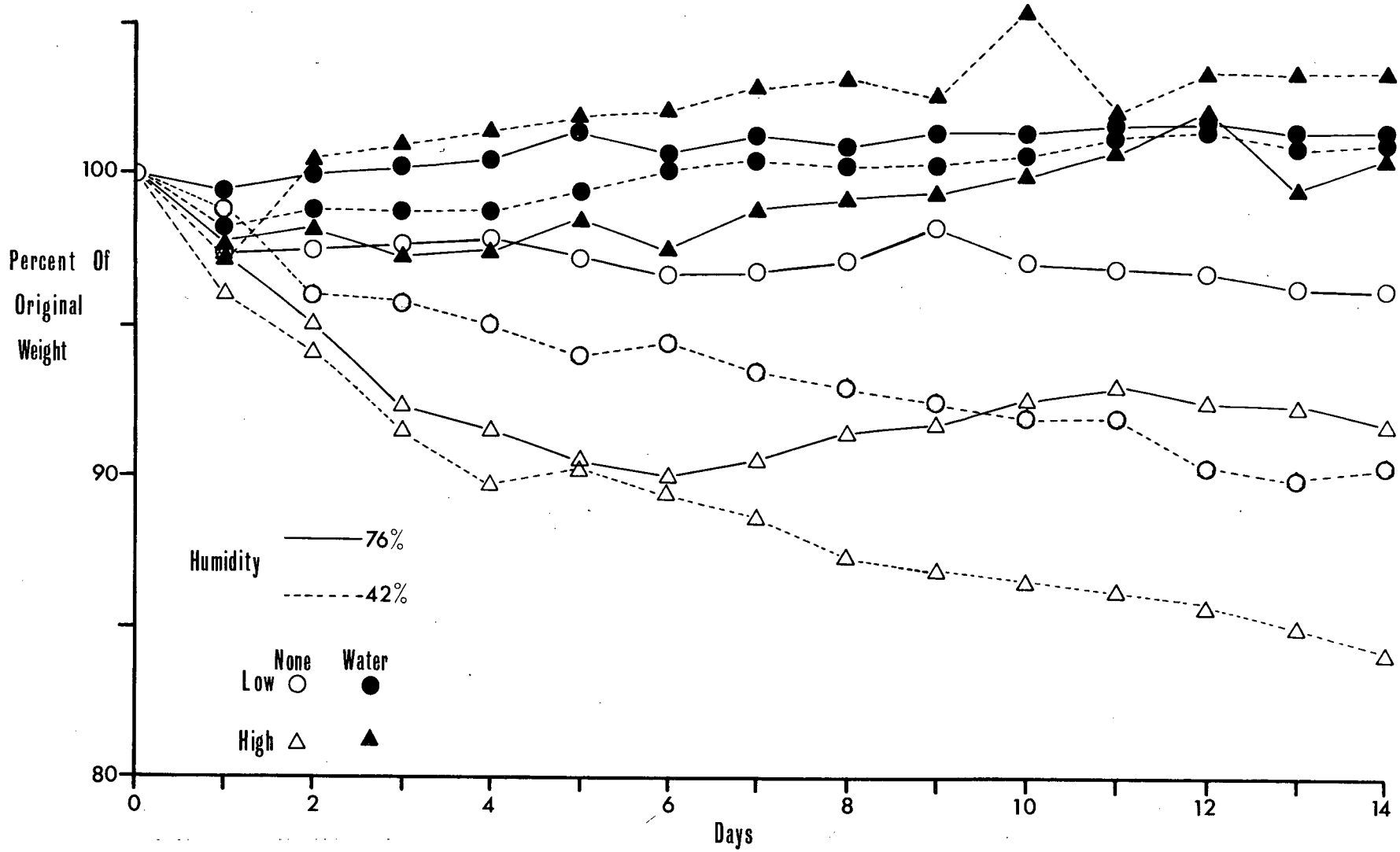


Figure 16. Percentage of original weight after time in animals from the high and low areas given different amounts of water and exposed to different humidities.

TABLE XXV. Results of a 3-way analysis of variance of percentage of original weight after 10 days in high and low populations of animals (A); deprived of water and given water, (B); at 42% and 76% relative humidity, (C); and a temperature of 20 C. All animals were fed an excess of pearl barley equilibrated to the humidity in question. The basic N was 12.

Comparison	High-Low A	Water no. B	42-76 C	AB	BC	AC	ABC
F value	6.17	35.55	1.86	.48	5.63	.97	.65
Significant A	≤.05	≤.001	≤.20		≤.05		

the effect of humidity falls short of the usual level of significance.

The only significant interaction is between animals given water and those not and between high and low humidity. This indicates that the combination of low water intake with low humidity produced a significantly different response in animals than high water intake and high humidity. This is the effect that would be expected since weight loss is dependent on the balance between water intake and water loss.

The difference between high and low populations seen in Figure 16 is in the direction expected on the basis of the environment. The effect of humidity is apparent and is in the direction expected. Examination of the curves for animals deprived of water show that the curves could be considered to be made up of two parts. The first part of the curve shows a steep decline followed by a slower decline, a levelling off or an increase. This is seen most clearly in the curves for the high area animals, where the inflection point is near the fourth day. In the low area animals the inflection point, if present, is in the first or second day. The inflection point could be considered the time at which the animal actively begins to conserve water.

Evidence presented to this point indicates that by the tenth day high area animals had lost more weight than low area animals, animals deprived of water had lost more weight than animals given water and animals at a low humidity deprived of water lost more weight than would be predicted from humidity or water deprivation curves alone. The weight loss curves, after the initial period of steep decline, can be examined to determine if the animals deprived of water and exposed to a relative humidity of 76% were losing weight and if the high and low area animals at 42% were losing weight at different rates.

Figure 17 presents the regression analysis of the weight loss

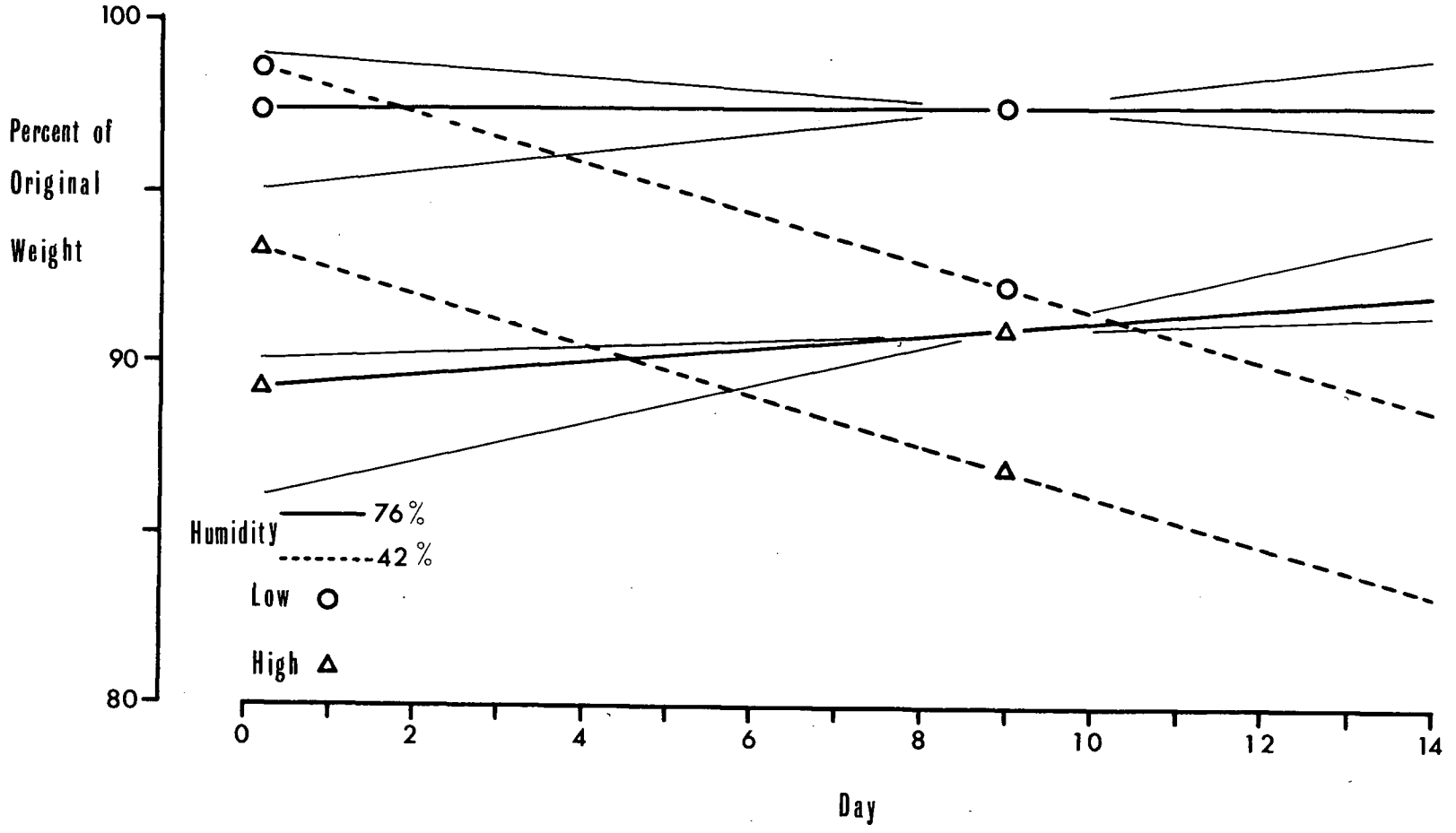


Figure 17. Regression of percent of original weight on time for high and low area water-deprived animals at 42 and 76% humidity. Confidence intervals ($P \leq .05$) are shown for the 76% humidity slopes. Calculated t for the comparison of high and low area animals at 42% humidity equals 0.0047 with 71 degrees of freedom.

curves from day 4 to day 14. The low area animals at 76% humidity show a rate of change in weight that is not significantly different from zero. They were not gaining or losing weight. The high area animals at 76% show a rate of change in weight that is significantly greater than zero. They were gaining weight. Both groups of animals at 42% humidity were losing weight but the difference between them is not significant.

It appears that the animals at 76% humidity were in neutral or positive water balance and could be expected to remain so indefinitely. The animals at 42% humidity were in negative water balance and show no signs of decreasing their rate of water loss. There is no reason to believe that at 42% relative humidity the animals would be able to avoid eventual death. On this basis it appears that the humidity below which positive water balance cannot be maintained lies somewhere between 42 and 76%.

The difference in amount of weight lost between high and low area animals was due to a more rapid response on the part of the low area animals. As discussed before, the inflection point in the weight loss curves for the high area animals is near the fourth day. In the low area animals it is on the first or second day.

Schmidt-Nielsen (1964) summarizes extensive work on water balance in the kangaroo rat (Dipodomys). He found, under conditions comparable to this study, that kangaroo rats from Arizona could maintain positive water balance down to a relative humidity of about 10% at 25 C when fed equilibrated pearl barley. The higher temperature in Schmidt-Nielsen's study would mean that the absolute humidity, which is the parameter which influences pulmonary water loss, would be higher than it would at 10% relative humidity at 20 C. This means that the difference between results of the studies are not as great as indicated.

The second phase of this experiment was designed to measure and compare water intake and loss through the different routes. The experimental design is shown in Table XXIV. The basic comparisons made were between high and low area animals deprived of and given water. Time since water deprivation was also included as a factor wherever possible.

Percent weight loss was measured in this experiment as an indicator of water balance. The weight loss curves (Figure 18a) are complicated by the fact that the controls did not maintain their weight. This weight loss was probably due to experimental conditions such as confinement to a small cage or lack of comfort when placed on a screen mesh floor. The effect of these conditions was greater on high area animals judged by the greater weight loss before water deprivation and the higher rate of weight loss in high area controls (Figure 18b).

High area water-deprived animals in this experiment lost significantly more weight than the low area animals (Tables XXVI, XXVII). This result is similar to the result of the prior experiment and was due to the same more rapid response to water deprivation in the low area animals. In this case lower response to other experimental conditions in the low area animals may have contributed to the effects. After water deprivation, however, the high area animals lost water at a lower rate (Figure 18b) than the low area animals.

This finding may be comparable to the results from the prior experiment where at 76% humidity the high area animals, to increase their weight, must have been losing less water than the low area animals, which were merely maintaining their weight. This would imply that in these two situations the high area animals were expending a greater effort to retain water than were the low area animals. The fact that weight loss rates at

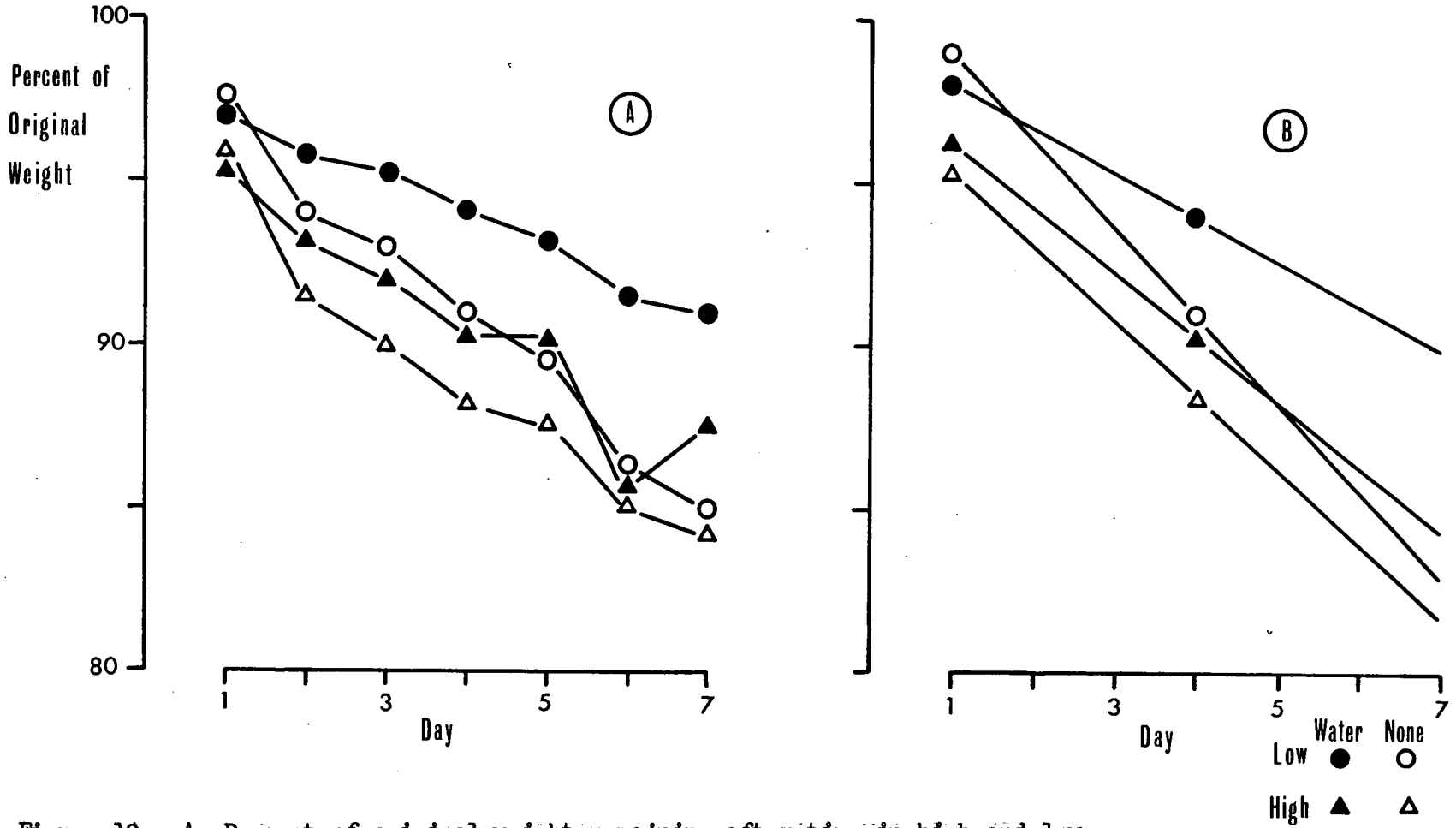


Figure 18. A. Percent of original weight remaining after time in high and low area animals, given and deprived of water. B. Regressions of percent of original weight on time. The slopes of the water-deprived groups are different at the .05 level ($t = 2.20$, 136 degrees of freedom), as are the slopes of the groups given water at the .02 level ($t = 2.42$).

TABLE XXVI. Calculated F values for analyses of variance conducted on results of the second group of experiments. Degrees of freedom in the numerator equal 1 except where noted ( ). Degrees of freedom in the denominator equal 36 in the two-way analyses and 72 in the three-way except for percent weight loss where there are 252 degrees of freedom in the denominator. The number of observations in each basic group is 10 (N = 10). Significance at .05 is shown by ^{s}.

	A High-Low Pop.	B Water or not	C Time	A-B Inter.	B-C Inter.	A-C Inter.	A-B-C Inter.
Starting weight	5.17	0.15		0.14			
Percent of original wt.	10.14^{s}	8.38^{s}	8.50^{s} (6)	42.53^{s}	0.24 (6)	23.19^{s} (6)	30.04^{s} (6)
Plasma Osmotic Pressure	7.89^{s}	2.54		0.90			
Urine-Plasma Ratio	0.80	38.08^{s}		0.14			
Urine Osmotic Pressure	0.09	34.03^{s}	0.33	0.82	15.25^{s}	0.87	1.95
Urinary water loss per day	0.72	26.40^{s}	7.47^{s}	1.13	15.10^{s}	0.31	0.77
Fecal percent water	0.00	1.38	0.00	11.60^{s}	0.24	0.34	0.21
Fecal water loss per day	2.00	2.44	2.85	0.27	0.27	0.14	0.00
Evaporative water loss	2.34	2.48		6.07^{s}			
Metabolic Rate	0.79	2.45		1.24			
Water intake in lettuce per day	0.02		0.08			0.23	
Water intake in food per day	15.32^{s}	0.56	11.90^{s}	9.39^{s}	3.08	7.47^{s}	1.30

TABLE XXVII. Means and standard error of the means for the results of the second group of experiments. N in all cases equals 10.

		High Area Given Water	High Area No Water	Low Area Given Water	Low Area No Water
Starting weight (g)		18.09±0.49	17.34± .80	19.90±0.98	19.90±1.34
Percent of original wt.	E	95.31±1.66	95.66±1.30	97.16±1.34	97.25±1.39
	L	87.38±3.32	84.60±1.90	91.06±2.59	84.76±2.28
Plasma Osmotic pressure (Osmol)		297.6±10.7	319.5±14.4	281.5±12.4	275.2±16.3
Urine-Plasma Ratio		6.16±1.22	12.46±0.92	6.72±1.21	13.81±2.78
Urine Osmotic Pressure (Osmol)	E	2.77±0.39	2.69±0.32	2.54±0.28	3.45±0.31
	L	1.71±0.31	3.90±0.28	1.68±0.26	3.67±0.24
Urinary Water Loss per Day (mg)	E	259.9±26	198.8±28	287.5±48	205.0±21
	L	556.7±118	151.4±29	748.5±119	120.5±14
Fecal Percent Water	E	53.40±1.80	41.82±2.76	45.32±2.24	49.83±3.86
	L	52.01±2.87	44.06±2.97	45.61±4.06	50.62±1.67
Fecal Water Loss per Day (mg)	E	108.6±19.3	76.0±16.1	114.8±15.0	95.6±18.6
	L	76.2±20.8	57.2±10.7	92.2±22.4	85.7±12.0
Evaporative Water Loss (mg H_2O/ml O_2)		0.68±0.003	0.58±0.003	0.66±0.002	0.68±0.002
Evaporative Water Loss per Hour (mg)		58.25±3.48	47.40±3.13	56.01±3.81	65.24±1.30
Metabolic Rate (ml O_2/gm/hour)		5.61±0.31	5.42±0.51	6.63±1.60	4.86±0.39
Water intake in Lettuce per Day (mg)	E	186.0±111.0		242.0±69.3	
	L	254.0±93.3		226.0±67.7	
Water intake in Food per Day (mg)	E	761.7±48.1	981.7±70.5	2165.8±465.0	1297.2±235.4
	L	589.7±149.0	968.3±122.0	991.0±135.7	872.6±195.8

42% humidity were not different indicates that, at least in this situation, low area animals were as capable of maintaining their weight as high area animals. If this interpretation of lack of maximum response on the part of low area animals is correct it indicates that these animals are not as sensitive to weight, or water, loss as are high area animals.

Plasma Osmotic Pressures

Evidence for greater sensitivity of high area animals to water deprivation is found in the increased osmotic pressure of the plasma of these animals (Figure 19). This is true particularly in the water-deprived group. Similarly high osmotic pressures have been found in plasma from severely water-deprived grasshopper mice (Schmidt-Nielsen and Haines, 1964) and Pack rats (Neotoma albigula) (B. Schmidt-Nielsen et al., 1948). In these cases the elevated osmotic pressures were due to higher plasma urea. Water-deprived kangaroo rats did not show elevated plasma urea or osmotic pressure levels (K. Shmidt-Nielsen, 1964). The references cited above indicate that only in very greatly dehydrated animals do the plasma osmotic pressures increase. The high area animals, therefore, even though they had lost little more weight at the time blood was collected, were showing signs of severe dehydration.

The urine:plasma ratios (Figure 19) were the same in the two populations, but a highly significant difference was found between water-deprived animals and those given water (Tables XXVI, XXVII). Both experimental groups were apparently reacting to dehydration very strongly by forming a much more concentrated urine than the control groups. The urine: plasma ratios for water-deprived animals are similar to those summarized by Schmidt-Nielsen (1964) for kangaroo rats and other desert animals.

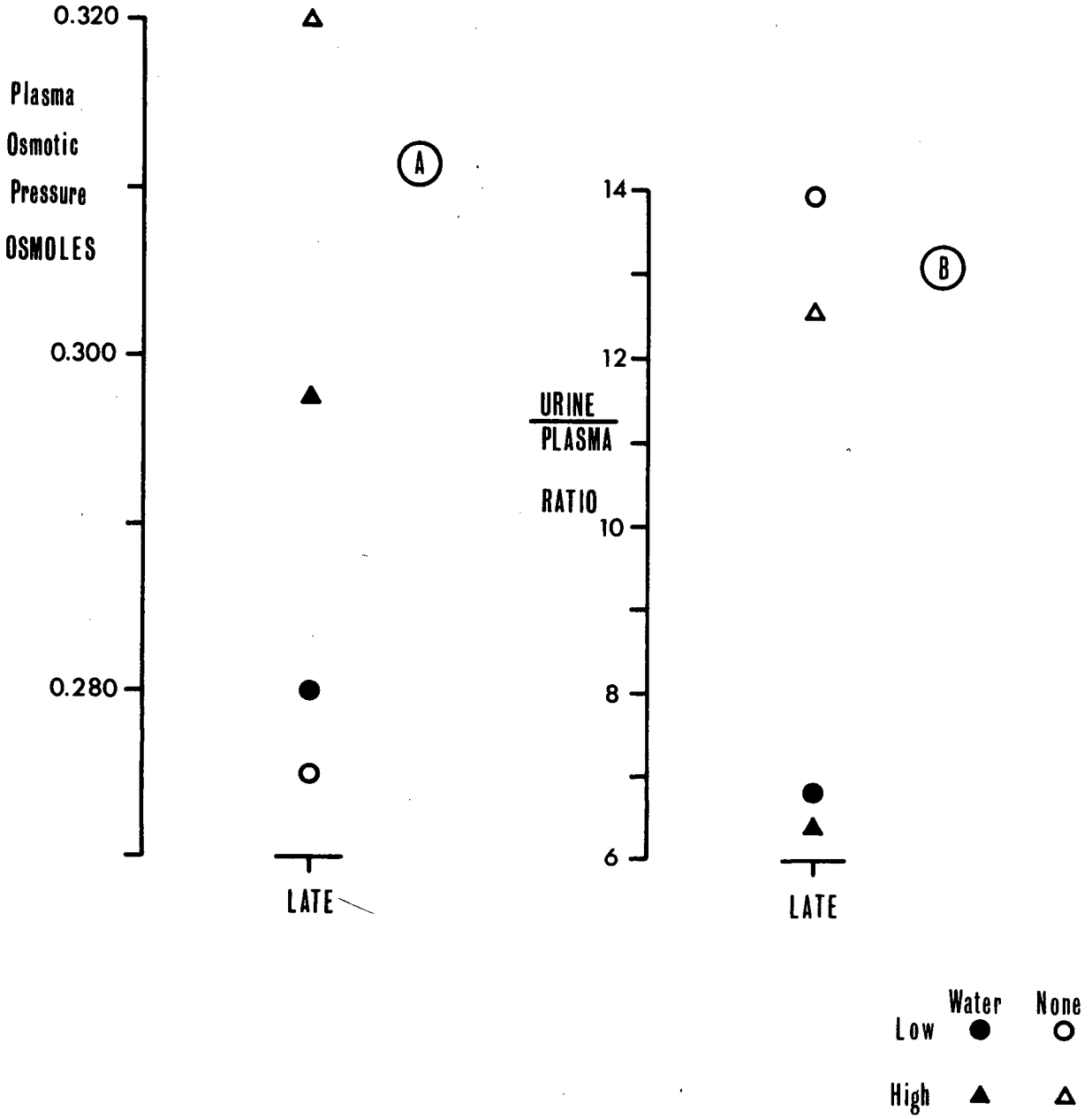


Figure 19. A. Mean plasma osmotic pressures, and (B). urine/plasma ratios of osmotic pressures of high and low area animals deprived of and given water.

Urinary Water Loss

Urinary osmotic pressures (Figure 20) showed a significant difference between animals deprived of water and those given water (Tables XXVI, XXVII). The difference became greater with time through an increase in concentration of urine in water-deprived animals and a decrease in controls. The increase in high area water-deprived animals was greater than in the low area water-deprived animals, primarily due to a lower early value. This may be the cause of the earlier inflection point in the weight loss curves of low area animals as was observed earlier.

Total urinary water loss per day (Figure 20) showed the same pattern of response. As in urine osmolarity the only significant difference was between water-deprived animals and controls. The difference becomes significantly greater with time (Tables XXVI, XXVII).

Fecal Water Loss

The only significant finding in water content of feces (Figure 21) is the interaction between population origin and water deprivation (Tables XXVI, XXVII). High area water-deprived animals had a much lower percent water in feces than the high area controls while the low area water-deprived animals had a slightly higher percent water in feces than did the low area controls. The high area water-deprived animals were apparently reacting to dehydration by concentrating their feces while low area animals were not.

Data summarized by Chew (1965) indicates that regardless of the percent water in the feces of hydrated animals (from 61.2% to 46.8%) dehydrated Jaculus, Dipodomys, Peromyscus and Rattus all showed fecal water percentages of 41 to 45%. The results for the control groups and the water-deprived low area animals fall into the range given by Chew for hydrated animals, while the result for the high area water-deprived animals falls

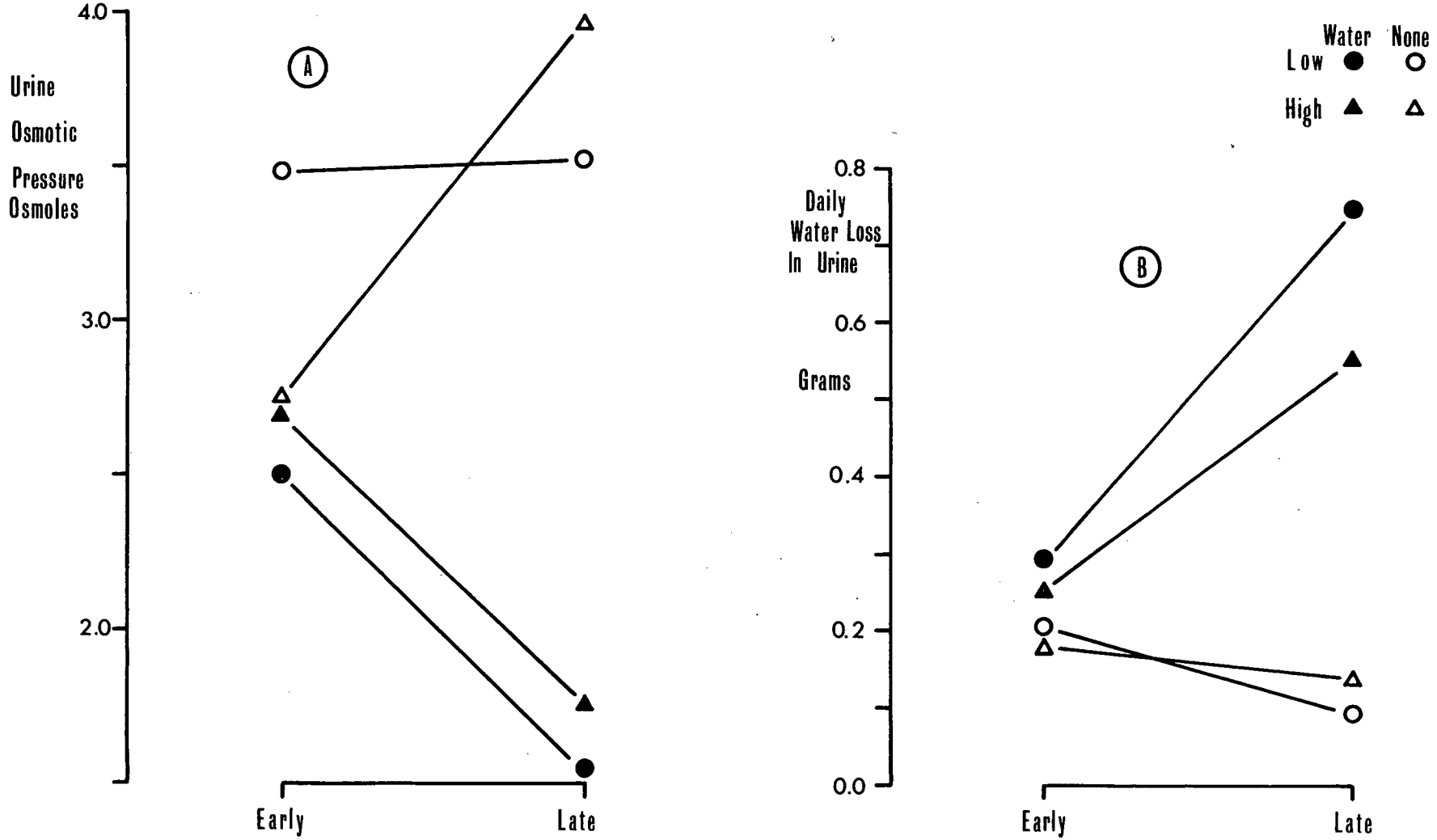


Figure 20. A. Mean urine concentrations and (B) daily urinary water loss in high and low area animals given and deprived of water.

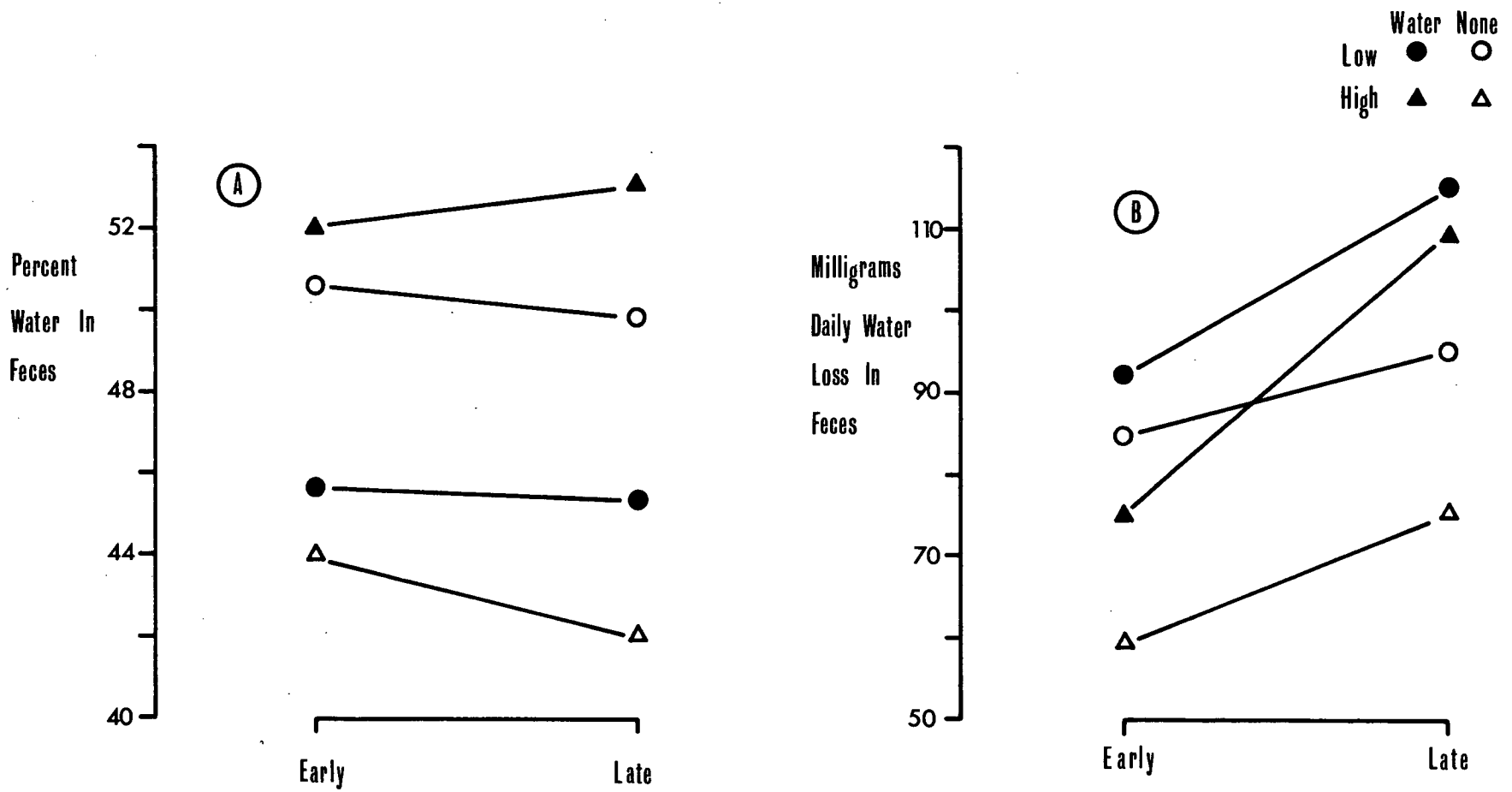


Figure 21. A. Mean percent water in feces, and (B). daily fecal water loss in high and low area animals given and deprived of water.

near the lower part of the range for dehydrated animals. This may be another indication of the greater effective dehydration of the high area animals.

Fecal water loss per day (Figure 21) showed no significant differences (Tables XXVI, XXVII). By the end of the experiment, however, both water-deprived groups were losing slightly less water in feces per day than were the control groups.

Evaporative Water Loss

Evaporative water loss, a combination of skin and pulmonary water loss, is shown in Figure 22. The only significant difference (Tables XXVI, XXVII) is between the high area water-deprived animals and the other groups. The function of this response is clear and it fits with the more general response of high area animals to water deprivation. The mechanism is far from clear however.

In Perognathus, and heteromyids in general, sweat glands are present in very low numbers and in localized areas such as the soles of the feet and the angle of the lip (Quay, 1965). They do not appear to be present in great enough numbers to play a significant role in temperature control or water loss. The method of evaporative cooling utilized by Dipodomys and Perognathus is to lick the fur at high temperatures. This was not a factor at the experimental temperatures.

The Schmidt-Nielsens (1950) concluded that evaporation of water which diffused through the skin was negligible in Dipodomys and Perognathus. Chew (1965) presents data which indicate that this may not be true and that water loss through the skin makes up about 16% of the total evaporative water loss (Chew and Dammonn, 1961). There is general agreement, however, that most of the water evaporated is lost from the respiratory surfaces. This, then, is where any significant conservation of water must occur.

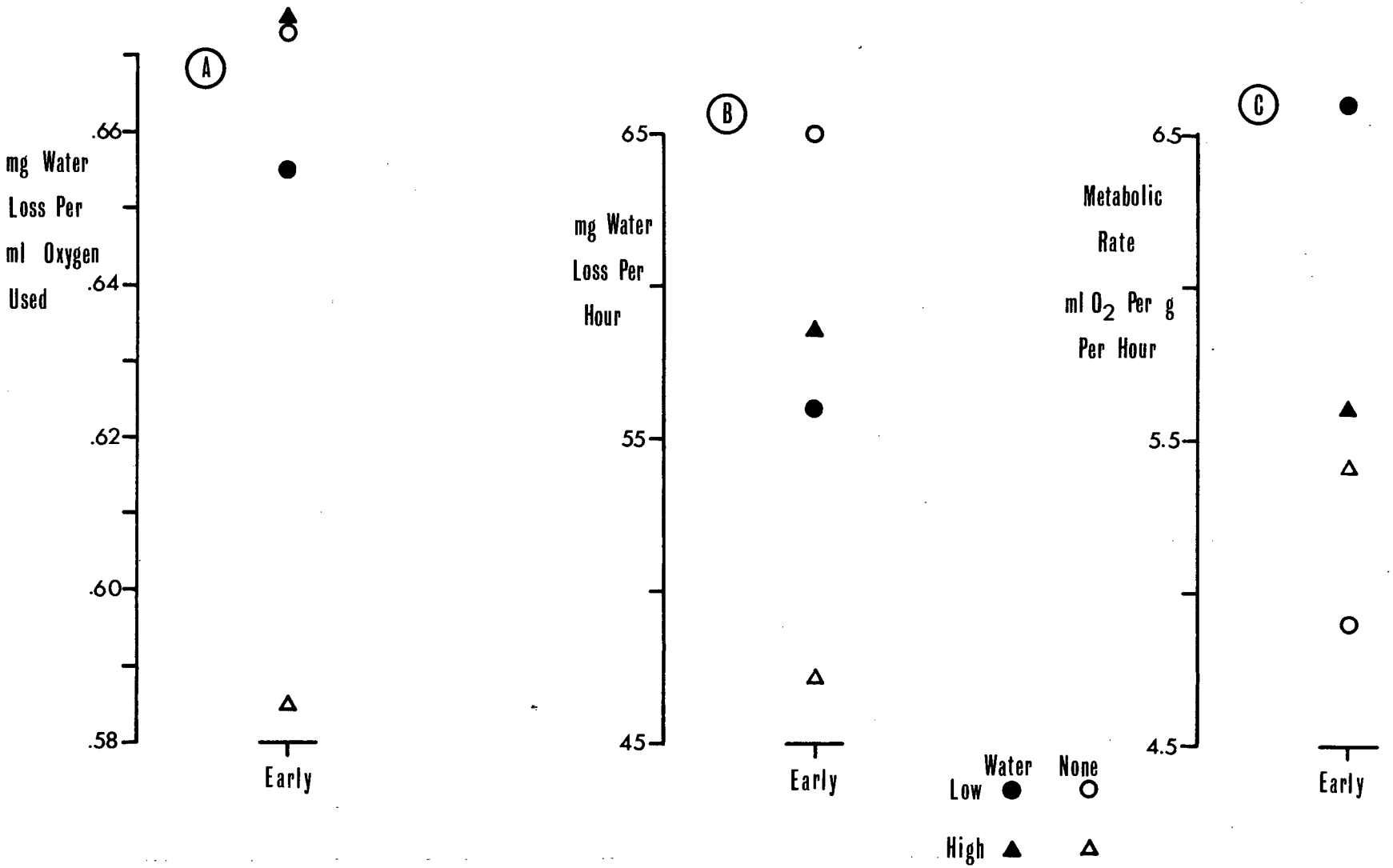


Figure 22. A. Water lost per ml of oxygen used, (B) water lost per hour, and (C) metabolic rate in high and low area animals deprived of and given water.

Respiratory water loss varies directly with metabolic rate in many animals (summarized by Chew, 1965). In this case the metabolic rate of the water-deprived animals was little lower than that of the controls. The other possibilities are that the temperature of the expired air was lower in this group of animals and/or that the volume of inspired air was less. These two possibilities are related in that Chew (1965) summarizes data which show that in a pattern of rapid shallow breathing the temperature of the expired air is higher and the respiratory volume, and therefore the percent of inspired air in alveoli, is less. Either or both of these effects could account for the observed difference.

Food Intake

Most mammals other than Mus and the heteromyids voluntarily reduce food intake when deprived of water (summarized by Chew, 1965). The value of this response is a reduction of urine volume and consequently a more favorable water balance. In agreement with the findings cited above, P. parvus from the high and low areas did not decrease food intake in comparison with control groups (Tables XXVI, XXVII, Figure 23). The reason for the failure to stop eating when deprived of water may be due to the ability to retain positive water balance on an air-dry diet. At humidities above 20% kangaroo rats can maintain positive water balance on air-dried foods (Schmidt-Nielsen, 1964) as can P. parvus above 76% humidity. No difference was found between the water intakes in the form of lettuce in the high and low area control groups (Tables XXVI, XXVII, Figure 23).

CONCLUSIONS

1. At 76% humidity water-deprived animals, when fed pearl barley equilibrated to that humidity, were able to maintain their weight; but water-deprived animals at 42% humidity lost weight.

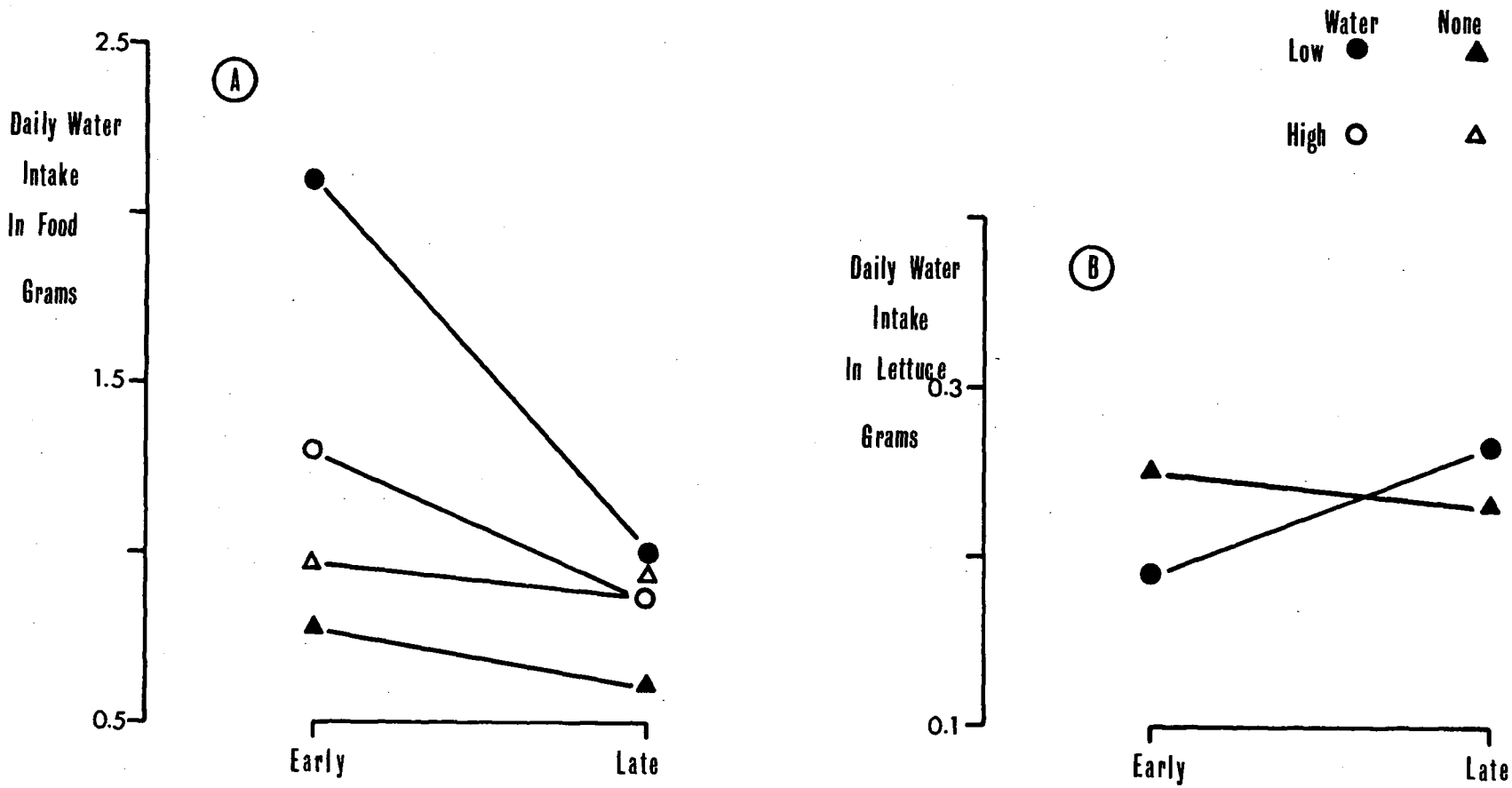


Figure 23. A. Free water intake in food per day in high and low area animals deprived of and given water. B. Free water intake in lettuce per day in high and low area control animals.

2. Low area animals lost less weight because they showed a shorter period of rapid weight loss when deprived of water. This difference appears to be due to the formation of near maximum observed concentrations of urine shortly after water deprivation by the low area animals, while the high area animals did not produce a comparably concentrated urine until several days after water deprivation.

3. After the initial period of rapid water loss at 76% the high area animals gained weight but the low area animals did not show a rate of change different from zero. At 42% humidity both groups of water-deprived animals lost weight at the same rate.

4. Both groups of water-deprived animals produced a highly concentrated urine.

5. High area water-deprived animals showed a higher plasma osmotic pressure, lower percent water in feces and a lower evaporative water loss than low area animals. This is interpreted to mean that high area animals were more sensitive to dehydration.

6. Osmotic pressures of urine and percent water in feces were similar to those found in other desert rodents, while evaporative water loss may have been higher.

DISCUSSION

Mammals that live in harsh environments can be divided into two basic categories: those which cope directly with the environment, and those which evade it. The pocket mouse, Perognathus parvus, is a highly adapted evader of desert conditions. It has evolved mechanisms for coping successfully with extreme temperatures, a variable food supply, and the results of low rainfall, and high evaporation. Its northern and altitudinal distribution in British Columbia may be limited only by two conditions it cannot avoid: the presence of trees and the short northern summer.

Adaptation

Deserts are characterized by two interrelated stresses they impose on organisms: low and undependable supplies of moisture, and extreme temperatures. The climatic conditions in the Okanagan Valley are intermediate between a semi-arid, cold steppe and an arid, hot desert. In this environment populations of animals along a gradient of altitude were studied. The effect of altitude, as such, was not examined. The effects that were of interest were the climatological parameters co-variant with altitude.

The lowest area is the most desert-like. With an increase in altitude the amount of rainfall and available water increases, maximum and minimum temperatures decrease, and the length of the frost-free period decreases.

ADAPTATION TO LACK OF WATER

Water is basic to life in all animals, but in mammals the main uses of water that remove it from the body are cooling, elimination of

wastes and maintenance of the absorptive surface of the lungs. It is advantageous for the animal to maximize water intake and minimize water loss with the expenditure of as little energy as possible.

Maximizing Water Intake

The main method available for the pocket mouse to maximize its water intake is to select food with high water content. Two such food materials are available; animal material and green vegetation. Although green vegetation contains only half as much free water as animal material it appears to be the source of water for low area animals. It may be used because it is more readily available or because it has a lower content of protein. A high protein content is disadvantageous both because more oxygen is used to produce a gram of water when metabolizing protein than when metabolizing fat or carbohydrate, and because more water must be used to eliminate the urea produced.

It has been demonstrated that diets of high water content allow certain animals to live in arid areas. The grasshopper mouse (Onychomys), an arid-land carnivore, can maintain its weight on a diet of meat alone without producing a highly concentrated urine (Schmidt-Nielsen and Haines, 1964). Pack rats (Neotoma) survive in the desert by feeding on Opuntia, a cactus which has a high water content, and are unable to produce a highly concentrated urine (Schmidt-Nielsen, 1964).

The behavioral mechanism of storing food in the burrow increases the amount of water in the food. This may be expected, since the relative humidity in the burrow may approach 100% (Cloudsley-Thompson and Chadwick, 1964). The amount of free water in a sample of seeds buried at burrow depth was doubled in comparison with that in the sample on the surface of the soil. This would be an important gain of water during the time the animals feed on

stored food, but its importance during the summer is unknown. The animals apparently carry quantities of seeds to their burrows but it is not known if they feed on the seeds immediately or eat them after storage.

Minimizing Water Loss

Evaporative, or insensible, water loss occurs through three main pathways: the production of sweat, diffusion through the skin, and evaporation from the lungs. The first of these is relatively unimportant since Quay (1965) has shown that heteromyids have very few sweat glands and Schmidt-Nielsen (1964) found that kangaroo rats utilize evaporative cooling only as a last resort. Evaporative cooling, by saliva spreading, has only been observed in Perognathus accidentally exposed to high temperatures in traps.

The rate of evaporation of water that has diffused through the skin has not been measured in Perognathus. In Dipodomys merriami, however, only about 16% of the total water evaporated is through the skin in resting animals (Chew and Dammann, 1961). It appears that the main pathway of evaporative water loss in heteromyids is from the surface of the lungs. The rate of loss depends on four factors: humidity and temperature of expired air, humidity and temperature of inspired air, amount of oxygen used, and the efficiency with which oxygen can be extracted from air in the lungs.

The humidity and temperature of inspired air are under the control of the animal only if it selects the best microhabitat. Deep burrows and nocturnal activity may provide environments which allow near maximal savings of evaporative water.

The white rat exhales air that is at its body temperature, but the kangaroo rat exhales air that is at a lower temperature than its body. The lower temperature results in a lower absolute humidity in expired air and a

saving of water by the kangaroo rat (Schmidt-Nielsen, 1964). A counter-current heat exchanger in the nasal mucosa has been suggested as the mechanism which produces this result. The temperature of expired air in Perognathus has not been measured but interpolated respiratory water loss at 28 C in P. californicus is no lower than in the white rat (Tucker, 1965a). The rate of respiratory water loss in P. parvus shown in this study is similar to that found by Tucker for P. californicus at 20 C (0.65 mg H_2O loss/ml O_2 used in P. californicus as compared to 0.67 in P. parvus). These data suggest that a special mechanism to decrease respiratory water loss is not present in P. parvus.

Another method of reducing evaporative water loss is to reduce the body temperature to near environmental temperature. P. parvus can enter torpor at room temperature as do other species of Perognathus (Bartholomew and Cade, 1957). Poor trap success in the low area during a hot, dry period in August 1965 suggests that the animals may enter torpor in response to extreme summer conditions. It is not known, however, if Perognathus enters torpor in response to water deprivation. The incidence of torpor in the water deprivation experiments was too low to allow statistical comparison but there appeared to be no difference between water-deprived and control animals. The water-deprived animals did not voluntarily starve and enter torpor as a result, because food consumption did not decrease in the water-deprived groups. MacMillan (1964) showed that cactus mice (Peromyscus eremicus), torpid at 15 and 20 C, evaporated only 35.5% and 38.7% as much water, respectively, as those active at the same temperatures. He suggests that water loss would be much less in a humid burrow.

Since water loss is, at least to a certain extent, proportional to oxygen uptake (Tucker, 1965a) any reduction in the amount of oxygen used would reduce the amount of water lost. The amount of oxygen used is under

the control of the animal to the extent of determination of the length of activity periods, entrance into torpor, and selection of foods with high oxygen-energy ratios. Schmidt-Nielsen (1964) found no evidence that kangaroo rats could extract a greater percentage of oxygen from inspired air than could other animals.

The relative importance of the routes of water loss is shown in the ratio of evaporative to urinary to fecal water loss per day. Animals given water at 20 C and 0% humidity have a ratio of 27:13:1. This ratio is a gross overestimate of the importance of evaporative water loss under any circumstances the animal might encounter in the field. A truer relationship in the field situation might be found by modifying the ratio with the results of Chew and Dammann's (1961) examination of the relationship between humidity and evaporative water loss in P. baileyi and P. intermedius. At relative humidities of 79% and 64% these species lost only 38% and 54%, respectively, of their water loss at 0% humidity. When these figures are applied to the ratio it becomes 14:13:1, at 64% humidity, or 7:13:1, at 79% humidity. Because of the high percentage of time P. parvus spends in its humid burrow the second ratio may be the most realistic.

Little water is lost in the production of feces and it was not found to vary between animals given water and those deprived of water. The percentages of water found in feces were similar to those found by Schmidt-Nielsen (1964) in dehydrated kangaroo rats and also similar to those found in other dehydrated animals (summarized by Chew, 1965). Schmidt-Nielsen suggests that fecal reingestion may plan an important role in water balance of kangaroo rats. It was not observed to occur in captive pocket mice but fecal material was observed in the stomachs and cheek pouches of wild-caught animals.

The production of highly concentrated urine appears to be the major short-term physiological adjustment to water deprivation in P. parvus. When deprived of water both high and low area animals produce urine more than twice as concentrated as they do when fully hydrated. The only difference found between the groups was that dehydrated high area animals were unable to maintain low osmotic concentrations in the plasma.

The ratio between evaporative, urinary and fecal water loss per day in dehydrated animals can be compared to the ratio calculated above for hydrated animals at 79% humidity. The ratio for hydrated animals is 7:13:1 and for dehydrated animals is 7:2.7:1, for a total saving of about 50%. In addition to being dependent on concentration, the amount of water lost in urine is dependent on diet and would be higher if salt-loaded vegetation or high protein animal material was eaten.

The main mechanisms which allow this animal to maintain positive water balance appear to be food selection, microhabitat selection and an ability to produce concentrated urine. Features of food selection are: prime dependence on seeds which have a high oxygen-energy ratio and low protein content, utilization of foods with high water content such as green vegetation, and the habit of storing seeds, which increases their free water content. Selection of microhabitat allows the animal to remain in situations of relatively high humidity and low temperature, thereby decreasing evaporative water loss and making evaporative cooling unnecessary. When these methods fail to keep the animal in positive water balance a highly concentrated urine can be produced which may result in about a 50% reduction in water loss. Entrance into torpor decreases the rate of water loss but it was not found to be an important response to the levels of desiccation observed in the laboratory. Its importance in the field as a response to negative water balance cannot be evaluated.

Water and Reproduction

The high need for water during lactation may explain why reproduction was delayed until the end of the comparatively dry months of April and May. Comparative water balance may also explain why high area females, living in a moister environment, came into reproductive condition before the low area females. The months of June, July and August produce growth of grasses in both areas, which provide a good supply of water to lactating females.

ADAPTATION TO EXTREME AND VARIABLE TEMPERATURES

The Okanagan Valley provides three temperature-related factors which are unfavorable to the survival of small mammals: high summer temperatures, low winter temperatures and the short summer season. These place different stresses on the animals and, in most cases, require different types of adaptations.

High Summer Temperatures

High summer temperatures pose their main threat indirectly to the water balance of the animals. Heteromyids have no special physiological adaptations to high temperature and can endure body temperatures no higher than most other animals. If exposed to high temperatures the animals must utilize evaporative cooling, which is a last resort. Schmidt-Nielsen (1964) summarizes information on soil temperatures, which shows that even in the hottest desert sampled the burrow temperature at a meter depth rarely reaches 30 C.

The diurnal change in temperature (Figure 2) means that by the time the animals emerge the temperature has fallen at least below 35 C. P. parvus avoids high temperatures, as do many other desert rodents, by the simple expedients of constructing a deep burrow and being nocturnal.

Low Winter Temperatures

The adaptations of these animals to low temperatures are much the same as to high temperatures. The animals are not active above ground during cold weather and the depth of the burrow protects the soil around the nest chamber from freezing. Even if the soil froze, the nest would provide a certain amount of protection against cold. The fact that the animals can arouse from a temperature as low as 2 C means that if the temperature in the nest falls to that point the animal need not expend energy maintaining its body temperature above ambient. The effectiveness of these mechanisms is reflected in the low winter mortality of adult animals. The stress low winter temperature places on the population is that young animals must excavate burrows to a certain minimum depth before the arrival of winter. If the minimum depth is not reached the insulating qualities of the soil will not be great enough and energy will have to be expended to maintain a temperature above 0 C. This stress would be expected to be greater in the high area, where the frost line is deeper and may be reflected in the earlier end of reproduction in the high area.

Short Summer Season

The stress of the short summer season, or conversely the long winter, expresses itself primarily in terms of energy. The animals must store enough energy in the form of body weight or stored food to survive the winter. To operate efficiently they must make every saving possible in the use of this stored energy. Winter in the high area is longer, as shown by the mean annual temperature, the time of first snowfall, and the time at which the populations cease being active above ground. A greater stress would therefore be placed on individuals of the high population. Adaptations to meet that stress are seen primarily in torpor and reproduction.

Perognathus avoids predators, shortage of food and low temperatures of winter by entering torpor. The basic adaptation of spending as much as 60% of the time at environmental temperature makes it possible for the animals to store enough energy to survive the winter. If torpor saves energy, and long periods of torpor save more energy than short periods, it is difficult to understand why the average torpor period is so short. It is possible that some selective pressure in the environment may maintain short periods of torpor but it is difficult to identify one that would operate in the northern part of the range of P. parvus. The most likely possibility appears to be that torpor was evolved to meet the stresses in the hot desert of the south, and sufficient time has not passed in a new environment for the periods to become much longer. Perognathus originated in the south (Eisenberg, 1963) and many of the southern species show shorter torpor periods than these found in this study. The high area animals show an initially longer average length of torpor when exposed to low temperatures. They also show a consistently greater percentage of time spent in torpor. These are both energy saving devices which have been developed to meet the longer winter period.

Temperature and Reproduction

The reproductive season in the high area started slightly earlier, and ended much earlier than it did in the low area. The cues that determine the time of onset and end of the reproductive seasons are unknown. The earlier start of the reproductive season in the high area may have been a result of a better supply of green vegetation, but the earlier end did not appear to be correlated with supplies of water. The earlier end of the reproductive season in the high area may have been due to the earlier onset, and greater length of the winter. To survive the winter the last litter of

the season must be born early enough to dig a burrow and accumulate a store of food. Not only does the winter start earlier in the high area but it is longer, requiring more stored food and a deeper burrow. The apparent inability of the high area animals to reproduce much earlier in the spring, combined with the earlier end to the season, means that fewer litters per summer per female can be produced.

Distribution

P. parvus appears to be strictly limited to dry grassland or desert. Burrows or tracks have never been found inside the edge of Ponderosa pine stands, even though the grasses appear much the same, or in irrigated or naturally wet areas. This strict habitat selection limits the animals to the dry valleys and unforested hillsides. There are areas, however, where the habitat appears suitable, stocking populations have access, but no P. parvus are found. Two such areas are the Fraser River Valley north of Ashcroft, and the very high altitude south-facing slope above Cawston.

In these areas there may not be enough time between the end of the April-May dry season and the onset of cold weather in the fall for reproduction to take place and the young to become established in large enough numbers to maintain the population. Three environmental factors work together to increase this general effect. The summer is shorter, the weather is colder, requiring deeper burrows, and the winter is longer, requiring more stored food. A possible test of this hypothesis would be to determine to what altitude, and environmental conditions, P. parvus ascends some of the higher southern mountain slopes.

Evolution

A discussion of the evolution of the two populations must be based on the assumptions that some of the observed differences developed in situ and are genetic. If the differences observed did not develop in the Okanagan, at least two invasions, one of lowland and one of highland type animals, must have occurred. Highland type animals could not have moved north solely on the highlands, because of the dissected nature of these areas and the many intervening valleys. The alternative would be that a highland type moved north following the retreating glaciers and was followed by lowland animals. This does not appear to be possible because the two types of animals are not reproductively isolated and so could not maintain their differences if they occurred in the same area. The most likely possibility appears to be that the Okanagan was colonized by a single type of animal, probably more like the low area form, and the differences have developed since colonization.

Many of the differences found might be genetic but might equally well be different reactions within the limits of reaction available to both populations. The results of the physiological experiments provide weak evidence that the populations are genetically different, while the analysis of morphological variation provides stronger evidence.

PHYSIOLOGY

Several differences, of apparent adaptive value, were found between the populations when torpor and water balance were examined. The subject of physiological ecophenotypes in mammals has been poorly explored, but I have seen no evidence to indicate that basic physiological values vary non-reversably with environment. It is possible that the early

experience of animals in the field may have had an effect on their ability to maintain low plasma osmotic pressure when dehydrated, or the length of their torpor periods, that was not eradicated by the holding experience in the laboratory. This possibility appears to be extremely unlikely and these differences may be accepted as weak evidence of genetic differentiation.

MORPHOLOGY

The strongest evidence for genetic difference between the populations is the morphological difference. Barnett (1965) found that first generation laboratory mice raised at -3 C had proportionately shorter tails than other animals of the same strain raised at 21 C. After 18 generations at -3 C, however, with selection only for reproductive success, the difference was no longer significant. This experiment shows that a temperature-caused ecophenotype can exist but is of doubtful application to a field situation. The mice withwhich the experiment was started were not adapted for the low temperature, but after 18 generations had been selected for reproductive success. In the field animals are not observed after one generation in a new environment but have had many generations to adapt. Little change in morphology, particularly of hard parts, has been observed when animals have been taken from the field and raised in the laboratory for several generations (Dice, 1949). The morphological differences observed in this study can therefore be accepted as being indicative of genetic differences in accordance with standard taxonomic practice.

In many instances of adaptive differentiation either long distances (Nevo and Amir, 1964; McNab and Morrison, 1963; and Murie, 1961) or geographic isolation (Fisler, 1965 and Benson, 1933) have restricted gene flow between the populations under examination. Although sometimes the

differences have become large in a short time (Fisler, 1965) in most cases the time factor is unknown and the differences are in degree, as was found in this study. Blair (1950) suggests that geographic isolation is the most important factor that has caused differentiation in the genus Peromyscus. Most of his evidence was collected, however, from the better known races of Peromyscus that live in regions where environmental conditions vary less sharply than in the Okanagan.

Although there is no reason to believe that speciation could occur in the populations under examination by anything less than geographic isolation, the evidence suggests that high selective pressures have played a greater role in differentiation than has restricted gene flow. This phenomenon may apply only to the populations examined or it may be of more general applicability in areas of harsh habitats and steep environmental gradients.

CONCLUSIONS

In nearly every aspect examined differences were found between the high and low altitude animals. In most cases these differences were apparently of adaptive significance when related to the difference between the environments. The low area animals, living in a warmer and drier environment with a longer summer season, produced more young per summer per female, had a higher mortality rate in young, ate more green vegetation, were better able to maintain their weight and a low plasma osmotic concentration when deprived of water, and spent less time in torpor at low temperatures, than did the high area animals.

The high area animals, living in a cooler and moister environment with a longer winter, were present in lower numbers, came into reproductive condition earlier in the spring, were unable to maintain low plasma osmotic concentrations when dehydrated, and spent more time in torpor at low temperatures. It is suggested that the distribution of the animals into colder regions is partially limited by the length of the season available for production and establishment of the young.

Analysis of morphological characters shows the existence of genetic differences between the populations. Concrete evidence of genetic differences in physiological characteristics between the populations is lacking, but a strong circumstantial case for the existence of such differences can be built. It is suggested that high selection pressures have been more responsible for the differentiation of the populations than has restricted gene flow.

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