ENERGY CONSUMPTION RELATIVE TO ENERGY REQUIREMENTS IN WILD DEERMICE (*PEROMYSCUS MANICULATUS*)

by

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B.Sc., Durham University, 1968

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Energy consumption relative to energy requirements in wild deermice (Peromyscus maniculatus)

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ABSTRACT

This study was carried out from October, 1968 to September, 1971 in a coastal Douglas fir forest at Haney in British Columbia.

Populations of deermice were captured over a period from about one hour after sunset until about one hour before sunrise over 12 months from September, 1970. Frequently captured individual deermice had activity times which averaged 82% of this period. Mice were active for longer periods during the winter than summer resulting in higher metabolic costs during the former season. The mean nocturnal defecation rate of a sample of 116 individuals was 4.0 mg dry weight/g mouse/h and the maximum total dry weight of feces recorded from an individual in a single night was 978 mg.

The average daily consumption of mice in the wild was 909 $\pm$ 109 kcal/ha/day. On the basis of this daily rate the total annual consumption was estimated to be 3.32×10^5 kcal/ha which was similar to Golley's (1960) estimate for Microtus but higher than that determined for small rodents in a European beech forest (Grodziński, Bobek, Drożdż and Górecki, 1970).

The energy quality of the food consumed by deermice

showed no consistent differences (a) between seasons or years, (b) between reproductive classes of individuals, or (c) between forest and slash areas. No consistent differences were found for the same comparisons in the protein/calorie ratio of the stomach contents. The mean caloric value of 404 stomachs was 6.07 $\pm$ 0.52 kcal/g ash free dry weight.

Stomach contents showed seasonal trends in food items consumed. In winter tree seeds predominated; in summer months, berries. Arthropods and fungi occurred in the diet throughout the year although the presence of fungi diminished in winter. There was no correlation between the occurrence of food items and the onset or cessation of breeding.

Metabolic requirements in relation to reproductive state were estimated from Hayward's (1965a) formula. These were compared with the estimates of consumption rates in the wild. Because estimates of the energy costs of pregnancy and lactation approximated closely the estimates of energy consumed during winter, it was suggested that deermice may not be able to obtain sufficient energy requirements for pregnancy and lactation throughout the year. Because the utilization of protein is dependent on adequate caloric intake and because quality of protein intake, in terms of

amino acids present, was not measured in this study, it was not possible to show that deermice can obtain their protein requirements for reproduction at all times of the year.

In

memory

of

Laura

"The best laid schemes o' mice an' men gang aft a-gley"

Robert Burns

ACKNOWLEDGEMENTS

I would like to express my gratitude to the many persons whose assistance and cooperation made this project possible. In particular I wish to thank my senior supervisor, Dr. R. M. Sadleir, for providing the opportunity to undertake this study, and for his continued encouragement and assistance. I am also indebted to the other members of my supervisory committee, Dr. A. L. Turnbull, Dr. G. H. Geen and also Dr. S. Haven, who initially assisted on this committee.

I am grateful to Mr. G. G. Brett and Mr. G. J. van Eerten, and many other members of the staff of the Department of Biological Sciences, for tolerating the nuances of this particular graduate student. My appreciation is extended to Mr. J. Walters (Director), Mr. B. Webster (Assistant Director) and the staff of the University of British Columbia Research Forest at Haney, for their cooperation throughout the project.

To Bruce and Tish Petticrew and Keith Casperson I am especially indebted for their ever-ready help in the field and laboratory. The diverse assistance of Karen Liskop, Jim Carr and Nancy Wallace, and the photographic work of Ron Long, is also acknowledged. To my wife, Donna, who assisted in many aspects of the project and who typed this thesis, I am very grateful.

Finally, to *Peromyscus maniculatus*; my deepest thanks!

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Page

PREFACE

The white-footed deermouse, Peromyscus maniculatus, is one of the most ubiquitous of North American rodents, and is represented in British Columbia by several subspecies. Because of its widespread distribution and the ease with which it can be kept and bred in the laboratory it has been the subject of many investigations. The present study investigates the daily energy consumption of wild Peromyscus maniculatus austerus and examines whether energy requirements for reproduction can be met throughout the year.

Although Golley and his associates in Georgia, U.S.A., Grodziński and his associates in Poland, and other workers in the U.S.A. and Britain have investigated the energetics of small mammal species, little previous work has attempted to measure energy parameters in the wild. The present study is mainly field orientated and reports the first measurements of fecal production rates of wild Peromyscus.

Subsidiary aims of the study include the determination of the extent of daily and seasonal out of the nest activity, the effects of weather on this activity, and seasonal fluctuations in type and energy quality of the diet. Because this study was part of a cooperative project involving three other workers (Casperson, Petticrew and Sadleir) there were several

joint research aims and overlaps in the gathering and analysis of data. Joint aims involved in the present study include the effect of total energy consumption on seasonal and annual population fluctuations, and the protein/calorie intake, on the reproductive performance of the deermice.

Chapter I of this thesis is an analysis of data relating to out of the nest activity and various parameters affected by this activity. This is exclusively my own work. Chapter II is an analysis of stomach content and weight data, some consideration of stomach weights relative to activity having been undertaken in Chapter I, but expanded in this chapter to include autopsy data gained from snap-trapped mice collected over a three year period. The analysis involved the categorization of the mice into reproductive classes as described by Sadleir, Casperson and Harling (1973). Chapter II also contains a discussion of the energy content of feces and estimates of individual and population energy consumptions. Mean body weights and numbers of mice per ha used in the population consumption estimates were obtained from the data of Petticrew (1973). The basic data relating to mouse weights and population fluctuations were collected by the research group as a whole.

Information on energy consumption of P. maniculatus was

published in a joint paper (Sadleir et al., 1973). This paper is embodied in Chapter III of my thesis.

Appendix A, a description of a trapping technique developed for determining duration of out of the nest activity of the mice, has been previously published (Harling, 1971). Also previously published is Appendix B, a discussion of the occurrence of Endogone macrocarpa in the stomach contents of the mice (Harling and McClaren, 1970).

This thesis therefore represents a portion of a cooperative project which researched several aspects of the ecology of the deermouse in British Columbia, Canada.

CHAPTER I

Activity, Stomach Weight Changes and Defecation Rates

INTRODUCTION

A knowledge of activity patterns in populations of rodents is necessary to estimate physiological rhythms that are determined by time. In this study information on activity patterns was needed to estimate consumption and assimilation of energy in wild deermice (Peromyscus maniculatus austerus) as reported in Chapter II and Chapter III. A new technique (Harling, 1971) enabled mice to be captured and released at known times in the field, providing a basis for estimating activity patterns. In addition to monitoring timed occurrence of activity, this study measured fecal production rates and changes in stomach content weights with time.

Several previous studies of activity patterns of Peromyscus in the wild have been reviewed by Falls (1968). There is general agreement that deermice exhibit an endogenous circadian activity rhythm, with activity out of the nest being nocturnal. The nocturnal period extends approximately from one hour after sunset to one hour before dawn, the period being correspondingly longer, but perhaps less continuous, in winter than summer. There is also the suggestion of a bimodal pattern in activity and feeding intensity during longer nights.

Short term and seasonal weather conditions are also known to affect the extent and distribution of activity. In winter, particularly in northern latitudes, deermice may spend considerable time in a state of torpor (Stebbins, 1968), a condition which severely restricts extent of activity.

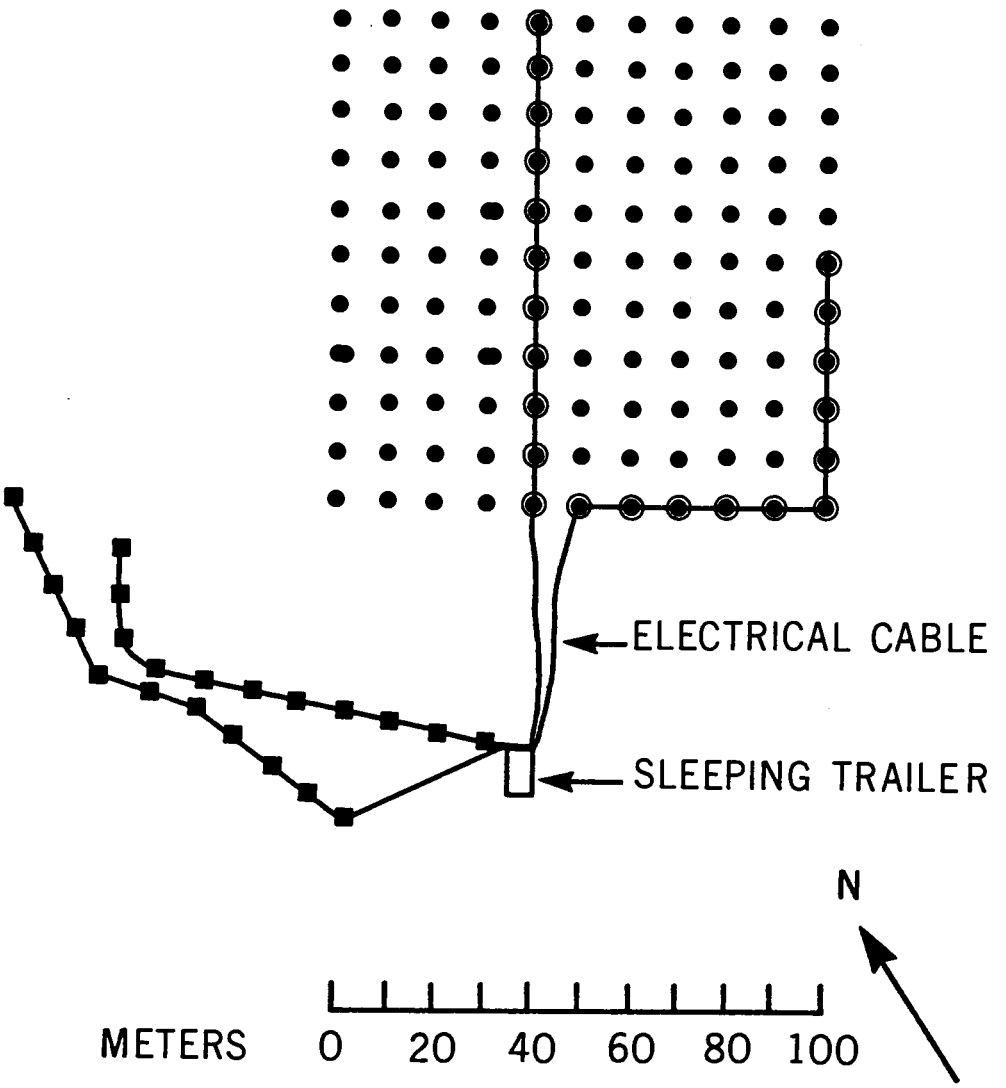
No studies of Peromyscus in the wild have reported variations in weight of stomach contents with time, or have measured fecal production rates during active periods. Only the elaborate laboratory experiments of Kavanau (1963, 1967) have monitored alimentary parameters and then only under conditions approximating a natural environment. Although it was not possible in the present study to measure activity parameters to the precision achieved by Kavanau, the data reported here were from deermice in their natural habitat that were only temporarily restrained in traps. Compared to Kavanau's studies therefore, these data may more accurately reflect variations of alimentary parameters experienced by wild rodents.

METHODS

Captures of deermice in the University of British Columbia Research Forest (Petticrew and Sadleir, 1970, 1973) were timed by using the technique described by Harling (1971). Initially, the method was used twice for 24 h periods in each of five months from February through June, 1970. This pilot study was carried out in two different areas north and east of the main study area described below. The technique also enabled the collection of other timed data relating to individual mice. Further data were subsequently collected during two consecutive 24 h trapping sessions in each month from September, 1970 through August, 1971 on trap lines (Fig. 1) on and near grid 2 of the live-trapping study (Petticrew and Sadleir, 1973).

From September, 1970 the first of the two consecutive 24 h trapping sessions was used to determine the time of captures and nocturnal changes in body weight of mice. Mice were handled as described by Sadleir (1965). A fecal sample for calorimetry was taken directly from the anus of each mouse and was frozen in a small vial for subsequent examination. An accurate recording of body weight was obtained by inserting the mouse into a plastic vial and weighing it, to the nearest 0.01 g, on an Ohaus M-5 portable field balance

Figure 1 - Map of grid 2 (Petticrew and Sadleir, 1973) showing location of electrical system trap sites.



● STANDARD LIVE TRAPPING GRID TRAP SITES

■ ELECTRICAL SYSTEM TRAP SITES

◉ TRAP SITES COMMON TO BOTH TECHNIQUES

(Ohaus Scale Corporation, Union, New Jersey, U.S.A.). Mice were released within minutes of their capture. On the second trapping session of each month timed distributions of captures and changes in body weight of the mice were again recorded. In addition the fecal production rates of individual mice were determined by collecting the feces produced by them whilst retained in traps for a minimum of one hour. Mouse chow pellets (Ralston Purina Company, St. Louis, Missouri, U.S.A.) were supplied in traps during this session.

During both sessions the location of each capture was noted so that the distance moved by individual mice between recaptures on the same night could be calculated. The shortest distances between successive capture points in a 24 h period were used in estimating distances moved. Summations of these distances for multiple captures of individual mice gave a minimum estimate of the total distance traversed per night for each of the mice. Meteorological conditions were recorded during trapping sessions.

Timed-capture data were treated in the following way. Captures and recaptures within each 24 h period were plotted against time of occurrence. The capture period of the total population for each month was taken as the length of time between the earliest and latest individual captures on the two

consecutive nights of that month. A comparison of the length of time between first and last capture for each month and the length of time between one hour after sunset and one hour before dawn was made. This comparison was made because previous workers (Falls, 1968) had suggested that nocturnal activity was limited to this time.

The time from first to last capture (t_i) of each individual mouse was calculated as a percentage of the total population capture period (t_p) in the respective month concerned ($t_i/t_p \times 100 = P_i$). These individual percentages (P_i) were then averaged for the whole year according to the number of captures made in the determination of t_i of each mouse (i.e. $P_i/3$ for 3 captures, $P_i/4$ for 4 captures, $P_i/5$ for 5 captures, etc.).

Because some authors (Golley, 1960 and Meese, 1971) have used mean stomach content weights in estimating consumption in wild mice I collected data on mean stomach content weights for comparative purposes. I also wished to determine the practicability of using mean stomach content weights in combination with rate of passage determinations in the wild to estimate consumption. Stomach content weights were determined by three methods. The first (Method A) involved the measurement of changes in body weight on the assumption

that the changes reflected primarily changes in stomach content weight. Body weight changes in each trapping session were calculated by taking the lowest recorded weight for the mouse that night as zero and rating other changes as increases in weight relative to it. The second (Method B) was a direct measurement of stomach content weights from individual mice trapped in the months February through June, 1970, and which had been selectively killed at known times of capture on specific nights. These mice were immediately frozen and kept until subsequent autopsy. Banks (1965) has shown that weights determined from frozen and thawed specimens of small mammals are almost identical to original capture weights. After autopsy stomach contents of these mice were removed, weighed wet, dried to constant weight at 100°C, and reweighed. The third (Method C) was also a direct measurement of stomach content weights. However these samples were from a dead-sample group which had been taken elsewhere in the same environment at unknown times of the night. They were processed in the same way described for Method B.

The fecal samples for calorimetry were thawed, weighed wet, dried to constant weight at 100°C, reweighed, and the percentage water content determined. The dried samples were burned in a microbomb calorimeter to determine their individual

caloric values, and percentage ash content. Duplicate samples were ashed at 600°C in a muffle furnace to check that complete combustion had occurred during bomb calorimetry.

Fecal production rates, measured between September and August, were determined by drying the collected feces to constant weight at 100°C and expressing the weight as mg feces/g mouse/h (based on live weight of mouse when fecal sample was taken). The percentage fecal water content could not be determined from the fecal production samples because of dehydration within the traps. The mean water content of the anal samples of the first session was used in each month to calculate wet weight production during the second session. The caloric and percentage ash values were also taken from session one in determining the dry weight caloric values of production in session two.

The total dry weight of feces produced by each of several representative mice, caught and retained in traps three or more times, was calculated by adding together the actual amounts of feces produced during each retention period of the respective mice.

RESULTS

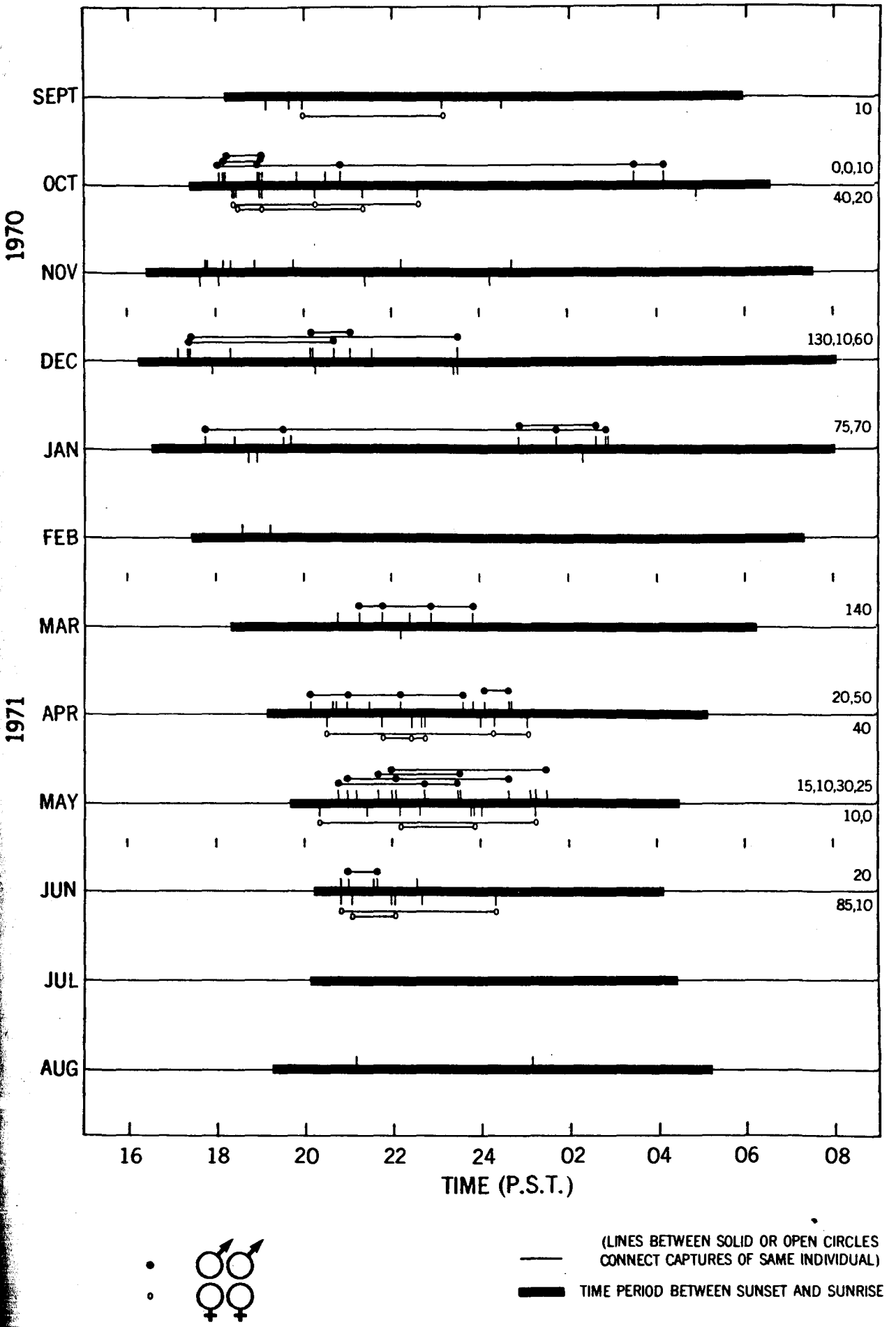
The times at which mice were captured during the hours of darkness during the first 24 h session (traps unbaited) of each month are shown in Fig. 2 and during each second 24 h (traps baited) session in Fig. 3. Because no mice were captured from 0800 - 1600 h these times were not included in these figures. The black horizontal bar indicates the time between sunset and sunrise. No deermice were captured during daylight hours.

The first capture of any night occurred about one hour after sunset, and the last capture about one hour before sunrise. A comparison of the length of time between first and last capture for each month and the length of time between one hour after sunset and one hour before dawn is presented in Table I.

Table II shows the mean length of time between first and last captures of individual mice, according to number of captures made, recorded as a percentage of the capture period of the population as a whole. Three mice each caught five or more times had a mean capture period of 82% of the total population capture period.

The minimum total distances moved in meters by individual mice in each trapping session are given in the right hand

Figure 2 - Distribution of captures in first 24 h trapping session of each month. The small vertical lines indicate individual captures. The solid (male) and open (female) circles joined by horizontal lines indicate recaptures of the same individual. The figures to the right are the minimum distances (in meters) moved by such animals.


1970
SEPT
10
OCT
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40,20
NOV
DEC
130,10,60
JAN
75,70
FEB
1971
MAR
140
APR
20,50
40
MAY
15,10,30,25
10,0
JUN
20
85,10
JUL
AUG
16
18
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22
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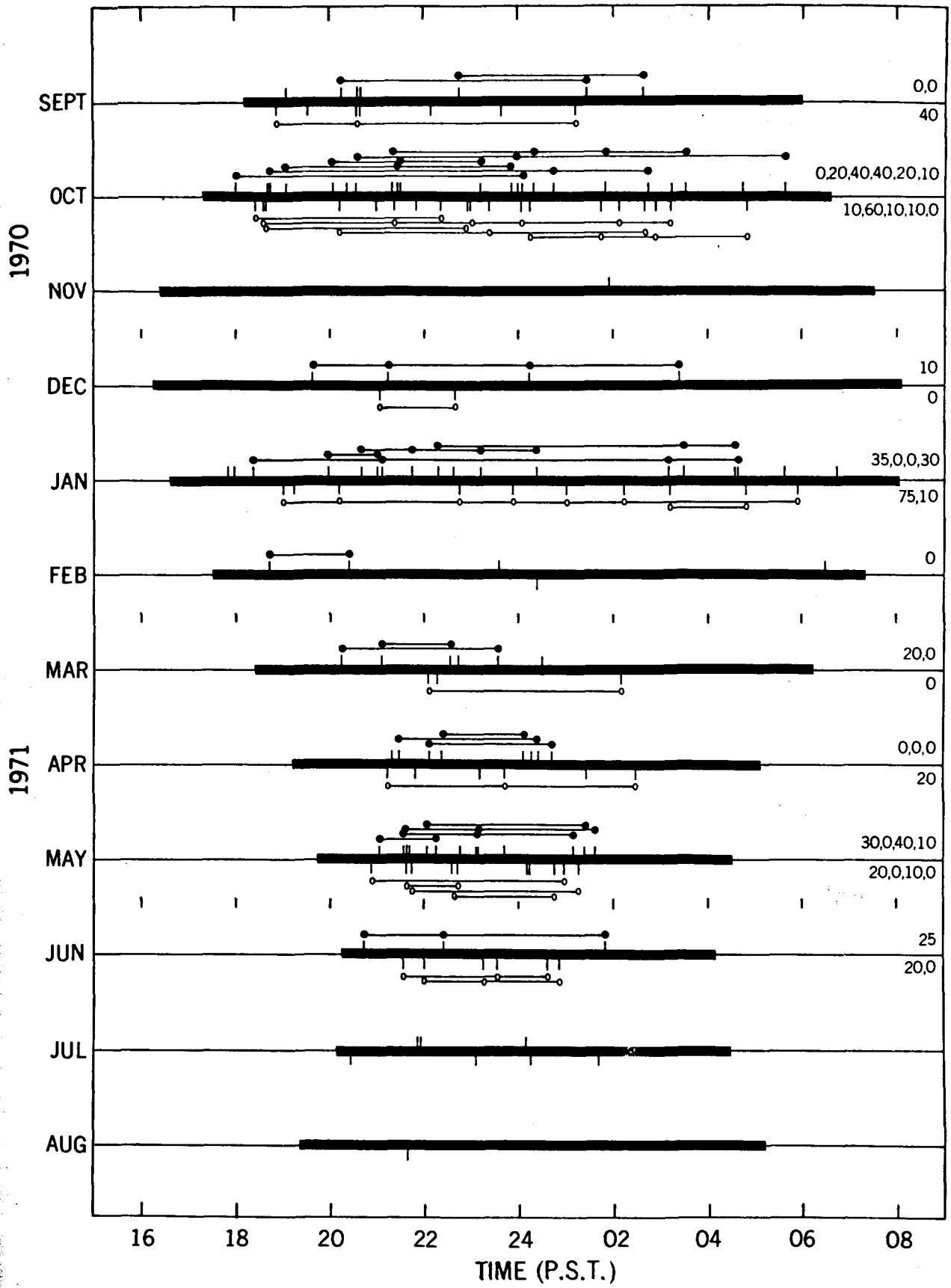
02
04
06
08
TIME (P.S.T.)
(LINES BETWEEN SOLID OR OPEN CIRCLES CONNECT CAPTURES OF SAME INDIVIDUAL)
TIME PERIOD BETWEEN SUNSET AND SUNRISE

Figure 3 - Distribution of captures in second 24 h trapping session of each month. Key as for Fig. 2.


SEPT
OCT
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1971
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40
0,20,40,40,20,10
10,60,10,10,0
10
0
35,0,0,30
75,10
0
20,0
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0,0,0
20
30,0,40,10
20,0,10,0
25
20,0
16
18
20
22
24
02
04
06
08
TIME (P.S.T.)
(LINES BETWEEN SOLID OR OPEN CIRCLES CONNECT CAPTURES OF SAME INDIVIDUAL)
TIME PERIOD BETWEEN SUNSET AND SUNRISE

TABLE I - Length of capture period of deermice per night.

	SEP (1970)	OCT	NOV	DEC	JAN (1971)	FEB	MAR	APR	MAY	JUN	JUL	AUG
(a) Time (minus two hours) in minutes from sunset to sunrise	570	675	780	840	780	720	600	495	405	345	375	450
(b) Time in minutes from first capture to last capture of mice	405	696	498	617	778	717	356	379	316	307	313	-
(b) expressed as a percentage of (a)	71	103	64	73	100	100	59	77	78	89	83	-

TABLE II - Mean length of time between first and last captures of individual mice caught more than once per night expressed as a percentage of the population capture period for the same nights.

Number of times captured		2	3	4	5	6	7
Mean capture period of mice as % of population capture period ($\bar{x}$ P_i)	Males	33	63	58	87	-	-
		(22)	(10)	(7)	(1)	-	-
	Females	45	55	40	-	75	84
		(14)	(9)	(1)	-	(1)	(1)

( ) Number in sample

columns of Figs. 2 and 3. Because mice could not usually be released during session 1 until approximately fifteen minutes after capture the total time available for movement was proportionately curtailed. In session 2 mice were retained in traps for periods of one hour so that the times available for movement were correspondingly shorter.

On night 1 in December (see Fig. 2) one mouse moved a minimum distance of 130 m in 55 minutes between release after first capture and its second capture. On night 1 in March (see Fig. 2) another individual moved a distance of 140 m between first and last capture, 120 m of which was between second and third captures. The 120 m were traversed in 58 minutes between release and recapture.

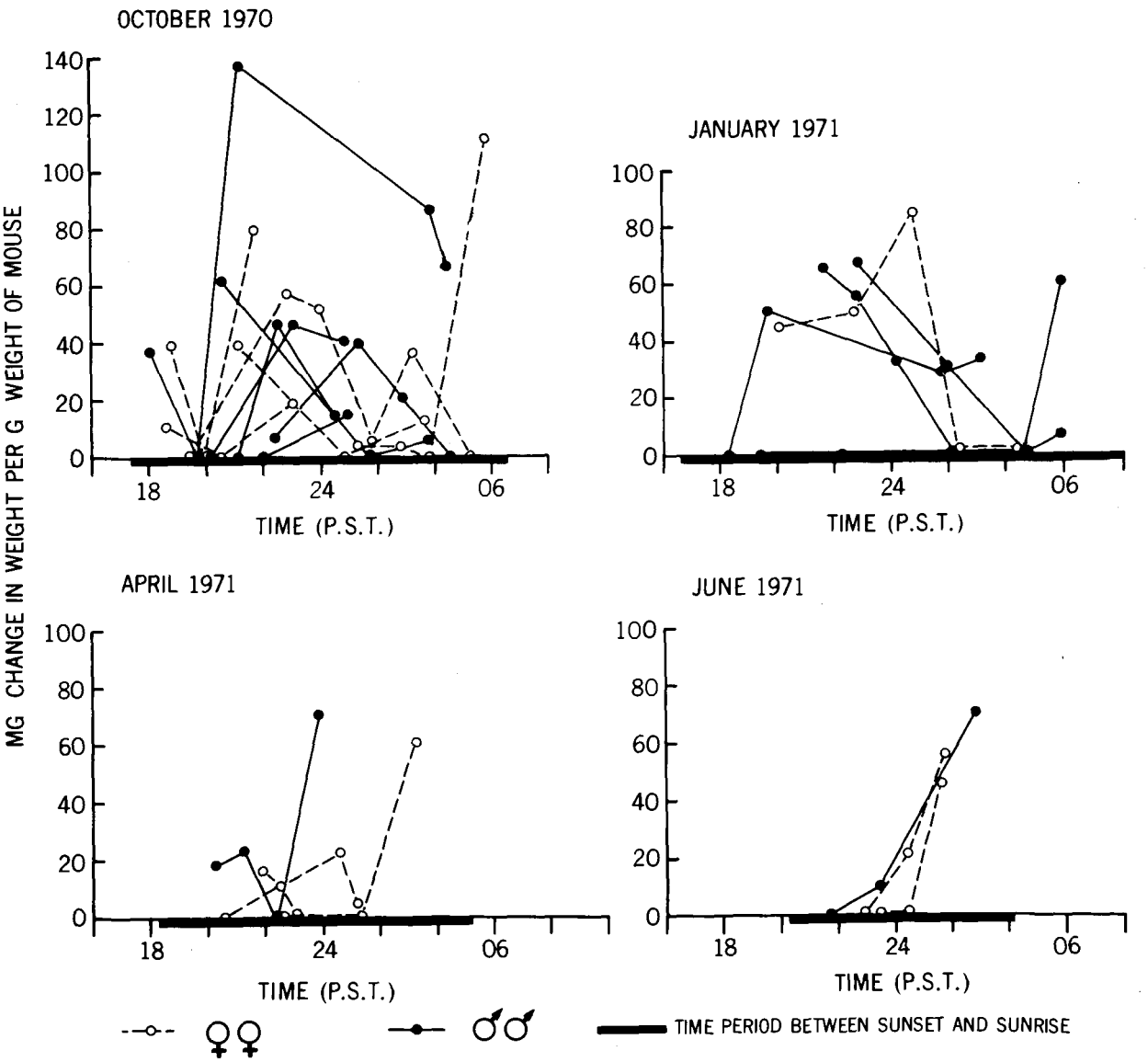
The occurrence of captures may have been influenced by the weather during trapping as the numbers of captures were generally higher on warm, dark nights. Trapping sessions in which such influences were suspected are shown in Table III.

Stomach content weights derived from body weight changes (Method A) were converted to change in weight (mg/g mouse) since previous capture, and plotted against the time at which each measurement was made (Fig. 4). Only those months where several individuals were frequently captured are shown. The mean change in weight, including zero values, was calculated

TABLE III - Trapping sessions during which weather conditions were particularly suspected to influence out of the nest activity.

Month	Trapping session	Weather	Number of individual mice captured	Total number of captures
OCT	1	Bright moonlight 2200-0300 h	9	20
	2	Overcast, showery, warmer than session 1	16	41
NOV	1	Snow falling after 2400 h	12	12
	2	Clear, cold, moonlight after 0230 h	1	1
DEC	1	Sleet turned to snow 2400 h	10	14
	2	Snowed heavily all night	2	6
JAN	1	Moonlight 2100-2400 h	7	12
	2	Overcast, only occasional moonlight	12	28
FEB	1)	Heavy rain after 2200 h	2	2
	2)		4	5
MAY	1	Rain showers after 0330 h	13	21
	2	Rain showers after 2400 h heavier after 0130 h	13	23
JUL	1)	Clear, moonlight after 0300 h,	0	0
	2)	Temp. 12^{o}-25^{o}C (daytime max. 32^{o}C)	7	7
AUG	1)	Overcast, heavy showers after	2	2
	2)	2400 h, Temp. 14^{o}-20^{o}C (daytime max. 21^{o}C)	1	1

Figure 4 - Individual body weight changes during four single nights. Lines join relative weight changes of the same individual deermouse.


OCTOBER 1970
JANUARY 1971
APRIL 1971
JUNE 1971
MG CHANGE IN WEIGHT PER G WEIGHT OF MOUSE
140
120
100
80
60
40
20
0
18
24
06
TIME (P.S.T.)
♀♀
♂♂
TIME PERIOD BETWEEN SUNSET AND SUNRISE

for all mice caught three or more times per session in each specific month. These results are given in Table IV. A frequency distribution of stomach wet weights derived from a large snap-trapped sample showed that this parameter was not normally distributed so that the usual statistical measures could not be applied. All stomach weight data were normalized by transforming stomach weights to their natural logarithms. The data in Table IV give the $\log_e$ means and their arithmetical values. Because the mice sampled in Method A were not killed it was impossible to determine if the lowest body weights recorded (included here as zero weights) actually reflected completely empty stomachs. In reality these zero weights may have represented stomachs with a portion of food in them. Because of this, the Method A "all samples" means, using zero values, may have given a biased estimate of the average stomach weight so these means were also calculated with zero values deleted.

The wet weights of stomach contents (Method B) were converted to mg/g mouse, the base weight for each mouse being its wet body weight minus the wet stomach content weight. These values were then plotted against time of capture (see Fig. 5) for each month (February through June, 1970). The mean wet weights per month for these mice, killed at known

TABLE IV - Mean monthly wet stomach content weights
(mg stomach content/g ± 1 S.D.).

			FEB (1970)	MAR	APR	MAY	JUN	OCT	DEC	JAN (1971)	MAR	APR	MAY	JUN
Timed captures live mice (Method A)•	All samples	1	-	-	-	-	-	6.27	6.50	6.01	6.48	5.58	5.95	5.12
		2	-	-	-	-	-	2.77	2.97	2.82	2.79	2.52	2.77	3.10
		3	-	-	-	-	-	4.3	5.3	3.5	6.2	1.9	3.2	1.8
		4	-	-	-	-	-	(40)	(4)	(21)	(4)	(13)	(12)	(9)
	Minus zero values	1	-	-	-	-	-	7.96	7.89	8.28	7.86	7.62	7.76	8.09
		2	-	-	-	-	-	1.03	1.23	0.49	0.14	0.89	0.82	0.81
		3	-	-	-	-	-	27.8	25.7	42.8	27.8	21.5	25.0	35.0
		4	-	-	-	-	-	(28)	(3)	(13)	(3)	(8)	(8)	(5)
Timed captures dead mice (Method B)		1	8.86	7.96	8.19	8.43	7.96	-	-	-	-	-	-	-
		2	0.73	0.98	0.55	0.21	0.63	-	-	-	-	-	-	-
		3	69.8	27.7	35.3	45.0	27.7	-	-	-	-	-	-	-
		4	(6)	(7)	(5)	(3)	(2)	-	-	-	-	-	-	-
Untimed captures snap-trapped dead mice (Method C)		1	8.47	8.07	8.17	8.21	7.37	8.21	8.09	7.97	8.26	8.72	8.41	8.66
		2	0.94	0.75	0.64	0.61	1.06	0.83	0.50	0.73	0.79	0.40	0.53	0.96
		3	46.9	30.9	34.2	35.7	14.8	35.6	31.6	28.0	37.4	60.3	43.9	56.5
		4	(17)	(11)	(10)	(11)	(7)	(21)	(43)	(30)	(19)	(6)	(20)	(20)

1 = Log_e (Wt. + 1) mg/100g; $\bar{x}$

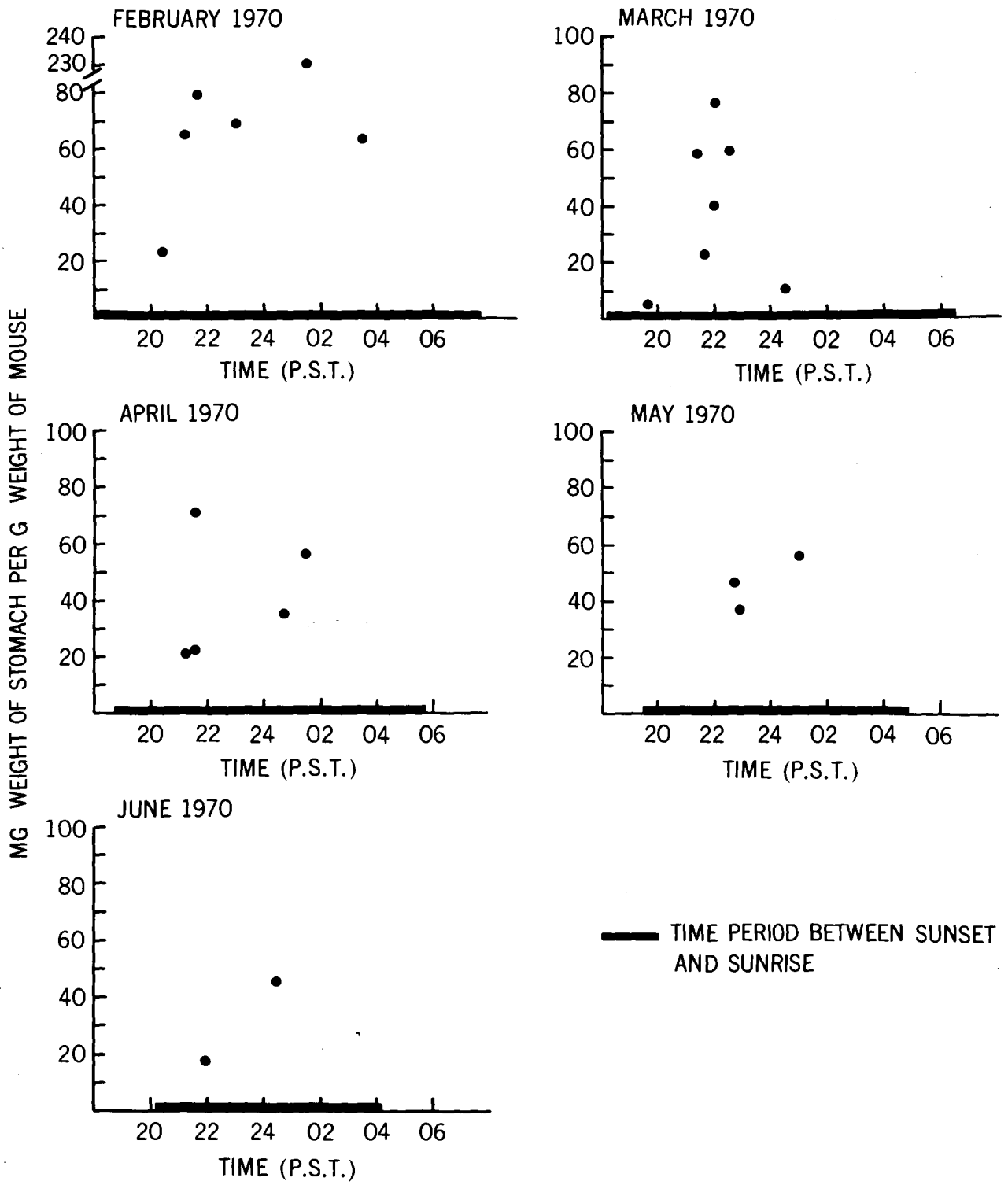
2 = Log_e value of ± 1 S.D.

3 = Wt., mg/g; $\bar{x}$

4 = Number in sample

• N.B. Based on body weight changes in consecutive captures of the same mouse

Figure 5 - Wet weights of stomach contents of mice killed at selective times of night in different months. Each dot represents a single stomach weight.


FEBRUARY 1970
MARCH 1970
APRIL 1970
MAY 1970
JUNE 1970
MG WEIGHT OF STOMACH PER G WEIGHT OF MOUSE
240
230
80
100
60
40
20
20 22 24 02 04 06
TIME (P.S.T.)
TIME PERIOD BETWEEN SUNSET AND SUNRISE

times (Method B), are given in Table IV where they can be compared with the mean wet weights derived from the untimed snap trap samples (Method C) and the mean body weight changes (Method A).

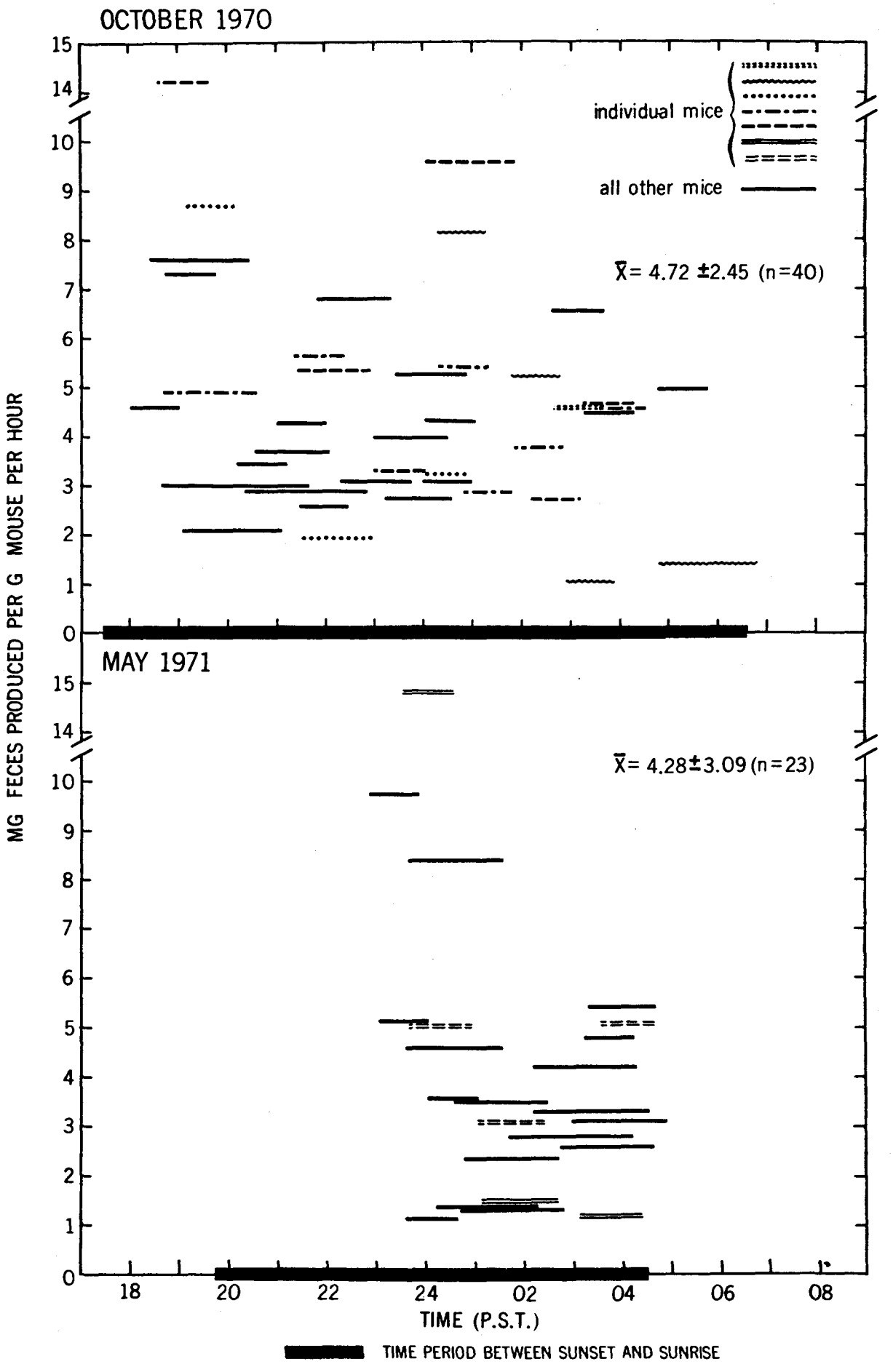
The mean hourly fecal production rates per g mouse for each month, and the mean percentage water contents, are given in Table V. None of the monthly mean fecal production rates was significantly different, at the 5% level ("t" test), from the overall mean production rate. The February fecal water content was significantly higher than the overall mean water content value ("t" test, t = 5.37). Mean fecal production rates of individual sex classes (Sadleir *et al.*, 1973) for October, 1970, a month in which there were recaptures of several individual mice, were tested ("t" test) against the month's overall mean to determine any significant deviation due to sexual condition. None of these was significantly different from the overall mean production rate ($\bar{x}$ 4.72 $\pm$ 2.48 mg/g mouse/h, n = 40) of the sex classes (lactating and/or pregnant, $\bar{x}$ 5.46 $\pm$ 3.51, n = 13, t = 0.67; non-vascular, non-lactating, $\bar{x}$ 4.87 $\pm$ 1.49, n = 6, t = 0.19; no discernible testes, $\bar{x}$ 4.23 $\pm$ 1.62, n = 21, t = 0.93). In October and May fecal production rates were plotted against time of occurrence (see Fig. 6) to determine the distribution patterns for

TABLE V - Mean monthly fecal production rates and % water content (± 1 S.D.)

	SEP (1970)	OCT	NOV	DEC	JAN (1971)	FEB	MAR	APR	MAY	JUN	JUL	AUG	Overall Annual Value
Fecal production rate (mg feces dry weight/ g animal /h)	5.23 ±2.27 (14)	4.72 ±2.48 (40)	4.85 - (1)	4.01 ±1.15 (6)	5.37 ±2.84 (27)	4.02 ±1.27 (4)	4.94 ±1.38 (9)	5.55 ±2.08 (13)	4.28 ±3.08 (23)	4.13 ±2.72 (9)	5.39 ±4.25 (7)	4.77 - (1)	4.86 ±2.59 (153)
% water content of feces	69.0 ±7.7 (4)	71.0 ±5.0 (18)	69.5 ±4.9 (6)	75.0 ±5.0 (12)	75.5 ±4.9 (12)	80.7 ±2.39 (4)	70.7 ±11.5 (7)	71.9 ±5.9 (18)	73.9 ±8.7 (21)	71.3 ±5.4 (11)	- - (-)	69.9 ±4.9 (2)	72.8 ±6.9 (115)
Fecal production rate (mg feces wet weight/ g animal /h)	16.87	16.28	15.93*	16.04	21.92	20.83	16.86	19.75	16.40	14.39	19.82†	17.87△	17.87

* Overall mean fecal production rate value used
† Overall mean % water content substituted
△ Overall mean value substituted
( ) Number in sample

Figure 6 - Fecal production rates of individual mice in October, 1970 and May, 1970. The horizontal lines span the time of restraint in the traps, and their distance above the Y axis, the fecal production rate.


OCTOBER 1970
individual mice
all other mice
$\bar{X}$= 4.72 ±2.45 (n=40)
MAY 1971
$\bar{X}$= 4.28±3.09 (n=23)
MG FECES PRODUCED PER G MOUSE PER HOUR
TIME (P.S.T.)
18
20
22
24
02
04
06
08
TIME PERIOD BETWEEN SUNSET AND SUNRISE

specific individuals and for the captured population as a whole. These two months were selected because determinations had been made on many individual mice.

Mean monthly caloric and ash values of feces are given in Table VI. Several significant differences were noted when the monthly caloric means were compared with the annual mean but the means fluctuated without any overt seasonal trends being obvious. Only the December, 1970 ash value was significantly different from the overall mean ash figure.

Summarized data relating to fecal production by six individual mice is given in Table VII.

TABLE VI - Mean monthly caloric and ash % values of feces (± 1 S.D.)

	SEP (1970)	OCT	NOV	DEC	JAN (1971)	FEB	MAR	APR	MAY	JUN	JUL	AUG	Overall Values Sep - Aug
kcal/g feces (ash free dry weight)	5.52 ±0.17 (4)	5.28 ±0.65 (14)	5.88 ±0.36 (5)	4.90 ±0.34 (12)	4.85 ±0.43 (11)	4.39 ±0.26 (3)	5.40 ±0.79 (6)	5.07 ±0.60 (18)	5.35 ±0.54 (20)	5.32 ±0.42 (10)	6.06 ±0.52 (3)	5.47 - (2)	5.22 ±0.59 (108)
% ash content feces	13.00 ±5.37 (4)	16.95 ±7.23 (15)	20.13 ±10.43 (5)	18.38 ±1.76 (12)	13.69 ±7.76 (11)	14.41 ±6.75 (4)	19.76 ±7.60 (6)	12.22 ±9.54 (18)	12.18 ±5.55 (19)	12.33 ±4.85 (11)	22.73 ±0.88 (3)	18.45 - (2)	14.97 ±7.25 (110)
kcal/g feces (dry weight)	4.80	4.39	4.70	4.00	4.19	4.44*	4.33	4.45	4.70	4.66	4.44*	4.44*	4.44

* Overall mean value substituted

( )Number in sample

TABLE VII - Summarized fecal production data for several individual mice.

Month & Year	OCT 1970		JAN 1971	JUNE 1971		
	♀	♂	♀	♀	♀	♂
Sex and condition	preg? lactating	no discernible testes	non-vascular non-lactating	preg? lactating	vascular non-lactating	large testes
Number of times captured	6	4	7	3	3	3
(a) Total time (mins.) retained in traps	440	240	577	180	231	182
(b) Capture period (mins.) of total population for this night*	675	675	780	345	345	345
(a) as % of (b)	65.2	35.6	74.0	52.2	67.0	52.8
Mean weight of mouse (g)	19.48	15.05	20.67	20.40	17.27	20.53
Total dry weight (mg) of feces produced by this mouse in time period (a) above	978	294	875	344	153	288

* Values taken from Table I

DISCUSSION

The data presented in this chapter are consistent with the presence of a circadian rhythm in Peromyscus maniculatus, activity being nocturnal and recommencing approximately 24 h after the commencement of the previous active period.

Except for July and August, when there were few captures, Figs. 2 and 3 indicate a strong pattern of nocturnal activity. It should be reemphasized that the live traps functioned during the daylight period between session 1 and 2 in each month and no deermice were trapped during this period. The capture period represents the maximum length of time of the activity period of the mice. Evidence of a nocturnal active period in Peromyscus has been well documented (Falls, 1968) as has the role of light as its effective zeitgeber (Ashby, 1972). A similar nocturnal activity pattern is found in Apodemus (Miller, 1955; Brown, 1956 and Kikkawa, 1964) a species with which Peromyscus is often compared.

Captures usually commenced approximately one hour after sunset and ceased no later than one hour before dawn; Table I shows that this is the time of capture prevailing for a period of several months. The periods of activity during other months, and on several nights in particular (see Figs. 2 and 3), may have been affected by prevailing weather conditions which

will be discussed in more detail later. There was no apparent difference in capture periods of the males and females (see Figs. 2 and 3). However Hawes and Hawes (Harling, 1971) caught pregnant and lactating females during the daytime in July in the same field area. The significance of this observation is discussed in Sadleir et al. (1973).

Very few studies have monitored Peromyscus activity completely in the wild, and those which have did not usually gather data on the timed activity periods of individual mice. Probably the best laboratory studies, being those in which the mice were allowed some control over their environment, were conducted by Kavanau (1962, 1963, 1966, 1967) and Brant and Kavanau (1965). Falls (1953) timed the departures and returns, in June and July, of four Peromyscus maniculatus bairdi from a nest on a beach, using an electric eye. The average first departures occurred 52 minutes after sunset and the last returns averaged 65 minutes before sunrise. Behney (1936), using enclosure cages from November through February, found that Peromyscus was most active from one half hour after sunset until about one hour before sunrise. Kavanau (1963, 1967) reported similar periods of activity in laboratory deermice. This evidence supports the previous conclusions of Harling (1971) and Sadleir et al. (1973). However, attention

is drawn to the subsequent analysis of data presented in Table II. Although the trap lines effectively sampled the total population of mice in the area, they were not spread extensively enough to regularly capture all the mice at large (Petticrew and Sadleir, 1970). Mice which were caught repeatedly were probably active most of their time in home ranges which were adequately sampled by the trap lines. Individual mice caught five or more times were caught 82% of the time of the population as a whole. It is probable that the home ranges of mice caught less frequently only bordered on the area sampled by the trap lines so that mice caught fewer than five times each rarely exceeded a mean total capture time of 55% of the length of capture times of the population as a whole. Data from animals captured frequently therefore give a more reasonable indication of the active periods of individual mice.

It is not known if the mice were continuously out of the nest over the time periods mentioned above but several other investigations indicate that Peromyscus spends continuous extensive time periods out of the nest. Falls (1968) cited studies indicating that Peromyscus probably is active during most of the time between one hour after sunset and one hour before dawn, with the length of activity out of the nest

being correspondingly longer but less continuous in winter than in summer. He also quoted several studies which suggested the presence of a bimodal pattern of activity during long nights and a single peak during short nights. During long nights the first peaks in activity occurred between sunset and midnight with a second peak just before dawn. In the present study most mice which were subsequently recaptured in any given night were initially captured soon after one hour following sunset. Thus the peak of captures was about this time.

Part of the interval between captures of individual mice was spent in movements over the trapping area, as can be discerned from the right hand columns of Figs. 2 and 3. The two individuals that each travelled over 100 m within one hour would probably not have much time to be inactive in their nests. As mentioned earlier, these distances are minimum distances moved. To monitor any exact movements would have required the use of techniques similar to those reported by Graham and Ambrose (1967) and Jahoda (1972). The use of radio telemeters as described by Rawson and Hartline (1964) for 25 g P. m. gracilis is not yet practical for P. m. austerus as the smallest transmitters presently available weigh about 1.5 g and are too large for realistic use in this 15-20 g

species.

The fact that Peromyscus moves considerable distances in a single night has been reported by Howard (1949), and others (see Falls, 1968). Particularly during dispersal, deermice are known to move long distances. The two mice reported above were not dispersing; they were previously, and subsequently, caught in the same general areas.

The energetic costs of such activity in wintertime would be high. The mouse trapped in December traversed 130 m while sleet was falling and the ground surface temperature was 0°C. Stebbins (1968) has discussed the function of torpor in overwintering Peromyscus; at the latitude of southern B.C., and in the coastal area, it seems unlikely that mice were spending a great deal of time in a torpid condition. Regular and abundant captures were made even in the coldest winter months. Petticrew (1973) has evidence of some torpor in the same trapping area but only occasionally, and only if mice had been retained in traps overnight in wintertime.

The mice in the present study predominantly ate tree seeds (Chapter II) in the winter months which entails more

extensive searching for new seed sources than the more varied and presumably more abundant food in the diet of summer. No heavy seedfall occurred during this study so that feeding on seeds necessitated extensive searching. It was likely that Endogone and other fungi, which were also food sources for Peromyscus, occurred infrequently during the period of low ground temperatures of winter months; very little was found in stomach contents of deermice at such times (Harling and McClaren, 1970). Endogone, however, is more readily available in summer months, as are the various arthropods eaten by Peromyscus, and allow the mice to obtain their required food in a shorter time period than in winter.

Seed storage may have alleviated some of the need for constant nocturnal searching but it is probable that large seed stores could only be built up at times of seed abundance. The mice may be able to cope with periods when activity out of the nest is restricted because of cold weather by utilizing stores of body fat as suggested by Caldwell and Connell (1968) although such reserves could only be tapped infrequently.

As previously mentioned, prevailing weather conditions may have affected the frequency of captures during several of the trapping sessions. Moonlight, varying ambient temperatures, and heavy rainfall are known to influence the extent

of the nocturnal activity of deermice (Falls, 1968). Gentry, Golley and McGinnis (1966) reported that the weather on the night of trapping had a greater effect on captures than the weather of the previous night. Several authors have commented on the effect of moonlight (Pruitt, 1959; Kavanau, 1966, 1967; Caldwell and Connell, 1968 and Falls, 1968) with the general conclusion being that increased illumination leads to a diminution of activity. Falls (1968) in comparing the results of Blair (1943) and Stinson (1952) with his own observations, suggested that moonlight may not have been as influential in reducing activity in shaded or densely vegetated areas. In this study the number of captures of deermice always dropped on bright moonlight nights indicating reduced activity out of the nest. The trapping was conducted in a logged-over area with very little cover. In the present study captures were notably less frequent on nights of moonlight such as occurred in October, November, January and July.

The effects of temperature on activity are complex. Temperature effects are linked with those of humidity, and if it is windy or dry those of evaporation as well. Falls (1968), summarizing the work of several authors, suggested that activity was greatest at intermediate temperatures with the effects of

humidity being variable.

In the present study reduced activity in terms of captures made, was observed on night 2 in November (see Table III) and Fig. 3) during the coldest trapping session; the ground surface temperature remaining around -6.5°C. The opposite situation, high temperatures during both night and day, may have decreased activity in July and August (Table III). These results tend to confirm the conclusions of Falls (1968).

Rainfall affects deermice captures when it becomes heavy or falls mainly before midnight (Falls, 1968). Light rain is associated with increased catches (Gentry and Odum, 1957) but this may be due primarily to the presence of cloud, and hence darker conditions that prevail at such times. In this study heavy rainfall probably decreased activity on both nights in February and intermittently on both nights in August.

Snow may affect activity in several ways. Heavy snowfall which remains on the ground for long periods of time may provide conditions in which deermice can be active in a subnivean environment of the type described by Pruitt (1958) and Coulianos and Johnels (1962). Snowfall which produces only a shallow cover on the ground may restrict mouse movements to well-defined trails under logs or other protective cover (Beer, 1961), and probably had such an effect in

November and December of the present study although such effects could not be separated from those of low temperatures. Heavy snow showers, like heavy rainfall, may inhibit mouse activity and were probably responsible, coupled with other factors mentioned above, for the diminished activity of November and December (see Table III).

Optimum conditions for activity occur when nights are warm, humid and moonless or cloudy with light rain. Such conditions were coincident with high frequency of captures during the second night in October and during the first night, and most of the second night, in May (see Table III).

The body weight changes shown in Fig. 4 were primarily a function of changes due to a filling and emptying of the stomach. Alterations in weight caused by urination and defecation, although of some importance, were probably of a lower order than is represented in this figure. Drinking may also have produced changes in body weight but variable water intake would have altered the percentage hydration of stomach contents. However, the average percentage water content of stomachs from autopsied deermice in different months remained fairly constant at 70%. The changes in body weight are considered to approximate the actual fluctuations in stomach contents with time. Stomachs of snap-trapped

"dead sample" mice (Method C, Table IV) were very rarely empty but for the body weight changes (Method A) several zero recordings of weight changes were made in each month. It was presumed that zero weight changes of mice did not necessarily represent an empty stomach but probably already represented stomach content weights of approximately 20 mg (see lowest weights recorded in Fig. 5). Mean weights of stomach contents were similar in some months as determined by the different methods, but this may have been purely coincidental, particularly considering some of the small sample sizes. Recording body weight changes (Method A), based on these meagre data, is not a reliable indicator of stomach content weights.

The relative changes in weight of some individual mice were of interest. The weights did not rise to a certain level and then remain static (see Fig. 4). In the four months represented there was an indication of initially low weights rising to variable weights later in the night.

The stomach contents removed from mice killed at selected times (see Fig. 5) were usually low in weight at the beginning of the night but subsequent weight changes were variable. More data of this type could not be collected because kill samples depleted the population until virtually no captures were made on a third trapping session in these months. There

was no significant difference ($p < 0.05$) between the stomach weights of these samples and the snap trap samples obtained elsewhere in the same environment, in the months of February, March and April when sample sizes were reasonably large. Because these samples were thus presumed to be from an identical population, the snap trap samples (Table IV) were probably taken at a similar range of capture times to the activity line samples. If they were not, i.e. if all dead samples were taken at the beginning of the night, then the mean weights would be lower because stomachs tended to be emptier at this time of night.

Because mice were rarely caught with what were considered to be full stomachs (see Chapter II) it appeared that most nocturnal activity was being monitored while mice were still searching for food. Practically all mice captured for the first time had lower stomach weights than occurred at subsequent captures. This suggests that the earlier captures were of hungry active mice which would be more likely to enter a trap. Consequently as the stomachs filled fewer mice may have been captured which would therefore have caused a bias in the determination of stomach content weights.

Attempts were made in the field to record the rate of passage of food items through Peromyscus by feeding captured

mice coloured food pellets and subsequently determining the period of time until coloured feces were produced. Sustained retention in traps would have reduced the reliability of measuring rate of passage in active deermice so they were released with the hope that subsequent captures would be frequent enough to record the duration of time over which coloured feces were produced. This technique did not succeed because of irregularity of captures and hence no reliable estimates of rate of passage could be made. Instead fecal production rates measured in the field were utilized in estimating consumption.

I have found no mention in the literature of fecal production rates being previously measured in wild rodents. The rates determined in this study were considerably higher than those observed in laboratory studies conducted at the same time. I have since found that mice reared in the laboratory and retained in traps for hourly nocturnal periods at laboratory temperature (25°C) produced approximately 40% less feces than mice which were reared in outdoor cages and retained in traps outside at 3°C in February. Although the outdoor-reared mice produced less feces than their wild counterparts, this could probably be attributed to a higher metabolic rate as a function of the need to be more active in the natural environment.

The mean fecal production rates, per hour, in any month did not differ significantly from the overall annual mean production value (see Table V), and neither did means of individual sex classes differ from their overall mean. However, the rates per hour, measured for specific individuals, varied considerably depending on the time of night (see Fig. 6). No consistent fecal rate per hour could be applied throughout any given night. Caloric values, water contents, and ash contents of feces were also variable (see Tables V and VI). The total caloric value of feces produced per night (see Table VII) was determined by the hourly rate of fecal production and not by variations in caloric value, and ash or water content.

Table VII shows the fecal production during the time retained in traps for certain individual mice. Because these mice had digestibility coefficients of approximately 87% (Sadleir et al., 1973) the amount which they consumed must have been in the order of eight times the fecal production weight. This would mean that the October lactating female whose fecal production whilst retained in traps was almost 1.0 g required an intake of approximately 8.0 g dry weight of food to produce this amount of feces. As reported earlier individual mice were on average active 82% of the time that

the total population was active. The October female was retained in traps for 65% of the total population time for that month; its total fecal production and total consumption must thus have been considerably higher.

Similar calculations on the October male (see Table VII) reveal that its metabolic costs were lower than for the female, reflecting the extra demands of the female's heavier weight and reproductive condition. The January female would have high metabolic costs because of her weight and the low ambient temperature conditions of that month.

The June vascular female produced less total feces whilst retained in traps than the individual totals of the two other June mice. Her lower body weight and sexual condition probably imposed lower metabolic demands than for the other June mice.

These results indicate that P. maniculatus had high metabolic costs in the wild when breeding late in the year or when active most of the night in winter.

CHAPTER II

Feeding Habits, Stomach Weights and Calories, and Population Energy Consumption Estimates

INTRODUCTION

The food items occurring in the stomachs of wild small rodents have often been studied (Dyke, 1971; Holisova, 1967; Jameson, 1952; Watts, 1968; Williams, 1959). The relationship between food items and their energetic values has also been well documented (Drożdż, 1966, 1968a; Grodziński and Sawicka-Kapusta, 1970). Some investigations have attempted to determine the energy flow through wild populations of small rodents. These are largely based on field determinations of population numbers and body weights (related to sexual condition) with extrapolations being made to the field situation from laboratory studies of other parameters, e.g. food consumption and metabolic rates (Golley, 1960; Grodziński, Bobek, Drożdż and Górecki, 1970).

The present study determined several of the above parameters for Peromyscus maniculatus austerus, the deermouse. In addition this study was designed to determine with more precision the energy consumption of wild deermice. This was accomplished, in part, by determining wild fecal production rates, and, knowing the approximate assimilation efficiencies,

predicting the necessary consumption required to balance this observed fecal production. Individual consumption estimates could then be estimated for a variety of seasonally occurring reproductive classes represented in the wild population; a more extensive interpretation of these results is given in Chapter III.

The present chapter reports the monthly mean mouse consumption values and monthly mean population (per ha) consumption values. In determining these values, habitat type was also considered; mice having been trapped in both mature forest and cut over (slash) areas. An analysis was made of the seasonal occurrence of food items consumed. The wet and dry weights of stomach contents were analyzed in relation to seasonal occurrence and the total amount of food required to meet metabolic requirements was estimated.

METHODS

The study was carried out in the University of British Columbia Research Forest at Haney, B.C., a coastal rain forest. Samples of deermice taken for autopsy were collected as reported in Sadleir et al. (1973). Food items occurring in slide preparations of a subsample of stomach contents (Harling and McClaren, 1970, Sadleir et al., 1973) were checked against a reference collection of vegetation samples collected from the sampling areas.

Wet weights of stomach contents from autopsied mice were grouped according to month of collection and categories of reproductive condition. The wet weights of stomach contents were not normally distributed, so each value was replaced by its $\log_e$ value which produced a normal distribution. They were calculated on a mg wet weight per g mouse basis (i.e. "relative weights"), the original total weight of a mouse being considered as its body wet weight minus the stomach content wet weight. The "absolute wet weights" (i.e. wet weight per whole mouse) of stomach contents were also calculated for each reproductive category.

The subsample for food item analysis was taken from the stomach contents before the remainder was dried and therefore the total dry weight of each stomach could not be directly

determined. It was derived instead from the known wet weight of the complete contents and the water content of the portion remaining after the food item subsample had been taken. The percentage water content was calculated by drying the remaining stomach content sample to constant weight at 100°C.

Live-trapping methods were as reported by Petticrew and Sadleir (1973). Some of their data (estimates of monthly populations per ha and mean monthly body weights) were utilized in the present study in calculating individual 24 h consumption and caloric consumption of the total population of deermice per ha per 24 h.

RESULTS

The frequency of occurrence in stomach contents of food items is shown in Fig. 7. Arthropod fragments (elytra, legs and larval stages) and annelid parts (small oligochaete sp.) occurred in stomachs at all times of the year except in December, 1970. Fungi, mainly Endogone sp. (Appendix B) occurred least frequently in the early months of any year. Green vegetation (leaves and stems) was found infrequently and usually only in spring. Berries (red and blue huckleberries (Vaccinium parvifolium and V. ovalifolium), salmonberries (Rubus spectabilis) and ground blackberry (Rubus ursinus)) occurred exclusively in summer and early fall months, and the presence of any berry species corresponded closely to its observable occurrence in the wild. Tree seeds (seed coats and endosperm of Douglas fir (Pseudotsuga menziesii), western hemlock (Tsuga heterophylla) and western red cedar (Thuja plicata)) were represented in samples from winter months, when they composed a major part of the diet.

Figure 8 shows the highly skewed distribution of the wet weights of all stomachs collected (n = 665). Table VIII shows the monthly mean wet weights ($\log_e \bar{x}$ and equivalent arithmetic $\bar{x}$), percentage water content, and dry weights of stomach contents. The stomach content weights were extremely

Figure 7 - Frequency of occurrence of major food items in stomach contents of deermice.

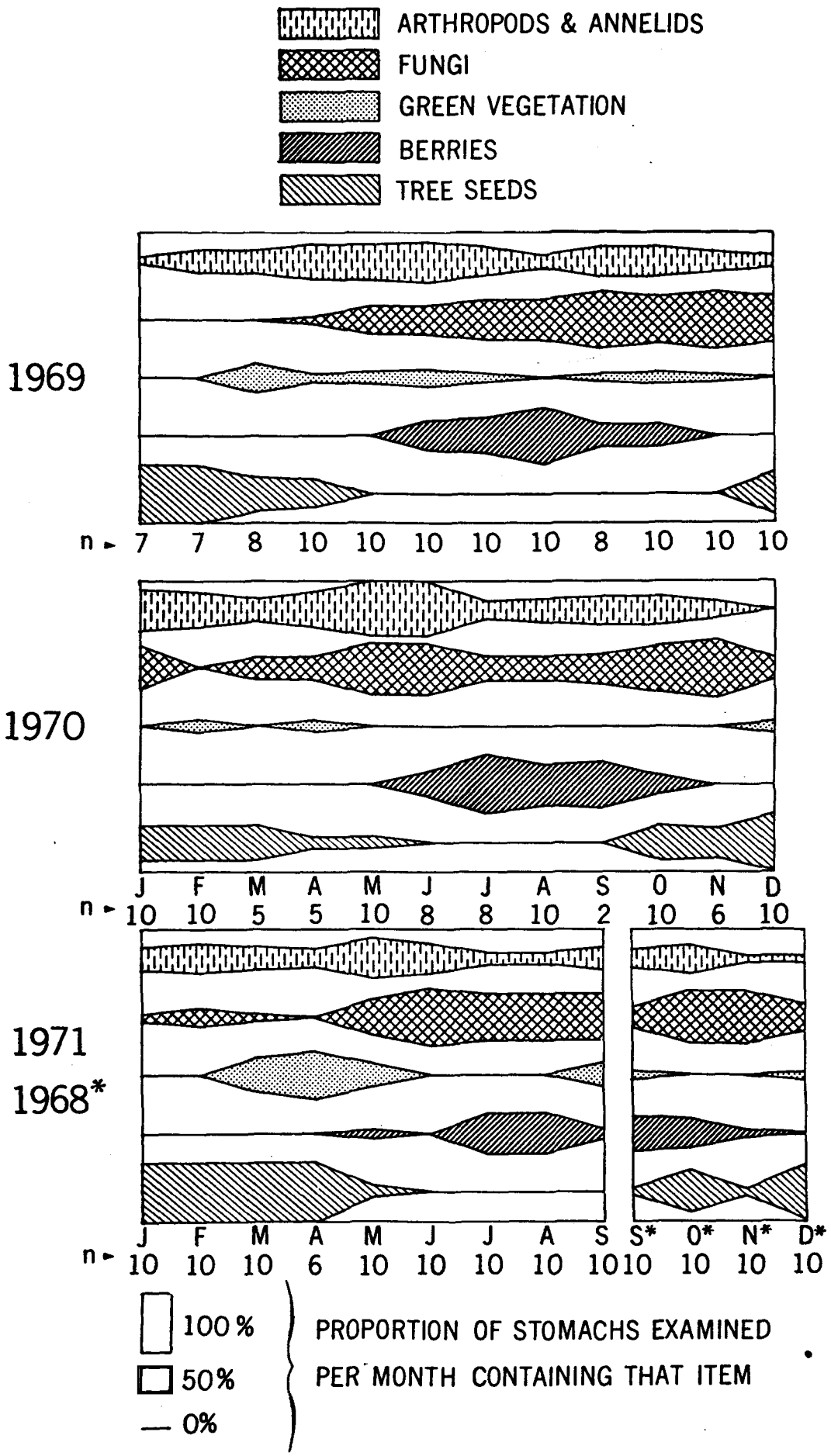

ARTHROPODS & ANNELIDS
FUNGI
GREEN VEGETATION
BERRIES
TREE SEEDS
1969
n ► 7 7 8 10 10 10 10 10 8 10 10 10
1970
J F M A M J J A S O N D
n ► 10 10 5 5 10 8 8 10 2 10 6 10
1971
1968*
J F M A M J J A S S* O* N* D*
n ► 10 10 10 6 10 10 10 10 10 10 10 10 10
100 %
50%
— 0%
PROPORTION OF STOMACHS EXAMINED
PER MONTH CONTAINING THAT ITEM

Figure 8 - Histogram of distribution of wet weights of all stomachs collected.

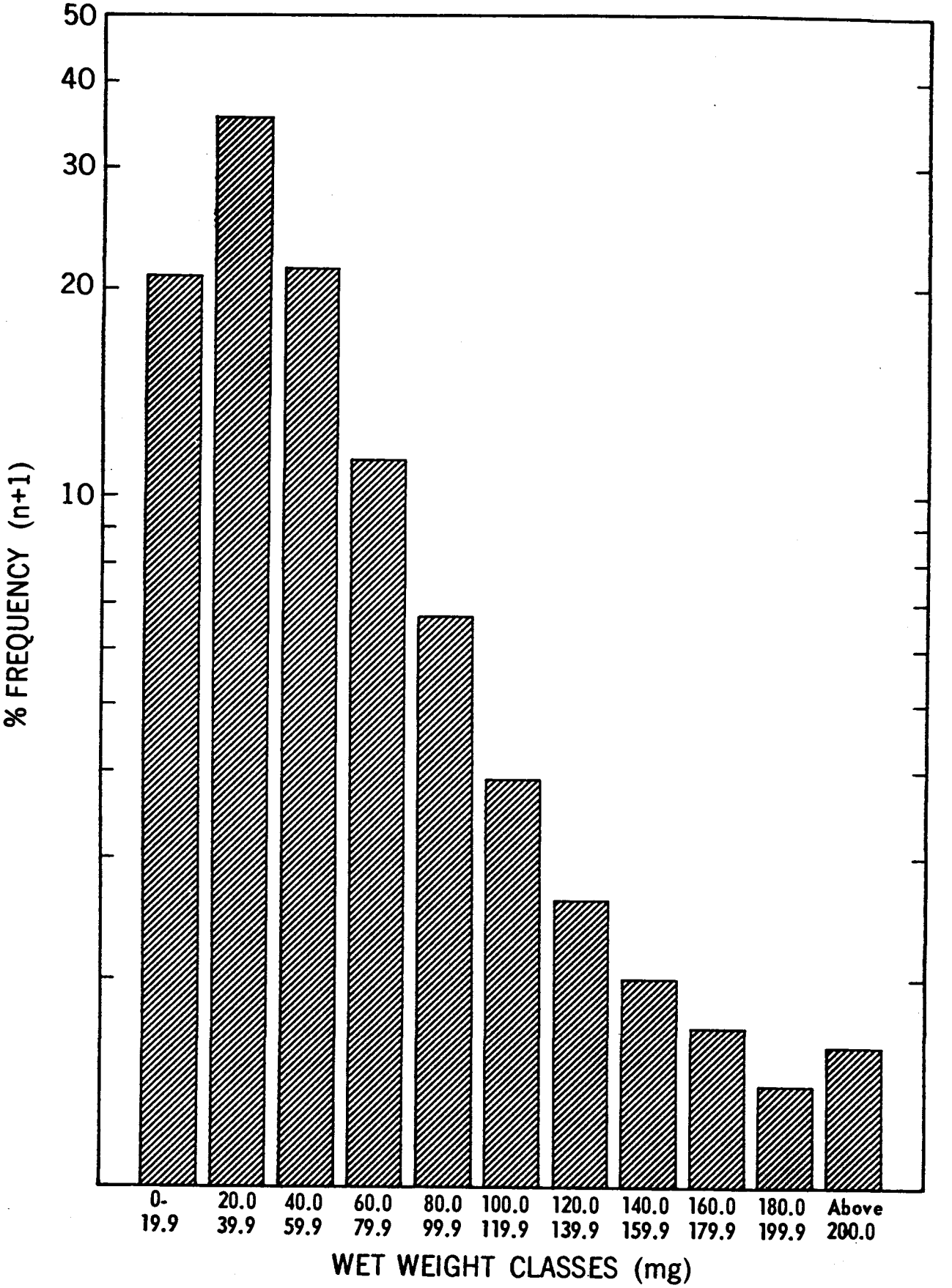

50
40
30
20
10
% FREQUENCY (n+1)
0-
19.9
20.0
39.9
40.0
59.9
60.0
79.9
80.0
99.9
100.0
119.9
120.0
139.9
140.0
159.9
160.0
179.9
180.0
199.9
Above
200.0
WET WEIGHT CLASSES (mg)

TABLE VIII - Monthly mean wet weights ($\log_e \bar{x} \pm 1$ S.D. and arithmetic equivalent), mean percentage water composition and mean dry weights of stomach contents.

			JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1969	Wet weight	1	8.11	8.74	8.01	7.75	8.12	8.26	8.31	8.03	8.37	8.30	8.49	8.49
		2	0.60	0.80	0.57	0.67	0.64	0.82	0.58	0.72	0.65	1.01	0.84	0.78
		3	(10)	(10)	(30)	(17)	(26)	(29)	(25)	(24)	(11)	(21)	(12)	(12)
		4	33.2	62.4	30.2	23.3	33.6	38.7	40.7	30.7	43.3	40.2	48.5	48.5
	% water		63.0	62.0	76.0	75.0	78.0	75.0	77.0	73.0	72.0	74.0	82.0	76.0
	Dry weight		12.3	23.7	7.2	5.8	7.4	9.7	9.4	8.3	12.1	10.5	8.7	11.6
1970	Wet weight	1	8.33	8.47	8.07	8.17	8.21	7.37	7.84	7.69	7.57	8.21	8.21	8.10
		2	0.57	0.94	0.75	0.64	0.61	1.06	0.67	0.80	1.10	0.83	0.87	0.50
		3	(14)	(17)	(11)	(10)	(11)	(7)	(18)	(18)	(3)	(21)	(10)	(43)
		4	41.6	47.9	31.9	35.2	36.7	15.8	25.4	21.9	19.5	36.8	36.8	32.6
	% water		72.0	67.0	71.0	76.0	73.0	75.0	73.0	69.0	70.0†	64.0	62.0	63.0
	Dry weight		11.6	15.8	9.3	8.4	9.9	4.0	6.9	6.8	5.9†	13.2	14.0	12.1
1971 (1968*)	Wet weight	1	7.97	8.05	8.25	8.72	8.41	8.66	8.45	8.43	8.32*	8.22*	7.81*	8.57*
		2	0.73	0.66	0.79	0.40	0.28	0.91	0.68	0.55	0.53	0.91	0.69	0.64
		3	(30)	(31)	(19)	(6)	(20)	(20)	(12)	(15)	(20)*	(24)*	(33)*	(25)*
		4	29.0	31.3	38.4	61.3	44.9	57.5	47.0	45.8	41.2*	37.1*	27.2*	52.7
	% water		60.0	65.0	62.0	65.0	66.0	65.0	67.0	72.0	71.0*	70.0*	74.0*	68.0*
	Dry weight		11.6	11.0	14.6	21.5	15.2	20.1	15.5	12.8	11.9*	11.1*	7.1*	16.9*

1 = $\log_e \bar{x}$ mg/100g mouse

2 = 1 S.D.

3 = Number in sample

4 = Arithmetic equivalent of $\log_e \bar{x}$, converted to mg/g mouse

† Calculated using $\bar{x}$ % water content determined for whole study ($\bar{x} = 70.0 \pm 9.0$, $n = 620$)

variable for all months in any given year and among specific months in different years (e.g. compare February 1969, 1970 and 1971).

Table IX shows the mean "relative weights" ($\log_e \bar{x}$ and equivalent arithmetic $\bar{x}$) of stomach contents for the different reproductive classes of deermice. There was variability in these weights between the different classes but no significant differences at the 5% level ("t" test) were present. The total wet weights (i.e. "absolute weights") showed the same pattern. The mean total wet weight of stomach contents of lactating females (whether pregnant or not) was found to be the heaviest.

In order to estimate the weight of a full stomach, the mean of the heaviest 10% values was calculated. The heaviest 10% values were considered to represent the weights of full stomachs because when autopsied, stomach contents weighing in this range appeared to fully distend the stomach wall. The mean weight of these stomachs ($\log_e \bar{x} \pm 1$ S.D. : 9.43 ± 0.28, $n = 66$, arithmetic equivalent of $\log_e \bar{x} = 125.0$ mg/g mouse) was almost three and one half times greater than the mean weight of all samples ($\log_e \bar{x} \pm 1$ S.D. : 8.18 ± 0.75, $n = 665$, arithmetic equivalent of $\log_e \bar{x} = 35.8$ mg/g mouse). The overall mean dry weight of all samples was 10.74 mg/g

TABLE IX - Wet weight of stomach contents ($\log_e \bar{x} \pm 1$ S.D., mg/g mouse and mg/whole mouse) in relation to reproductive class.

		♂♂ and ♀♀	♂♂			♀♀				
		Juveniles	No Discernible Testes	Small Testes	Medium or Large Testes	Outside Breeding Season	Inside Breeding Season Cycling Only	Pregnant	Pregnant and Lactating	Not Pregnant But Lactating
Wet weight of stomach contents (mg/g mouse)	1	8.15±0.79	8.31±0.68	8.08±0.77	8.07±0.72	8.22±0.82	8.31±0.59	8.15±0.52	7.98±1.17	8.24±0.68
	2	34.8	40.8	32.5	32.2	38.1	40.9	34.9	27.2	38.9
		(114)	(148)	(44)	(146)	(99)	(46)	(22)	(17)	(21)
				8.07±0.73					8.12±0.93	
				32.2					33.8	
				(190)					(38)	
								8.13±0.80		
								34.1		
								(60)		
Wet weight of stomach contents (mg/whole mouse)	3	6.00±0.86	6.34±0.72	6.17±0.67	6.24±0.71	6.28±0.84	6.38±0.64	6.40±0.53	6.29±1.19	6.59±0.56
	4	404	573	479	513	534	590	602	539	728
		(114)	(148)	(44)	(146)	(99)	(46)	(22)	(17)	(21)
				6.22±0.70					6.45±0.90	
				503					633	
				(190)					(38)	
								6.44±0.78		
								627		
								(60)		

1 Log_e value ± 1 S.D. (mg/100g mouse)

2 Arithmetic equivalent of $\log_e$ value converted to mg/g mouse

3 Log_e value ± 1 S.D. (mg/whole mouse)

4 Arithmetic equivalent of $\log_e$ value (mg/whole mouse)

( ) Number in sample

mouse.

The caloric values of stomach contents were normally distributed and the monthly mean values are shown in Fig. 9. The monthly means in the combined data were not significantly different ($P < 0.05$) from the overall mean of the whole study. Monthly samples were collected alternately from slash (recently logged) and forest habitats. When caloric values of stomach contents of mice from each habitat were combined by year groups (Table X) a significant difference ($P < 0.05$) was found only in 1969. The overall mean caloric value of mouse food in slash (all years) was not significantly different from the overall mean in the forest (all years). Therefore, habitat differences did not consistently contribute to specific caloric differences in stomach contents.

The mean caloric values in different reproductive classes (Table XI) were not significantly different from the overall mean. However, when caloric values were grouped according to the seasonal breeding condition for males and females (Table XII) some significant differences were revealed. In 1969, breeding females had a significantly higher ("t" test, $P < 0.05$) mean caloric value for stomach contents than breeding males but this difference was not evident in other years. The comparison between male or female breeding or non-breeding

Figure 9 - Monthly changes in mean caloric value of stomach contents.

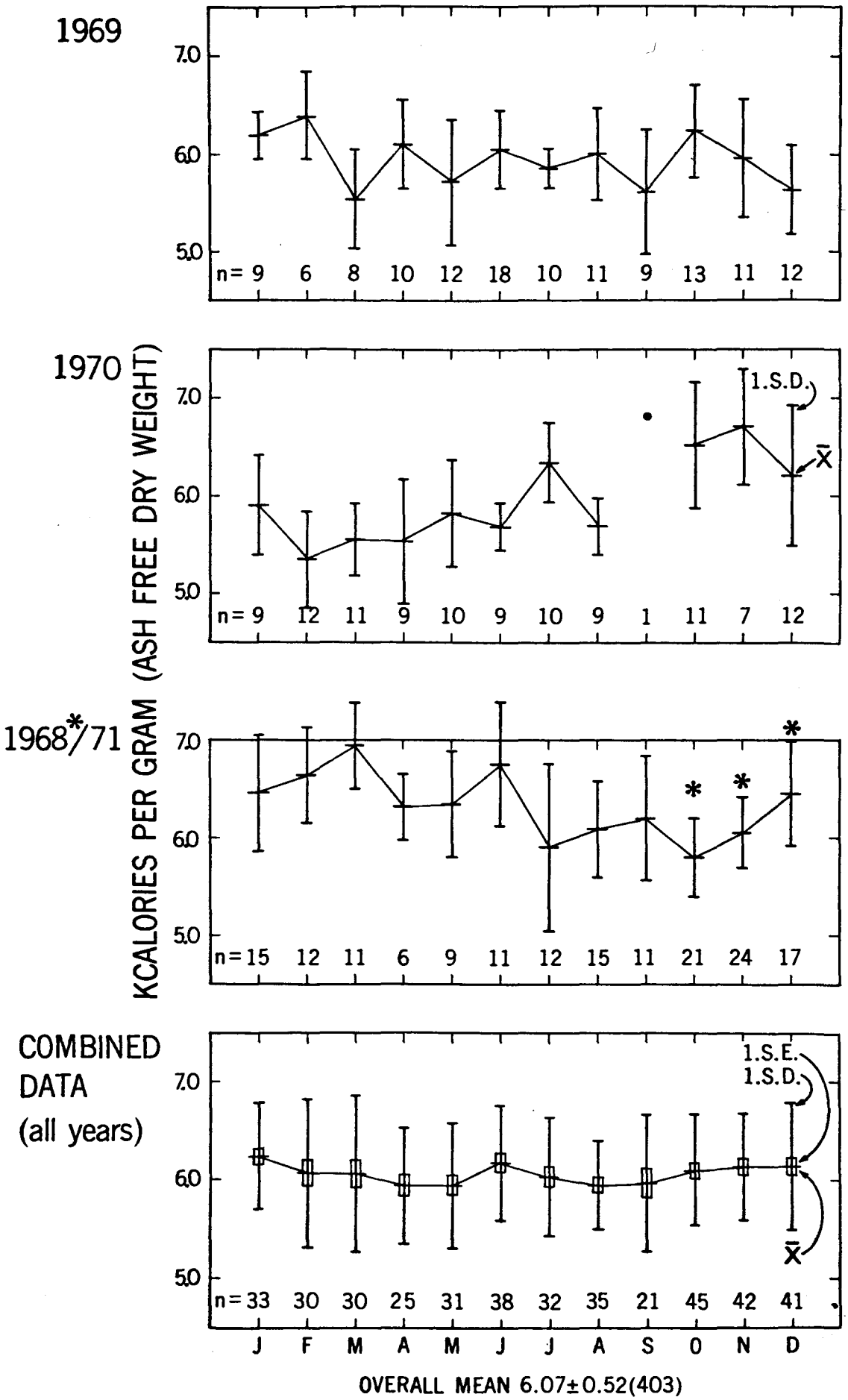

1969
1970
1968*/71
COMBINED DATA (all years)
KCALORIES PER GRAM (ASH FREE DRY WEIGHT)
7.0
6.0
5.0
n= 9 6 8 10 12 18 10 11 9 13 11 12
n= 9 12 11 9 10 9 10 9 1 11 7 12
n=15 12 11 6 9 11 12 15 11 21 24 17
n=33 30 30 25 31 38 32 35 21 45 42 41
1.S.D.
1.S.E.
1.S.D.
X̄
*
J F M A M J J A S O N D
OVERALL MEAN 6.07±0.52(403)

TABLE X - Annual caloric values ($\bar{x} \pm 1$ S.D.) of stomach contents collected separately from slash and forest habitats.

	1968	1969	1970	1971	All Years
1. Slash	6.09* ±0.57 (38)	6.04 ±0.48 (70)	5.85 ±0.67 (62)	6.43 ±0.57 (44)	6.07 ±0.61 (214)
2. Forest	6.05 ±0.37 (24)	5.81 ±0.55 (57)	6.03 ±0.61 (48)	6.41 ±0.72 (47)	6.06 ±0.64 (176)
"t"	0.331	2.481†	1.456	0.145	0.160

* Caloric values expressed as kcal/g ash free dry weight

† Significant difference at 5% level

TABLE XI - Caloric values ($\bar{x} \pm 1$ S.D.) of stomach contents of different reproductive classes of deermice.

♀ ♀	non-breeding	6.12† ± 0.60 (66)
	cycling	6.25 ± 0.69 (33)
	pregnant	5.88 ± 0.53 (21)
	pregnant and lactating	6.20 ± 0.45 (12)
	lactating	6.01 ± 0.43 (17)
♂ ♂	non-breeding	5.94 ± 0.65 (98)
	intermediate	6.14 ± 0.54 (24)
	breeding	5.99 ± 0.76 (73)
♀ ♀	juveniles	6.20 ± 0.60 (36)
♂ ♂	juveniles	6.16 ± 0.53 (23)
overall mean		6.07 ± 0.52 (403)

† Caloric values expressed as kcal/g ash free dry weight

TABLE XII - Caloric values ($\bar{x} \pm 1$ S.D.) of stomach contents, by breeding season, of male and female deermice and their comparisons with the overall mean (Table X).

Year	Breeding condition		Stomach content caloric value	Significant difference of individual values compared to overall mean (6.07 ± 0.52)
1968/69	Non-breeding	♀♀	6.13† ± 0.39 (17)	
		♂♂	6.11 ± 0.57 (30)	
1969	Breeding	♀♀	5.99 ± 0.44 (33)	
		♂♂	5.63 ± 0.81 (28)	*
1969/70	Non-breeding	♀♀	5.85 ± 0.51 (26)	*
		♂♂	5.75 ± 0.62 (44)	*
1970	Breeding	♀♀	5.81 ± 0.53 (19)	*
		♂♂	5.91 ± 0.53 (33)	
1970/71	Non-breeding	♀♀	6.63 ± 0.71 (13)	*
		♂♂	6.30 ± 0.72 (13)	
1971	Breeding	♀♀	6.51 ± 0.63 (25)	*
		♂♂	6.47 ± 0.58 (33)	*

† Caloric values expressed as kcal/g ash free dry weight

* Significant difference at 5% level

groups with the overall mean showed several significant differences ("t" test). There was, however, no overt regular pattern to these differences.

A frequency distribution of caloric values of fecal contents was normally distributed and monthly means are shown in Fig. 10. When fecal samples from mice caught in slash areas were compared with those from forest mice in each year (Table XIII) forest samples were significantly higher ("t" test, $P < 0.05$) in caloric value in two out of the three years represented. The overall caloric value of feces for mice sampled from the forest was also significantly higher ($P < 0.05$) than the caloric value in slash. Such differences are not considered important in later estimating consumption from this parameter because defecation only amounts to 10% of consumption (Sadleir et al., 1973).

Figure 10 - Monthly changes in mean caloric content of feces taken from deermice at autopsy.

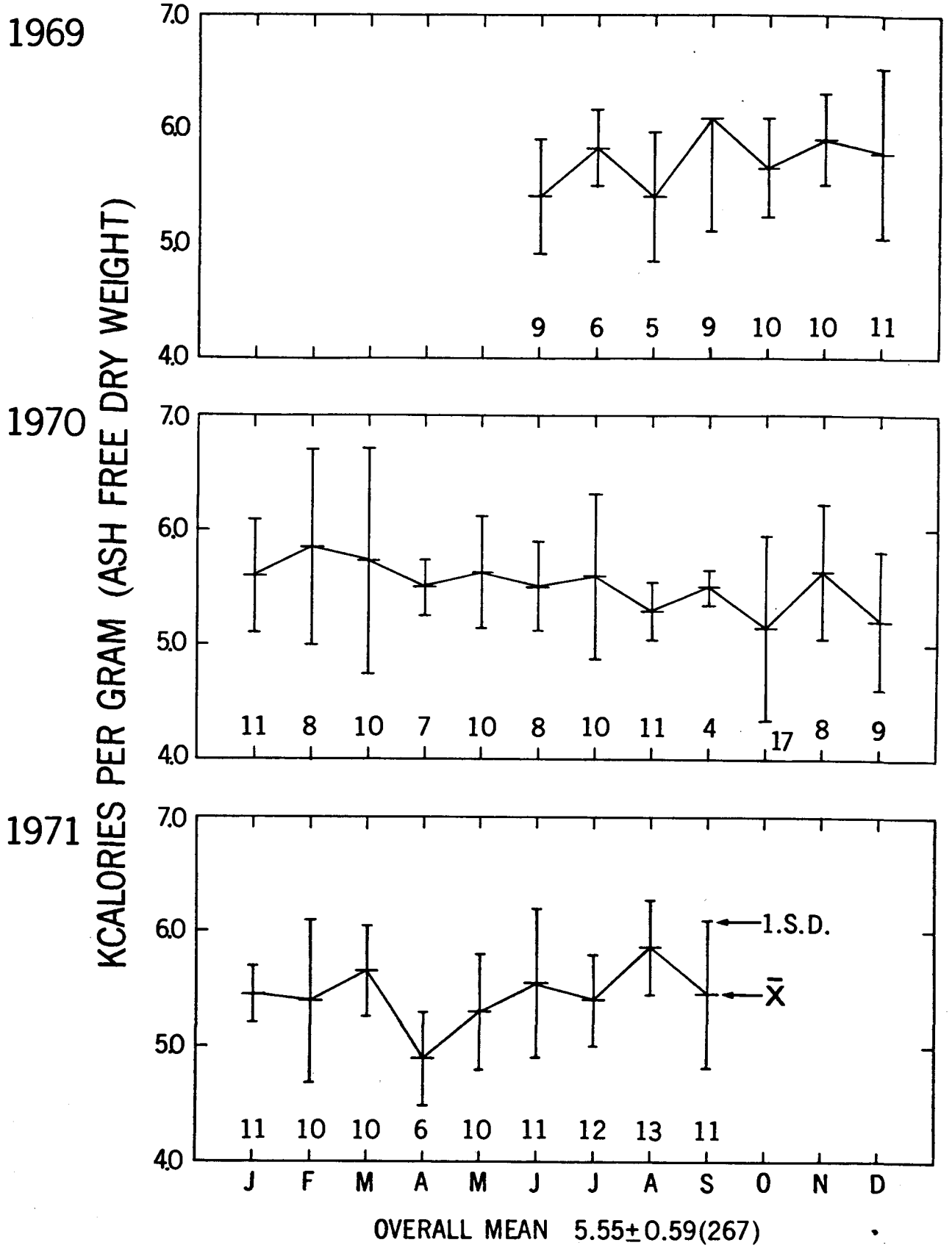

1969
1970
1971
KCALORIES PER GRAM (ASH FREE DRY WEIGHT)
7.0
6.0
5.0
4.0
9 6 5 9 10 10 11
11 8 10 7 10 8 10 11 4 17 8 9
11 10 10 6 10 11 12 13 11
1.S.D.
$\bar{X}$
J F M A M J J A S O N D
OVERALL MEAN 5.55±0.59(267)

TABLE XIII - Annual caloric values ($\bar{x} \pm 1$ S.D.) of fecal contents collected separately from slash and forest habitats.

	1969	1970	1971	All Years
1. Slash	5.61† ±0.58 (35)	5.38 ±0.64 (61)	5.52 ±0.63 (40)	5.48 ±0.62 (136)
2. Forest	5.97 ±0.65 (25)	5.63 ±0.63 (53)	5.46 ±0.44 (54)	5.63 ±0.59 (132)
	*	*		*

† Caloric values expressed as kcal/g ash free dry weight

* Significant difference at 5% level between 1 and 2

DISCUSSION

The frequency of occurrence of food items in stomach contents, as shown in Fig. 7, indicated distinct seasonal trends in consumption which appeared to be correlated with their availability in the wild. Tree seeds were consumed as a major item primarily in winter and were replaced in summer by berries. Consumption of green vegetation occurred mainly in springtime, bridging the gap between the availability of tree seeds and berries. Arthropods and annelids were staple items and may have been consistently available in the burrow systems of the mice, thus providing some available food all year. The fungi were probably also available in the burrows almost all year. The occurrence of fungi as a food item is discussed more fully in Harling and McClaren (1970). Dyke (1971) and Williams (1959) have also found fungi in stomachs of wild deermice. My results suggest that Peromyscus is an extremely mobile feeder in any habitat it occupies and does not appear to exhibit a pronounced dependence on specific food items. This agrees with the view of Dyke (1971).

The slight seasonal fluctuations in percentage water in the stomach contents (Table VIII) was probably due to the proportions of particular food items present. As tree seeds are drier than berries the stomach contents tended to be drier in winter months (compare the percentage water content with

occurrence of seeds in Fig. 7).

The data given in Tables VIII and IX and shown in Fig. 8 indicated that the frequency distribution of stomach content wet weights represented in the autopsy samples collected did not conform to the normal curve. Initially it was suspected that this skewed distribution was due to capture of a majority of mice soon after the onset of their activity when feeding had just commenced so that their stomachs were relatively empty. However, as explained in Chapter I, it is considered that this distribution is representative of stomach content weights of mice active out of the nest over the night period. During the first captures the mice had relatively empty stomachs. The likelihood of capture would be effectively reduced subsequently as the stomachs filled and searching activity decreased.

It is difficult to define a "full" stomach. In the majority of the 665 stomachs examined the stomach walls were partially collapsed and the volume of food therein occupied much less than half the possible stomach capacity. The small number of heavy stomachs in the top 10% of the weight range were distended and the stomachs seemed full to capacity. It was thus considered that the mean of the top 10% weight range represented the weight of food in a full stomach. The overall

mean wet weight of stomach contents was considerably less than half of the top 10% mean. If this situation is common for wild rodents then Meese (1971), following Golley's (1960) suggestion that the average weight of stomachs could be taken as half the full weight, probably underestimated the daily energy consumption of the bank vole (Clethrionomys glareolus). Alternatively, the stomach of the more omnivorous P. maniculatus fills in a different manner to that of the relatively herbivorous bank vole. Golley (1960) does not comment about the normality of the distribution of his samples and hence may have seriously underestimated the correct mean value of his samples. Thus the difference between mean and full content weight is an important factor to interpret correctly in estimating consumption by wild rodents.

As reported in Chapter I an attempt to determine rate of passage for deermice in the wild was not successful. In the absence of such data it was not possible to relate mean stomach weights to rate of passage in calculating a reliable estimate of wild consumption. It is to be noted that the consumption estimates of Golley (1960) and Meese (1971) were not based on a field estimate of rate of passage, but on one determined in the laboratory. If the rate of passage in the wild is different to that in the laboratory their estimates of consumption might

be further influenced.

I suggested in Chapter I that deermice were active almost all night. Since deermice had low stomach content weights during most of the night it appears that they are feeding almost all night in order to meet energy requirements. The mean content dry weight determined in this study was 10.74 mg per g mouse. This dry weight had an "absolute" value of 0.068 kcal, based on the overall stomach caloric value per g dry weight given in Sadleir et al. (1973). Thus the total 24 h dry weight (per mouse) consumption would have to be in the order of 30 times greater than the mean dry weight of stomach contents in June and 42 times greater in December to satisfy the 24 h consumption estimates given in column K of Table XIV. It should be noted, however, that the mean "relative" 24 h consumption on which this is based is for the maximal possible activity period of the animal (Sadleir et al., 1973). It is possible that the mean weight of stomach contents is not a satisfactory parameter in combination with rate of passage information for estimating consumption in the wild because mice with full stomachs may not be entering traps but returning to nests. Hence a bias in determining mean stomach weights would result. Also because the rate of passage of food items through Peromyscus was not satisfactorily deter-

mined in the wild it was not possible to relate the consumption amounts mentioned above to the maximum consumption which could possibly occur in the wild.

Gębczyński (1966) and Grodziński and Górecki (1967) have suggested that the European Apodemus, an ecological counterpart of the North American Peromyscus, is less active in winter and hence has a lower energy budget than in summer. If Peromyscus followed this pattern, it could be suggested that the mouse would emerge and feed for only a short time, (longer exposure to cold temperatures would increase the energy budget) and ingest food rapidly. If this were true, one would expect the autopsy stomach content weights to be higher in winter months because the incidence of fuller stomachs would be increased. Such a pattern did not emerge in the present study. Therefore, I conclude that deermice were feeding during a major portion of their out of the nest activity period in any given night of the year. As full stomachs were rare, it appears that feeding maintains contents at about the mean weight observed in this study.

Only pregnant, or pregnant and lactating females, showed indications of higher stomach content weights (see Table IX)

when determined on a whole body weight basis, suggesting that they probably fed faster and consumed more food over a shorter period. Pregnant and lactating females were also trapped in daytime in mid-summer (Harling, 1971). The night feeding of lactating females would be interrupted because they were suckling young in their nests. Such females also needed extra food to meet their increased energy budget required by pregnancy and lactation (Sadleir et al., 1973). All of the above factors could have contributed to the feeding pattern of such females extending into the daytime.

Because the caloric value per g ash free dry weight of stomach contents was similar at all times of the year (see Fig. 9) and did not consistently differ between slash and forest habitats (Table X), there would be no major difference in the caloric value obtained from the same weight of food eaten at different times of the year. If searching time for specific foods differed from season to season, then it is possible that the same gross caloric value might be obtained more readily at some times of the year than at others. If, for example, tree seeds were more rapidly obtained in winter than berries were in summer, the energy requirement would be more quickly met in wintertime

and the mice could be less active over a winter night. However, as shown in Chapter I the mice were active throughout winter nights. Also if, for example, more food was obtained per "outing" in wintertime one would expect to capture more mice with heavier stomach contents, but as mentioned previously this condition was not evident.

None of the breeding classes (Table XI) appeared to selectively choose foods of higher caloric value. Thus, time spent feeding would probably be the same for each class to obtain an equal amount of energy. It has already been noted that lactating females fed for longer periods to obtain their extra energy requirements. Because there were no consistent annual patterns for fluctuations in caloric values of stomach contents in different years, I concluded that no specific energy selection was occurring. The differences probably reflected only the variability in seasonal occurrences of the various food items.

Because there was no large difference in fecal caloric values throughout the year, or from slash to forest habitats (Table XIII and Fig. 10), the caloric content (per g feces) should not influence the assimilation efficiency of the mice at any time of the year. Thus, there should be no large increment, or decrease, in time required to obtain food as a

result of the assimilation efficiency changing.

Because of cooperative data collection undertaken in this research project it was possible to utilize data reported by Petticrew (1973) in his parallel study on deermice population dynamics, in estimating the total caloric consumption of a deermouse population over an entire year. In Table XIV the mean weight (column W) and the population density (column N) are derived from Petticrew (1973) who trapped on three separate grids over a three year period. The relative individual caloric consumption (column K) was derived from the estimated assimilation shown in Table XIX (Chapter III) by adjusting for the 87% digestibility coefficient. The daily caloric consumption, by months, of individuals (column Ci) and of the population as a whole (column Cp) are also shown in Table XIV.

The individual consumption figures are at a maximum in winter months and at a minimum in summer months because of seasonal differences in energy requirement. The total population consumption figures remained relatively constant from January through September and then increased and remained constant at a higher level from October through December.

TABLE XIV - Monthly mean data pertaining to individual and total population caloric consumption.

	W	N	K	Ci	Cp
Month	Mean mouse weight (g)	Mean number of mice per ha	Mean 24 h consumption (kcal/ g body weight)	Consumption per mean mouse (kcal/24 h)	Consumption of total population (kcal/24 h/ ha)
JAN	15.48	20	2.77	42.88	859
FEB	15.76	22	2.67	42.08	926
MAR	17.22	21	2.47	42.53	894
APR	17.94	22	2.26	40.54	893
MAY	15.81	26	2.10	33.20	863
JUN	16.20	24	2.06	33.37	801
JUL	15.61	24	2.06	32.16	773
AUG	14.63	26	2.21	32.33	842
SEP	15.56	22	2.42	37.66	828
OCT	15.10	28	2.57	38.81	1087
NOV	14.91	26	2.78	41.45	1079
DEC	15.38	24	2.88	44.29	1063
			Overall mean value	38.44	909
			S.D.	±4.55	±109
			$\bar{x}$ annual consumption	3.22×10^5 kcal/ha	

The increase in population consumption reflects the increase in density which occurs in deermouse populations in fall and early winter. The population then drops steadily and by the following spring it is at its smallest size when the reproductive season recommences.

On average the total population consumed 909 ± 109 kcal/ha/day (Table XIV), giving an annual consumption of 3.32×10^5 kcal/ha. This is a maximum estimate for reasons discussed in detail in Sadleir et al., (1973). Thus the actual consumption figure may be lower than this but it corresponds approximately to the annual consumption of 2.50×10^5 kcal by a Microtus population estimated by Golley (1960). It is noted, however, that his Microtus population had a higher biomass per ha than my Peromyscus population. The value derived in the present study differs considerably from the 1.28×10^5 kcal for small rodents in a European beech forest, as estimated by Grodzinski, et al., (1970). This difference is primarily due to their assumption that the rodents are on a decreased energy budget in winter, whereas Peromyscus in the present

study is assumed to be on a higher energy budget in winter. This difference is discussed in more detail in Chapter III.

CHAPTER III

Intake and Requirements of Energy and Protein Relative to Breeding Duration

INTRODUCTION

The influence of nutrition and temperature on breeding in wild rodents in temperate zones has not been adequately determined, although it has been frequently suggested that these parameters govern the length of the reproductive season. Many workers have documented varied lengths of breeding in different years (reviewed in Sadleir, 1969a, 1969b) and some have suggested, a posteriori, that extended breeding seasons resulted from a surplus of natural food or mild temperatures (Ashby, 1967; Fuller, 1969). Much is known of metabolism rates in small rodents under various temperature conditions in the laboratory (Grodziński, 1961; McNab, 1963; Górecki, 1965; Hayward, 1965a; Gębczyński, 1966; Johnson and Groepper, 1970) as well as the increased energy costs of pregnancy and lactation (Migula, 1969; Kaczmarski, 1966). There have been, however, few attempts to document seasonal variation in food consumption in wild rodents. As a result, little is known as to whether the metabolic requirement for breeding can be met at all seasons of the year.

This chapter reports an attempt to determine the rela-

tionship between energy and protein requirements and consumption for breeding in the deermouse Peromyscus maniculatus. The hypotheses were 1) that deermice can obtain their energy requirements for reproduction at all times of the year and 2) that deermice can obtain their protein requirements for reproduction at all times of the year.

Although there have been previous measurements of diel activity of deermice in the laboratory and in field pens (reviewed by Falls, 1968), little is known of the situation in the wild. The use of activity lines (Harling, 1971) allowed measurement of the duration of nocturnal activity and the fecal production rate of small mammals in the field. These measurements in conjunction with laboratory data enabled the derivation of an estimate of consumption rates in the wild.

Johnson and Groepper (1970) reported on the protein contents of stomachs of small numbers of samples of several species of rodent (including P. maniculatus). This appears to be the only previous investigation of protein ingested by small mammals in the wild. The role of protein in the reproduction of laboratory rodents is well known (Russell, 1948) but its effects on reproduction of feral species are undetermined. Although nitrogen balance was not measured in this study, it was possible to compare the protein requirements of reproduc-

tion in wild deermice with estimates of their protein consumption.

METHODS

This study was carried out in the University of British Columbia Research Forest at Haney, B.C., a coastal rain forest. Samples for autopsy were taken within an altitude range of 90 m and 250 m from October, 1968 to September, 1971 in habitats similar to those described by Petticrew and Sadleir (1970). Samples were taken in alternate months from logged and unlogged areas. Snap traps were baited with oil-soaked string to eliminate bait consumption. Snap-trapped deermice were frozen until autopsy.

Defecation rates were determined from September, 1970 to August, 1971 by holding wild caught deermice for approximately one hour periods in Longworth live traps.[1] In order to facilitate fecal removal bedding was not provided in the traps. Electrically monitored trap lines (Harling, 1971) showed the exact times of capture so that fecal production rates could be determined. Over the same period animals were trapped and immediately released to determine the length of their nocturnal activity. Two or three nights of observations in each month showed that the average time of first capture was one hour after sunset and all captures ceased no later than one hour

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[1] Detailed in Chapter I.

before sunrise. The activity period was therefore taken as the length of night on 15th/16th of the month minus two hours (see Table XV).

Autopsies were carried out immediately after thawing. Deermice were weighed, mammaries inspected and the stomach, liver and reproductive tract removed. A sample of feces was taken from the lower colon of the eviscerated animal and dried for 24 h at 100°C to determine water content.[1] The stomach contents were weighed wet and homogenized. A temporary slide mount was prepared for inspection of food items (Harling and McClaren, 1970) from a subsample. The remainder was weighed, dried similarly, reweighed, and a further subsample taken for caloric determination using a Phillipson microbomb calorimeter (Phillipson, 1964). A fecal sample from each deermouse was similarly treated. Complete combustion in the calorimeter was checked by duplicate ashings in a muffle furnace at 600°C. A final subsample of stomach contents and the entire liver were dried at 100°C, ground up and their nitrogen content determined on a Perkin-Elmer 240 Elemental Analyser. The nitrogen values were converted to protein by multiplying by 6.25 (Brody, 1945). Testes were removed and fixed in Bouin's fluid, imbedded, sectioned at 7 μ, and stained with Harris's haemotoxylin and

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[1] Detailed in Chapter II.

eosin. Ovaries were removed from female tracts, and after the number and condition of the corpora lutea were noted, they were preserved by similar techniques and serially sectioned. Uteri were spread on cards and the number of embryos and/or implantation scars noted. They were then preserved and cleared in methyl salicilate by the method of Brown (1964).

Males were considered to be breeding when spermatozoa were seen in the testis tubules. Non-breeding males exhibited no sign of spermatogenesis. Males whose tubules showed either some stage of spermatogenesis (without the process being completed -- developing), or signs of decreasing in size (crinkled basement membrane -- regressing), were classified as being in intermediate breeding condition. Adult females were classified as non-breeding when their ovaries showed no developing follicles or exhibited only persistent corpora lutea of the type described by Brown and Conaway (1964). Cycling females were not pregnant but had either enlarging follicles, developing corpora lutea, or both. Pregnant females had detectable embryos in utero.

The relationship between 24 h food consumption and 24 h fecal production was determined on laboratory deermice in metabolism cages (see Fig. 11) at 20°C with Purina mouse chow and water supplied ad lib. Consumption and production were

Figure 11 - Metabolism cage used in feeding experiments.

strongly correlated ($r = 0.98$, $P < 0.001$, $n = 123$) and had the following regression formula: $y = 0.13x - 0.03$ where y = g dry weight feces produced/g mouse, and x = g dry weight food consumed/g mouse. The slope (β) had a S.E. of 0.0065. The proportion of feces produced at night was determined in two experiments (24 determinations each) where deermice were fed for 6 h in an 8 h night (summer conditions) or for 14 h in a 16 h night (winter conditions). The dry weight of feces present was determined when food was removed, 2 h later, 4 h later and for the 24 h period. In the 6 h experiment, 66% of the total 24h feces were produced by the time food was removed, a further 6% (72%) 2 h later and a further 22% (88%) 4 h later. In the 14 h run, the comparative figures were 88%, 90% and 92%, indicating that with a lengthened night, deermice produce a higher proportion of their 24 h fecal production during nighttime. Thus the estimates of 24 h fecal production of field animals were based on a weighted length of activity called the fecal production time as shown in Table XV. This time was taken as the time in which 88% of the total 24 h feces was produced.

Energy consumption and assimilation and protein consumption in the field were estimated for each month using the data in Table XV and the separate monthly values for stomach calories

TABLE XV - Seasonal variation in activity period, temperature correction factor, fecal production rate and time.

Month	Length of activity period (night length - 2) (h)	Fecal production time (h)	Mean rate of production x 10^{-2} g dry wt/h/g body wt	Temperature factor (36.2°C - Ambient T°)		
				68*/71	69	70
JAN	13	13 1/2	0.54 (27)	35.2	36.2	34.2
FEB	12	13	0.40 (4)	33.2	33.2	30.2
MAR	10	12	0.49 (9)	33.2	30.2	30.2
APR	8 1/4	11	0.56 (13)	28.2	28.2	29.2
MAY	6 3/4	10 1/4	0.43 (23)	23.2	22.2	25.2
JUN	5 3/4	9 3/4	0.41 (9)	23.2	19.2	20.2
JUL	6 1/4	10	0.54 (7)	19.2	19.2	19.2
AUG	7 1/2	10 3/4	0.49 - †	18.2	21.2	19.2
SEP	9 1/2	11 3/4	0.52 (13)	24.2	22.2	25.2
OCT	11 1/4	12 1/2	0.47 (40)	*27.2	26.2	27.2
NOV	13	13 1/2	0.49 - †	*30.2	30.2	31.2
DEC	14	14	0.40 (6)	*35.2	31.2	34.2

† ,Calculated on basis of mean value for whole study

and fecal calories (Table XVIII). Rates of fecal production had only been determined for a twelve month period beginning in August, 1970. The monthly rates for this period were applied to the respective months prior to August, 1970 (e.g. the 1970 October fecal production rate of 0.47×10^{-2}g dry weight/h/g body weight was applied to calculate the October estimate of assimilation in 1968 and 1969). Fecal production times were a function of average day length in the month which was obviously constant for each respective month in the different years. The fecal production rate (F_wg/h/g mouse) was multiplied by the fecal production time (t) (Table XV) and corrected for daytime fecal production to give an estimate of 24 h production: 1.136 $F_w t$ g/g mouse. On the basis of the consumption/fecal production relationship described in the preceding paragraph an 87% dry matter digestibility coefficient was used to estimate the weight of food consumed: 8.74 $F_w t$ g/g mouse. Drożdż (1968b) found similar digestibility coefficients for Apodemus sylvaticus and A. flavicollis on both laboratory and mixed natural diets. The number of calories consumed was estimated by multiplying this figure by the caloric value of the stomach contents (S_c kcal/g) to give 8.74 $F_w t S_c$ kcal/g mouse. As consumption was measured in terms of dry weight, monthly caloric values (determined on an ash free basis) were

adjusted to dry weight but all others were left on an ash free basis. The number of calories assimilated was determined by subtracting from this estimate the calories lost in feces (weight of feces (1.136 $F_w t$ g/g mouse) x fecal caloric content (F_c kcal/g) = caloric value of feces (1.136 $F_w t F_c$ kcal/g mouse). A correction factor was also applied to compensate for a 4% urine loss (Drożdż, 1968b). The protein consumption was estimated in turn by multiplying the stomach content caloric values by the protein/calorie ratio (mg protein/kcal).

The estimates of metabolic requirements of deermice in the field are based on their body weight, average body temperature, and the ambient temperature. Over a 12 month period, the mean monthly soil temperature at 8" in the field area (which can be taken as burrow temperature - Hayward, 1965b) were the same as the mean monthly air temperatures taken in a Stevenson screen at a permanent meteorological station in the research forest. This latter measure was therefore considered as the ambient temperature for each month of the study with a single exception. In January, 1969, the mean air temperature dropped below 0°C but snow cover would have maintained the burrow temperatures at not less than this figure. The theoretical BMR for a 24 h period for resting deermice (at ambient temperature 0° - 27°C) was calculated from formula 2 in

Hayward (1965a) as based on a temperature correction factor using the ambient temperature minus the average body temperature of 36.2°C (Table XV). This was converted to kcal and increased by a standard 20% for all deermice to include the metabolic increment due to activity (McNab, 1963). This gave an estimate of the active metabolic rate expressed here as maxADMR.

Unfortunately I had no direct information as to the increased metabolic costs of pregnancy and lactation in P. maniculatus. Approximate calculations based on the biomass of young at parturition and weaning, and the use of Górecki's (1965) figures for the caloric content of newborn and weaned A. flavicollis, gave estimates of extra metabolic costs (above normal activity) of 28% per day as an average during pregnancy and of 98% per day during lactation. Kaczmarski (1966) showed that the increased energy requirements above normal activity for Clethrionomys glareolus were on average 32% per day during pregnancy and 92% per day during lactation, while Migula (1969) reported 24% and 133% respectively for Microtus arvalis. As these figures are of the same order as those calculated empirically for P. maniculatus, the maxADMR's of pregnant deermice were estimated by increasing the active metabolic rate by 28% and of pregnant and lactating, or lactating deermice,

by 98%. Protein requirements were calculated from the caloric figures by applying a correction factor of 2.90 mg nitrogen excreted per kcal maxADMR (Brody, 1945, p. 380 - for Mus musculus). This estimates the minimal protein converted from nitrogen which is required to maintain a nitrogen balance.

RESULTS

The energy and protein values of the stomach contents are shown in Table XVI.[1] There is no consistent pattern of differences ("t" test) between breeding and non-breeding seasons. The lack of statistical differences ("t" test) between the various reproductive classes in Table XVII[1] indicates no food selection as a function of reproductive condition.

The concentrations of calories and protein in stomach contents and of calories in feces for each month are shown in Table XVIII.[1] The values shown are the means for both sexes using adults only. As previously mentioned they were used in calculating the estimates of assimilation and consumption in Figs. 12 and 13. Table XIX shows assimilation estimates for each month of the year which are based on the fecal production times shown in Table XV, and on the following means (and S.D.'s) which were determined from the entire sample:

1. Energy value, stomach contents.....5.871 $\pm$ 0.36 kcal/dry weight (n = 404)[2]

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[1] The data in these tables are also included in Tables XI and XII and Figs. 9 and 10. They are repeated here in order to show the derivation of the protein/calorie ratio.

[2] These values are given here as kcal/g dry weight because the consumption/defecation relationships were measured in terms of dry weight. Elsewhere in this thesis the corresponding values are expressed as kcal/g ash free dry weight.

TABLE XVI - Variation in stomach contents, liver and whole body protein in relation to reproductive season ($\bar{x} \pm 1$ S.D.).

Reproductive Season		Stomach Contents: Calories kcal /g Ash Free Dry Weight	Stomach Contents: Protein %	Stomach Contents: Protein/Calorie Ratio*	Liver Protein Content mg Protein/g Body Weight	Whole Body (Eviscerated) Protein Content mg Protein/g Body Weight
Non-breeding	♀♀	6.13±0.39 (17)	31.6±6.9 (16)	52±13 (16)	14.19±1.84 (9)	---
(1968/1969)	♂♂	6.11±0.57 (30)	27.6±8.3 (29)	46±14 (29)	12.50±1.62 (20)	---
Breeding	♀♀	5.99±0.44 (33)	28.7±8.7 (29)	48±14 (29)	14.06±2.31 (20)	222.6±15.7 (37)
(1969)	♂♂	5.63±0.81 (28)	29.4±11.1 (25)	53±20 (24)	12.81±1.61 (30)	214.7±10.4 (72)
Non-breeding	♀♀	5.85±0.51 (26)	30.0±7.4 (19)	51±15 (19)	11.63±1.44 (18)	232.1±12.6 (32)
(1969/1970)	♂♂	5.75±0.62 (44)	29.2±9.9 (41)	52±20 (37)	10.44±2.06 (33)	227.4±5.9 (69)
Breeding	♀♀	5.81±0.53 (19)	32.4 (5)	54 (4)	12.38±1.94 (22)	234.7±7.9 (23)
(1970)	♂♂	5.91±0.53 (33)	30.8±8.2 (16)	54 (7)	12.31±2.19 (38)	232.4±7.0 (56)
Non-breeding	♀♀	6.63±0.71 (13)	26.9±10.8 (15)	31 (1)	12.13±1.38 (16)	232.9±6.2 (34)
(1970/1971)	♂♂	6.30±0.72 (13)	22.5±12.7 (17)	78 (2)	11.13±1.38 (42)	232.1±5.3 (43)
Breeding	♀♀	6.51±0.63 (25)	30.1±6.5 (13)	43 (9)	11.63±2.19 (11)	238.1±11.2 (33)
(1971)	♂♂	6.47±0.58 (33)	29.8±12.5 (31)	56 (7)	12.88±1.63 (21)	233.7±11.2 (69)

( ) Number in sample * Determined from individual ratios

TABLE XVII - Variation in stomach contents, liver and whole body protein in relation to reproductive class ($\bar{x} \pm 1$ S.D.).

	Reproductive Class	Stomach Contents: Calories kcal /g Ash Free Dry Weight	Stomach Contents: Protein %	Stomach Contents: Protein/Calorie Ratio*	Liver Protein Content mg Protein/g Body Weight	Whole Body (Eviscerated) Protein Content mg Protein/g Body Weight
♀♀	Non-breeding	6.12±0.60 (66)	29.2±8.7 (61)	48±16 (47)	12.31±1.93 (50)	230.2±11.0 (89)
	Cycling	6.25±0.69 (33)	28.0±9.8 (24)	29±9 (21)	12.69±1.69 (18)	228.9±18.4 (41)
	Pregnant	5.88±0.53 (21)	33.1±7.3 (10)	57±14 (9)	13.56±2.56 (13)	234.5±11.4 (22)
	Pregnant and Lactating	6.20±0.45 (12)	31.4 (5)	48 (5)	12.31±2.63 (11)	233.9±8.8 (15)
	Lactating	6.01±0.43 (17)	28.4±6.2 (17)	48±11 (17)	12.81±2.75 (11)	229.7±9.4 (14)
♂♂	Non-breeding	5.94±0.65 (98)	28.0±10.7 (97)	51±20 (77)	11.85±1.81 (99)	229.0±6.5 (128)
	Intermediate	6.14±0.54 (24)	29.3±11.0 (29)	51±16 (13)	12.37±1.94 (32)	229.8±12.0 (43)
	Breeding	5.99±0.76 (73)	30.0±11.1 (46)	55±19 (27)	12.75±1.87 (57)	225.2±12.9 (161)

* Determined from individual ratios

TABLE XVIII - Monthly variation in mean values of stomach calories and protein, and fecal calories.

Month	Stomach Contents									Feces		
	Calories kcal/g Dry Weight			% Protein			Protein/Calorie Ratio			Calories kcal/g Dry Weight		
	68*/71	69	70	68*/71	69	70	68*/71	69	70	68*/71	69	70
JAN	6.32	6.07	5.74	29.28	34.40	28.67	46.31	56.67	49.91	4.84	4.94	5.04
	(15)	(9)	(9)	(18)	(9)	(13)	†	(9)	(9)	(11)	△	(11)
FEB	6.51	6.22	5.09	25.01	29.12	31.12	38.43	46.84	61.19	4.73	4.94	4.69
	(12)	(6)	(12)	(18)	(6)	(8)	†	(6)	(6)	(10)	△	(8)
MAR	6.76	5.40	5.35	26.96	21.40	35.05	39.88	39.62	65.47	5.01	4.94	4.50
	(11)	(8)	(11)	(8)	(11)	(5)	†	(8)	†	(10)	△	(10)
APR	6.11	5.88	5.28	28.91	28.28	29.07	47.32	48.07	55.03	4.70	4.94	4.47
	(6)	(10)	(9)	△	(11)	(2)	△	(9)	†	(6)	△	(7)
MAY	6.12	5.55	5.59	35.49	34.12	37.39	57.98	61.43	66.89	4.70	4.94	4.63
	(9)	(12)	(10)	(7)	(13)	(5)	†	(10)	(5)	(10)	△	(10)
JUN	6.62	5.86	5.41	29.68	30.00	28.91	44.81	51.22	53.41	5.03	4.88	5.01
	(11)	(18)	(9)	(8)	(14)	△	†	(14)	△	(11)	(9)	(8)
JUL	5.65	5.67	6.18	25.74	33.82	36.61	45.53	59.70	59.28	4.81	5.51	5.15
	(13)	(10)	(10)	(7)	(9)	(6)	(7)	(9)	†	(12)	(6)	(10)
AUG	5.96	5.79	5.48	25.83	26.21	25.57	43.34	45.30	46.66	5.27	4.81	4.95
	(15)	(11)	(9)	(15)	(12)	(8)	(15)	(11)	†	(13)	(5)	(11)
SEP	6.01	5.39	5.89	33.85	33.00	28.91	56.32	61.25	49.11	4.78	5.47	4.95
	(11)	(9)	△	(11)	(9)	△	(11)	(8)	△	(11)	(9)	(4)
OCT	*5.67	5.86	6.15	*31.02	28.62	23.60	*54.73	48.87	38.41	*4.94	5.08	4.37
	(21)	(13)	(11)	(21)	(13)	(7)	(21)	(13)	†	△	(10)	(17)
NOV	*5.94	5.50	6.46	*26.85	25.32	28.91	*45.20	46.04	44.79	*4.94	5.56	5.23
	(24)	(11)	(7)	(25)	(10)	△	(24)	(10)	△	△	(10)	(8)
DEC	*6.31	5.38	6.04	*28.33	30.04	25.21	*44.93	55.85	41.72	*4.94	5.27	4.60
	(17)	(12)	(12)	(19)	(7)	(24)	(17)	(7)	†	△	(11)	(9)

† Determined from mean calories and mean protein for that month

△ Calculated on basis of mean values for whole study

Figure 12 - Comparison of estimated assimilation of energy and theoretical metabolic energy requirements for each month of the study. The solid line in the assimilation estimate indicates the period over which monthly determinations of fecal production rates were measured. These monthly rates were also used in calculating assimilation estimates in respective months prior to August, 1970 (dotted line).

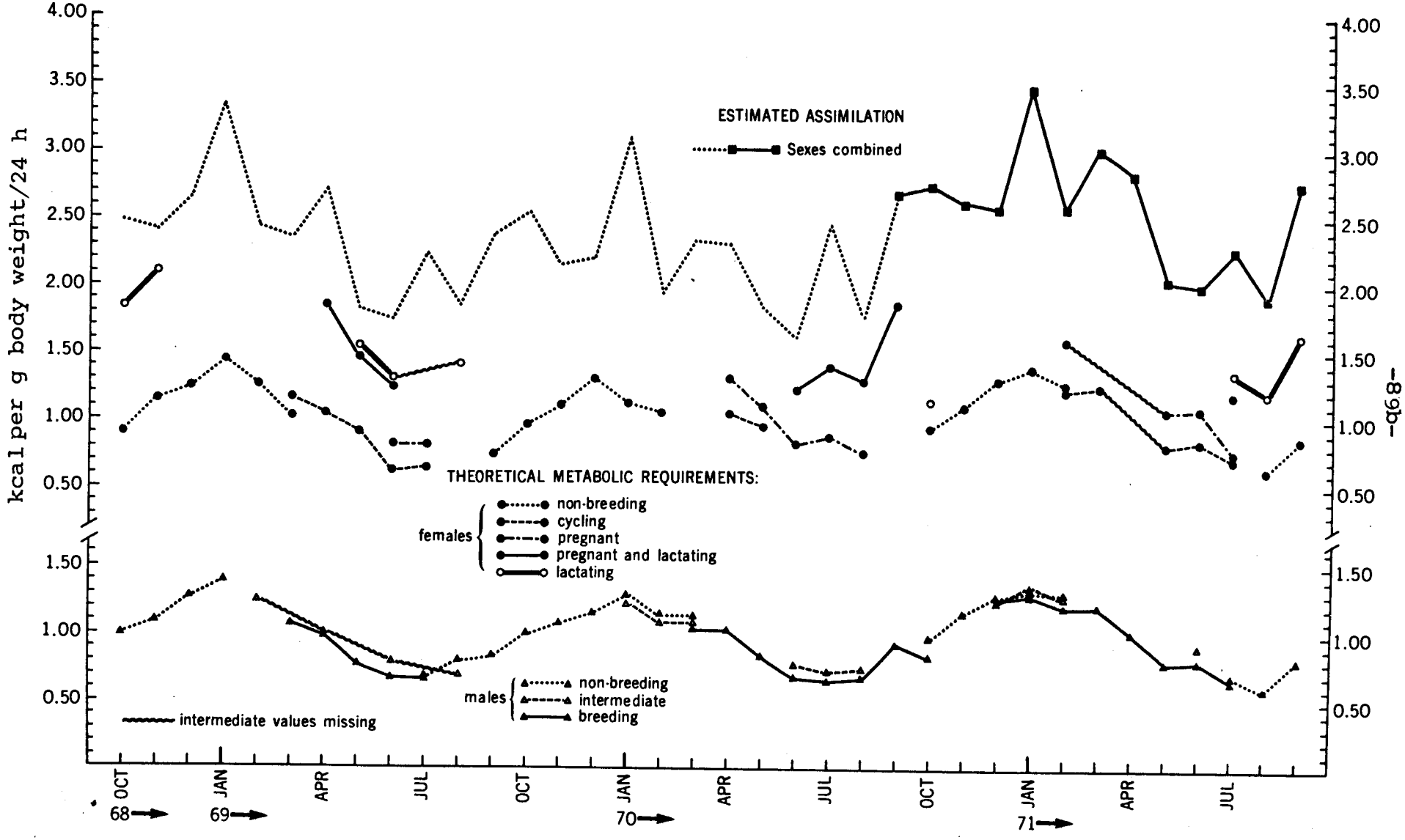
kcal per g body weight/24 h
4.00
3.50
3.00
2.50
2.00
1.50
1.00
0.50
ESTIMATED ASSIMILATION
Sexes combined
THEORETICAL METABOLIC REQUIREMENTS:
females
non-breeding
cycling
pregnant
pregnant and lactating
lactating
males
non-breeding
intermediate
breeding
intermediate values missing
OCT
JAN
APR
JUL
68
69
70
71
-89-

Figure 13 - Comparison of estimated consumption of total protein and theoretical protein requirements for each month of the study. Symbols as in Fig. 12. The solid line on the consumption estimate indicates the period over which monthly determinations of fecal production rates were measured. These monthly rates were also used in calculating assimilation estimates in respective months prior to August, 1970 (dotted line).

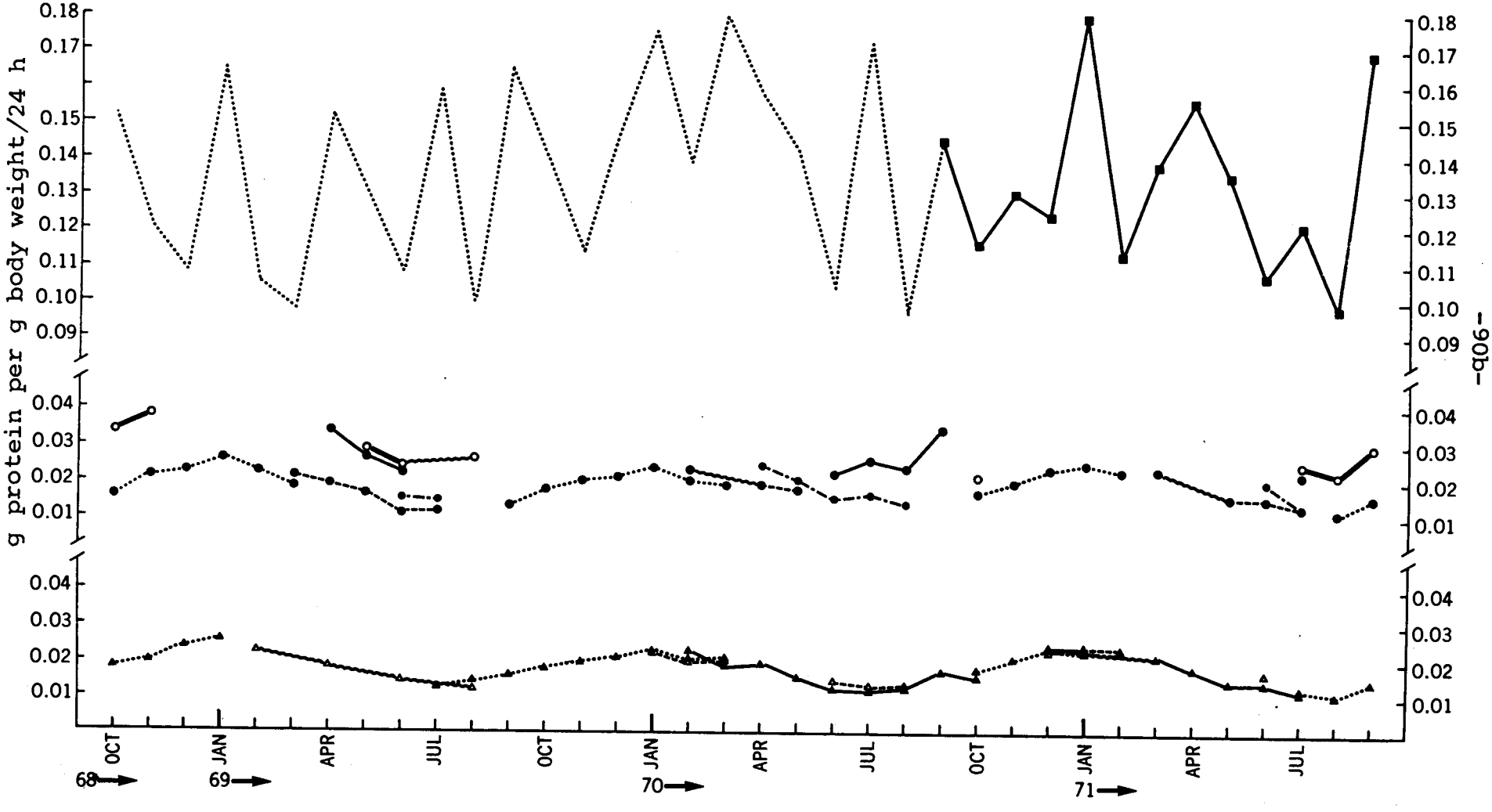
g protein per g body weight/24 h
0.18
0.17
0.16
0.15
0.14
0.13
0.12
0.11
0.10
0.09
0.04
0.03
0.02
0.01
OCT
JAN
APR
JUL
68
69
70
71

TABLE XIX - Comparison of monthly theoretical metabolic energy requirements (kcal/g body weight/24h) of two types of female deermice with estimated monthly assimilation (kcal/g body weight/24h).

Month	Active non-breeding female (17.0g)	Active pregnant and lactating female (22.0g)		Estimated assimilation
	At monthly mean temperature	At monthly mean temperature	At 3°C below monthly mean temperature	
JAN	1.22	2.06	2.24	2.37
FEB	1.14	1.92	2.11	2.28
MAR	1.13	1.89	2.07	2.11
APR	1.02	1.70	1.89	1.93
MAY	0.92	1.54	1.72	1.80
JUN	0.81	1.36	1.53	1.72
JUL	0.69	1.16	1.35	1.76
AUG	0.70	1.18	1.37	1.89
SEP	0.83	1.40	1.58	2.07
OCT	0.95	1.59	1.78	2.20
NOV	1.13	1.90	2.08	2.37
DEC	1.22	2.04	2.23	2.46

2. Energy value, feces.....4.919 ± 0.44 kcal/g dry weight (n + 267)[1]

3. Fecal production rate.....$\log_e$ value 5.98 ± 0.56 (Arithmetic value 0.40 x 10^{-2})g dry weight/h/g body weight (n = 116)[2].

The estimates of metabolic requirements in Table XIX were determined for an active non-breeding female of representative weight (17.0 g) and for an active pregnant and lactating female of representative weight (22.0 g). The ambient temperature used in the calculations was taken as the mean monthly temperature (monthly average maximum + monthly average minimum/2). These were based on 10 year averages (1958-1967) taken at the meteorological station at the U.B.C. Research Forest main gate.

The protein requirements of each individual deermouse was calculated on the basis of its maxADMR. The monthly averages of each reproductive class are shown in Fig. 13.

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1 As per footnote 2, page 85.

2 A better fit to the normal curve was obtained for this data by conversion to a $\log_e$ base. As a result the arithmetic value of the $\log_e$ mean differs from the uncorrected mean which was reported in Harling (1971) (see Appendix A).

The quantity of protein stored in the liver and in the eviscerated body are shown in Tables XVI and XVII. There were no significant differences for these parameters between reproductive seasons or between reproductive classes of deermice.

DISCUSSION

Before considering the data in terms of the original hypothesis, the procedures used in estimating consumption and requirements will be discussed. The major variable used in determining consumption was the fecal production rate in the field. Retention of a deermouse in a trap could increase this variable as a result of fright or to elevation of its metabolic rate because of cold stress. If fright raises the fecal production rate, it could be reasonably expected that the weight of feces produced during the initial capture would be higher than that produced during subsequent captures on the same night. As this did not occur, it would appear that fright is not a major stimulus to fecal production under the conditions of trapping. It should be noted that the fecal rates were applied to production times which assumed that the deermice were actually defecating for the entire period of activity. The mean fecal production rates in the field were higher ($t = 16.62$, $P < 0.001$) than those determined for laboratory animals. If the field rates were too high, the assimilation and consumption estimates in Figs. 12 and 13 and in Table XIX will be considerable overestimates.

Assimilation and consumption estimates were also dependent upon the digestibility coefficient of 87%. It is

known that coprophagy occurs in P. maniculatus and I have seen individuals consuming feces directly from the anus. Consequently, the digestibility coefficient is not altered. It is possible that field conditions could alter this coefficient. However, it is extremely unlikely that the coefficient would be significantly higher than 87% in the field so that again the figures give a maximum estimate of consumption.

The final variables used in the consumption estimates were the energy and protein values of the stomach contents. It was not possible to carry out replicate determinations on the contents of each separate stomach, so that monthly means were chosen as the best estimate. This assumed that the food found in the stomachs sampled represented the range of food types available inside that month. The estimate of total protein required assumes that amino acids are not limiting and is therefore an oversimplification of the field situation. The seasonal variation in food items consumed was described and discussed in Chapter II.

The major variables involved in the individual determination of basal metabolic requirements in Figs. 12 and 13 and in Table XIX were the body weight and ambient temperature. The increase in BMR due to activity over a 24 h period depends on the nature and length of activity, which is difficult to

monitor in the field. Although individuals were active throughout the night, no information is available on how continuously deermice were absent from their nests. Exact adjustments of metabolic rate for ambient temperature would involve monitoring the activity of a number of individuals in and out of the nest, the numbers of individuals in the nest at any one time, and the surface and ground temperatures throughout the night. P. maniculatus would not use artificial nestboxes and natural nests were very difficult to find, so that no attempt was made to monitor this activity nor were corrections for these factors applied. The maxADMR's are therefore overestimates as they are the requirements for an individual mouse maintained over 24 h at the monthly mean temperature. Torpor is also known to occur in deermice (Morhardt, 1970) but since its incidence and duration were unknown, no corrections could be applied.

As a result of measuring the maxADMR by the above methods, the estimates in Table XIX indicate a higher maxADMR in winter than in summer. This result differs from that obtained by several Polish workers (Gębczyński, 1966; Grodziński and Górecki, 1967) on rodents in eastern Europe where this seasonal pattern was reversed. There are three reasons for this discrepancy. Firstly, these workers have applied corrections for the estimated effects of nest temperature and

huddling in determining the daily energetic requirements during winter. I have no substantial data on this point and have therefore applied no such corrections. Secondly, Gębczyński (1966) claimed that the daily energy requirement of Apodemus flavicollis, a very similar species to P. maniculatus, was lower in winter than in summer. The data in his paper does not show statistically significant differences and when corrected to actual body weight the differences disappear. For A. agrarius, Górecki (1969) reported that if breeding effects were not included the daily energy requirements were higher in winter than in summer. Thirdly, and most importantly, the Polish workers have generally assumed that rodents have much shorter activity period in winter than in summer. They have used winter activity periods of as short as two hours. The data presented here and in Chapter I, and that of other workers on Peromyscus reviewed by Falls (1968), shows clearly that deermice have much longer periods of external activity in winter than in summer. It thus appears that P. maniculatus may have a different pattern of seasonal metabolism than some small mammal species reported in eastern Europe.

The conversion from maxADMR to an estimate of the protein requirements necessary to maintain nitrogen balance was done

on the basis of previously published information obtained on resting animals. The maxADMR involves an activity component for all animals and a reproductive component in pregnant and lactating females. The effect of activity on endogenous nitrogen requirement is not known. However, the extra protein costs of pregnancy and lactation (Poo, Lew, and Addis, 1939; Payne and Wheeler, 1968) will certainly be of the same order, if not greater, than the known extra energy costs.

The approach in using the estimates of consumption and requirements throughout the study has been to apply maximum estimates of both to determine the practicality of deermice breeding under these conditions. The consumption is almost certainly overestimated. More precise measurements of the variables used in determining assimilation and consumption would reduce the estimates given in Figs. 12 and 13 and Table XIX which thus represent the amount of food deermice could obtain under the best possible conditions. Similarly a known overestimate of the energy and protein requirements has been used which enables a comparison of the greatest metabolic needs of deermice with their maximum consumption.

To disprove the original hypothesis in terms of energetic intake, it is necessary to demonstrate that deermice cannot obtain sufficient energy to breed at certain times of the year.

Females which are pregnant and lactating have the highest energy demand. Table XIX shows that during summer their requirements are realized, but in the winter months (November - March) requirements rise more closely to their consumption, particularly if the mean temperature was 3°C lower in a given year. An increment of 98% was added for pregnancy and lactation. This may have been the only underestimate in the theoretical metabolic energy requirement because, as previously mentioned, the 98% correction is for lactation alone. In absence of any information on the extra cost of both pregnancy and lactation, no additional correction was used. However the increase may be in the order of 10 - 20% and would thus further elevate the theoretical requirement of the pregnant and lactating female such that her requirement could exceed the maximum estimated assimilation.

It is difficult to assess the profit/loss nature of the energetic costs of obtaining food. The maxADMR estimates would decrease relative to consumption if accurate temperature corrections could be applied on the basis of deermice remaining in nests during daytime. These relative proportions would probably not alter if deermice stayed in nests for increasing periods of the night, because consumption itself would therefore decline. Alternatively, pregnant and lactating females could

extend their activity periods into the daylight hours as the consumption estimates assume night activity only. It should be remembered, however, that the lactating female must spend some time actually suckling her young. In July, 1971, D. and M. Hawes (Harling, 1971) trapped on the study area, pregnant and lactating P. maniculatus during the day. Although such activity can occur in warm weather, the benefit that could be derived from daylight feeding in winter months would be very small. No such activity was observed in the winter.

Because the metabolic energy requirements of pregnant and lactating females rise close to the estimated maximum assimilation in winter months, and because as described above the 98% increase for pregnancy and lactation is certainly underestimated, these females could have extreme difficulty in meeting their energy requirements in winter. If, additionally a colder than normal mean temperature persisted for more than a few days, a condition which must frequently occur in the wild, these females would not be able to meet their requirements. I therefore conclude that it is unlikely that pregnant and lactating females can always meet their energy requirements to continue breeding throughout winter months.

Other workers on P. maniculatus and a similar European species, Apodemus sylvaticus, have reported that breeding can

continue late into winter in years of extensive seed fall or when artificial food was supplied. During this study, deermice have bred in outside cages during winter when food was supplied ad lib. Fordham (1971) reported an extended breeding season in wild populations of deermice supplied with artificial food, and Linduska (1942) reported winter breeding of deermice under stooks of corn. In years of good acorn crops, A. sylvaticus had an extended breeding season into winter (Smyth, 1966). Such observations indicate that when food is very plentiful, the metabolic costs of obtaining nutrition are sufficiently reduced that reproduction can occur. Deermice in the coastal regions of B.C. live in forest where heavy seed falls occur irregularly at approximately 6 year intervals (Gashwiler, 1969). No such fall occurred during this study but it is reasonable to predict prolonged breeding when it does.

Various studies of reproduction in P. maniculatus (Jameson, 1953; Brown, 1966; Terman, 1966; Fuller, 1969; Sadleir, 1970, 1973) have shown that breeding seasons can start in different months at the same locality. There have been few studies of photoperiodic control of breeding in P.

maniculatus. Whitaker (1940) found little evidence of such control in a closely related species, P. leucopus. It would seem that temperature variation between years may alter the season during which the energetic costs of obtaining food are lowered relative to their benefits. This would account for the irregularity of breeding seasons in P. maniculatus and perhaps other myomorph rodents.

The limiting effect of available calories on reproduction in deermice precludes any additional effect of protein quality or quantity, as the utilization of such protein is dependent on adequate caloric intake. It should be noted that Fig. 13 indicates protein consumption but it has quite possible that there are seasonal fluctuations in the nitrogen balance of this species. Tables XVI and XVII show no seasonal or reproductive differences in the amount of total protein stored in the liver or eviscerated body. Even during periods when caloric intake is sufficient for breeding, it remains possible that the quantity of total protein and its quality (in terms of amino acids) could affect reproductive performance. Thus it is not claimed that the second hypothesis is disproved.

Finally, it is useful to consider the type of evidence which could disprove the suggestion that deermice cannot obtain

sufficient energy to lactate throughout the year in cool temperate regions. I have suggested that winter breeding does not occur as the metabolic costs are too great to obtain the extra energy required for pregnancy and lactation. In more southerly regions, P. maniculatus can breed almost throughout winter (Jameson, 1953) where the higher ambient temperatures reduce metabolic costs of winter activity. The suggestion could be disproved, if deermice were found to breed and lactate throughout a winter of normal temperature and normal food supply.

SUMMARY

1. A new trapping technique developed for use in this study confirmed that deermice populations were nocturnally active out of the nest from approximately one hour after sunset until approximately one hour before dawn throughout the year. Individual deermice were active up to 82% of this time period. No mice were caught in this study during daylight but pregnant and lactating females were caught in July afternoons in areas adjacent to this study by other researchers.

2. Some mice moved distances of more than 100 m between captures in the same night. Several individuals were recaptured four or more times within a single night. Prevailing weather conditions affected out of the nest activity of the mice; bright moonlight and heavy rainfall were the most inhibiting to activity. Darker, warmer and drier nights tended to produce more intensive periods of out of the nest activity.

3. The occurrence of food items in stomach contents indicated seasonal trends in consumption. These trends appeared to be correlated with the availability of foods in the wild. Tree seeds were a major item in winter months and were replaced by berries in summer. Green vegetation was

consumed mainly in spring months. Fungi and arthropods were staple items, occurring frequently in stomachs throughout the year.

4. Stomach content wet weights determined from autopsied mice, normalized by use of a $\log_e$ conversion, had a mean of 35.8 mg/g mouse (n = 665). This was considerably less than one half of a mean "full stomach" wet weight of 125.0 mg/g mouse (n = 66). The heaviest 10% of stomachs sampled were considered full. The overall mean dry weight of all stomachs sampled was 10.74 mg/g mouse. Stomachs were usually empty early in the evening. It is suggested that stomachs were partially filled during most of the night with "full" weights only occurring towards dawn when mice returned to nests. Thus captures of mice with full stomachs were infrequent. There were no consistent significant differences between stomach wet weight contents of the various reproductive classes, or between mice caught in forest or slash environments in different years, or between different months of sampling within a given year or between the same months of different years.

5. The caloric values per g of stomach contents were normally distributed. The overall mean caloric value was 6.07 $\pm$ 0.52

(n = 404) kcal/g ash free dry weight. There were no consistent differences between the caloric contents of the various reproductive classes, or between mice caught in forest or slash environments in different years, or between different months of sampling within a given year or between the same months of different years.

6. A frequency distribution of caloric values of feces conformed to the normal curve. The overall mean caloric value was 5.55 ± 0.59 (n = 267) kcal/g ash free dry weight. The forest overall mean caloric value (5.63 ± 0.59) was significantly higher ($P < 0.05$) than the slash overall mean caloric value (5.48 ± 0.62) but such a difference was not considered to be of major importance in later calculations of energy budgets because defecation only amounts to 10% of consumption.

7. Fecal production rates determined in wild deermice, normalized by use of a $\log_e$ conversion, had a mean of 4.0 mg dry weight/g mouse/h (n = 116). This was significantly higher than those determined from laboratory deermice ($t = 16.62$, $P < 0.001$). The mean fecal production rate was maintained by the various reproductive classes in all months of the year. The maximum total dry weight of feces recorded for an individual mouse in

a single night was 978 mg.

8. The overall mean 24 h energy consumption of wild deermice was determined to be 38.44 $\pm$ 4.55 kcal/mean mouse. The overall mean 24 h energy consumption of the total population/ha was determined to be 909 $\pm$ 109 kcal. Total annual population consumption amounted to 3.22×10^5 kcal/ha.

9. Because the metabolic energy requirements of pregnant and lactating females rise close to the estimated assimilation in winter months and could potentially exceed requirements in very cold months it was concluded that these females would be unlikely to always meet their energy requirements to continue breeding throughout winter.

10. Because of the limiting effect of available calories on reproduction this precluded any additional effect of protein quality or quantity, as the utilization of such protein is dependent on adequate caloric intake. Although it appeared that adequate amounts of total protein were consumed at all times of the year to meet requirements, no measure was made of quality, in terms of amino acids, in the protein diet consumed. Thus it is not claimed that an hypothesis that deermice can obtain their protein requirements for reproduction at all times of the year was disproved.

APPENDIX A

A technique for precisely timing captures of *Peromyscus maniculatus*

A technique for precisely timing captures of *Peromyscus maniculatus*

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An electrical system is described which precisely times the captures of wild deermice in Longworth traps. This enables the immediate handling of trapped animals and permits more accurate determinations to be made of activity, body weights, and rate of fecal production. Subsequent release of deermice allows multiple recaptures in a single night, providing a better indication of movement patterns. Some results collected over a 12-month period indicate the value of the technique.

On décrit un système électrique qui détermine avec précision le temps où les souris *Peromyscus maniculatus* se sont prises dans des trappes Longworth. Ce système permet de suivre les animaux aussitôt après leur capture et de déterminer avec précision leur activité, le poids de leur corps et le taux de leur production fécale. La libération subséquente des souris entraîne de multiples recaptures dans une seule nuit et donne ainsi une meilleure indication sur l'ensemble de leurs déplacements. Des résultats recueillis sur une période de 12 mois donnent une bonne idée de la valeur de cette technique.

To evaluate activity patterns and energy budgets of small mammals, it is desirable to study them in their natural environments. Activity patterns and various parameters of energy budgets are often studied under laboratory conditions (Park 1935; Hatfield 1940; Miller 1955; Erkinaro 1961; Kavanau 1966; Górecki 1969; Hansson and Grodziński 1970). Elton *et al.* (1931) and Brown (1956) both studied activity patterns of *Apodemus* and *Clethrionomys* by making periodic visits to live traps throughout 24-h periods. Ashby *et al.* (1969) studied the distribution and activity of water voles by following and observing specifically marked individuals. Camera recording devices have also been used for monitoring of activity at specific sites (Pearson 1959; Dodge and Snyder 1960; Ray 1967). The technique described here precisely timed the captures of deermice (*Peromyscus maniculatus*) and permitted them to be examined, handled, and released almost immediately. Thus precise and immediate determinations of body weights were made, and timed collections of fecal samples were taken. As mice were released immediately after capture, multiple recaptures were possible within a single night, allowing a more accurate determination of movements.

Captures were timed by using Longworth traps (Chitty and Kempson 1949) connected via multiple conductor electrical cables to a panel of flashlight bulbs (see Figs. 1 and 2). A lighted bulb indicated that a single specific trap had been set off. A buzzer connected in series also informed the operator that a trap had been triggered.

The traps were spaced at 10-m intervals along four separate 100-m lines on a 3-ac slash site (Petticrew and Sadleir 1970) within the University of British Columbia Research Forest at Haney in Southern British Columbia (49°N, 122°W). Permanent cables were installed along the trap lines. Traps were removed for storage between monthly trapping sessions. The monitoring panel was housed in a mobile sleeping trailer situated a few meters off the trapping area.

The system has been in operation for several nights of each month over a 12-month period. Deermice activity began about 1 h after sunset and ceased no later than an hour before sunrise throughout the year, indicating that the out-of-nest activity was exclusively nocturnal. The monthly nighttime fecal output approximated 478 mg dry weight per 100 g of mouse, per hour, throughout the year, and was estimated by collecting feces from traps in which the mice had been left for known time intervals before release. The fecal output rate was usually higher in the early part of the activity cycle and diminished towards dawn. Fecal water content was determined from samples collected directly from the anus of live animals and averaged 73% by weight. Autopsies on selectively killed individuals provided data on stomach content weights. From February through May, 1970, these weights

ranged, on average, from 0.10 g dry weight on first capture to 0.43 g on final capture. They had an average water content of 66% by weight. Caloric values of stomach contents and feces are being estimated, using a microbomb calorimeter, to determine energy budgets of deermice.

The sequence of multiple visits to specific traps within one night by the same mouse, and by different mice, was recorded. Estimations of home range by this technique compared with trap-revealed home ranges on the same area showed considerable differences. These will be reported in a later publication.

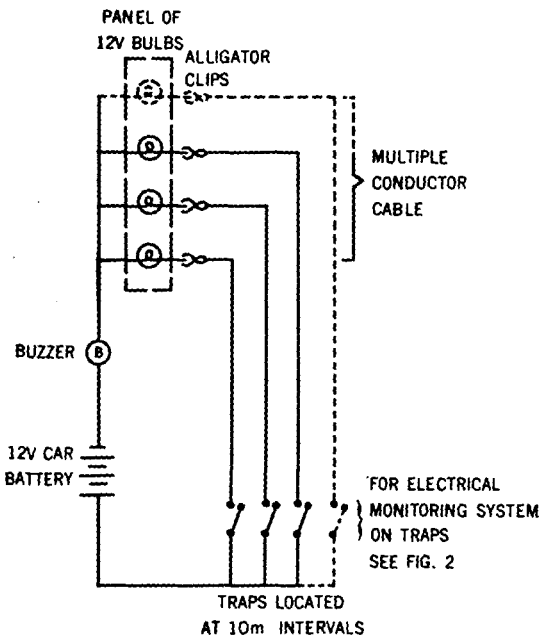

FIG. 1. Circuit diagram of timed capture trapping system.

Addendum

Since this paper was submitted, D. and M. Hawes (personal communication), who have been studying the activity of shrews, *Sorex* sp., and microtines in the same area, have captured, during July, pregnant and lactating female *P. maniculatus* between 1400 and 1730 h. This abnormal activity will be further investigated.

Acknowledgments

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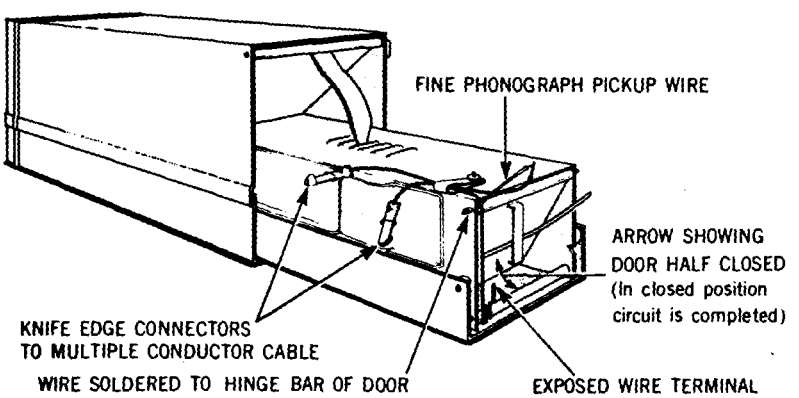

FIG. 2. Modified Longworth trap.

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APPENDIX B

The occurrence of *Endogone macrocarpa* in stomachs of *Peromyscus maniculatus*

The occurrence of *Endogone macrocarpa* in stomachs of *Peromyscus maniculatus*

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Chlamydospores of *Endogone macrocarpa* Tul. were found in the stomach contents of deermice (*Peromyscus maniculatus* Wagner) trapped in the University of British Columbia Research Forest over a 14-month period. A seasonal variation in frequency of occurrence was noted, but spores were found in more than one-third of 103 stomachs. No correlation was observed between the presence of *Endogone* and other plant or animal remains in the stomach contents.

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Introduction

Spores of *Endogone* species have been reported frequently in the stomach contents of animals such as rodents and arthropods. Thaxter (1922) observed apparently intact spores of *Endogone* in the stomach contents of shrews and millipedes. Diehl (1931) reported the zygospores of a species of *Endogone* in the stomach contents of two shrews, *Sorex fumeus* and *S. cinereus*. He speculated that they may have ingested the spores by feeding on earthworms which had in turn eaten *Endogone*. Later reports (Dowding, 1955; Bakerspigel, 1956, 1958; Williams and Finney, 1964) described spores of several species of *Endogone*, notably those of *E. fasiculata* Thaxter and *E. pulvinata* Henn. in the stomach and cæcal contents of deermice (*Peromyscus maniculatus*) and eight other species of rodent. In this study observations were made on the frequency of *Endogone* spores in stomach contents of 103 deermice trapped in British Columbia.

Materials and Methods

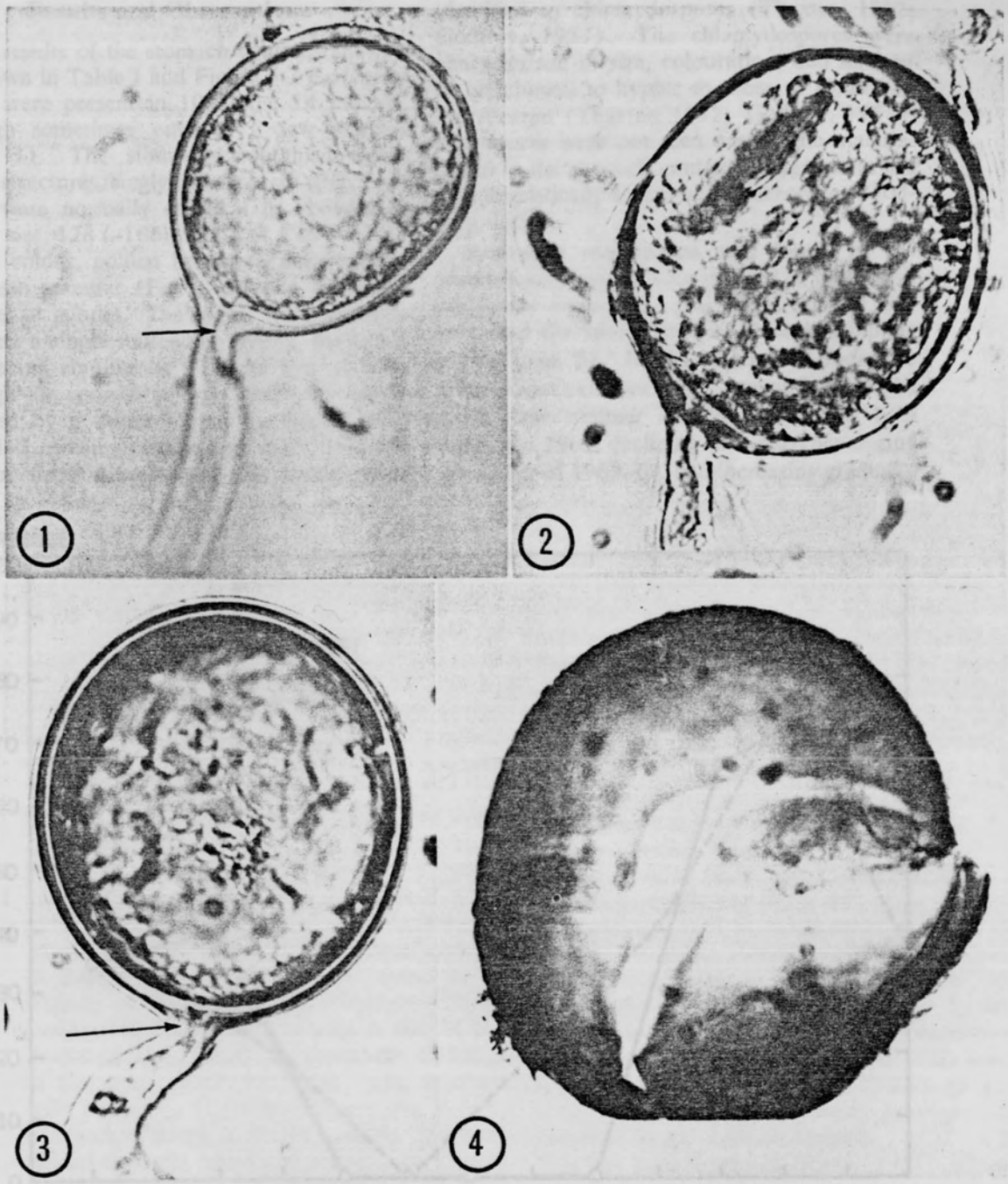
Deermice were trapped over an area of about 6 square miles in the University of British Columbia Research Forest at Haney, British Columbia (49° N, 122° W). They were trapped during alternate months from September 1968, until October 1969, in a coastal western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest from 50 to 100 years old (*FOREST*), and during the other months on areas which had the same cover type but which were logged from 0 to 10 years ago (*SLASH*). All mice were caught in baited snap traps and were frozen until autopsy. After thawing, stomach contents were removed and either stored in 70 per cent ethanol (Sept. 1968, only), processed directly, or dried at 60 C and then rehydrated. The contents were then spread evenly on slides, mounted in permount, and examined microscopically.

TABLE I

Occurrence of *Endogone macrocarpa* chlamydospores in stomach contents of *Peromyscus maniculatus*

Month and year		Number of stomachs	
		Examined	Containing *Endogone*
Sept. 1968	(F)*	14	5
Oct.	(S)†	12	4
Nov.	(F)	5	2
Dec.	(S)	5	1
Jan. 1969	(F)	5	0
Feb.	(S)	5	0
Mar.	(F)	5	0
Apr.	(S)	5	1
May	(F)	5	0
June	(S)	5	2
July	(F)	9	6
Aug.	(S)	8	6
Sept.	(F)	9	7
Oct. 1969	(S)	11	4
Total		103	38 (37%)

* F=Forest; † S=Slash.



FIGURES 1–4. FIG. 1, *Endogone macrocarpa* chlamydospore; arrow indicates continuity between hyphal wall and endospore of chlamydospore; ×300. FIG. 2, chlamydospore with very granular cytoplasm, ×300. FIG. 3, chlamydospore showing thickening of hyphal wall at the point of contact with the spore (*arrow*), ×300. FIG. 4, chlamydospore with ruptured wall; the interior appears devoid of cytoplasmic contents; ×450.

Results and Observations

The results of the stomach contents analysis are shown in Table I and Figure 5. *Endogone* spores were present in 10 of the 14 months, although sometimes only in a few animals (Table I). The stomachs contained thick-walled structures, singly or in masses (Fig. 1–3) which were normally elliptical to obovoid in shape; size, 128 (–166)–212 μ × 116 (–132)–200 μ; colour, golden brown to dark brown; cytoplasm granular (Fig. 1–3) with numerous vacuoles or gutules. The spores were regularly borne on a single subtending hypha, the endospore being continuous with the hyphal wall, although the connection was sometimes nearly obscured by a thickening of the hyphal wall (Fig. 1–3, *arrows*) below the spore. On the basis of these observations the spores were identified as chlamydospores (Thaxter, 1922; Godfrey, 1957). The chlamydospores were characteristic in size, colouration, and manner of attachment to hyphæ to those of *Endogone macrocarpa* (Thaxter, 1922; Godfrey, 1957). Zygospores were not seen among the material found in the stomach contents. Zygospores are characteristically absent in *E. macrocarpa* (Godfrey, 1957).

Endogone macrocarpa was found in the stomach contents of mice trapped in both slash and forest areas and equal proportions of animals had the spores present at each sampling period (Fig. 5). It was noted that *Endogone* chlamydospores were most common in stomachs during late summer and fall months of both 1968 and 1969, declining in occurrence during the winter of 1968–69, and increasing gradually

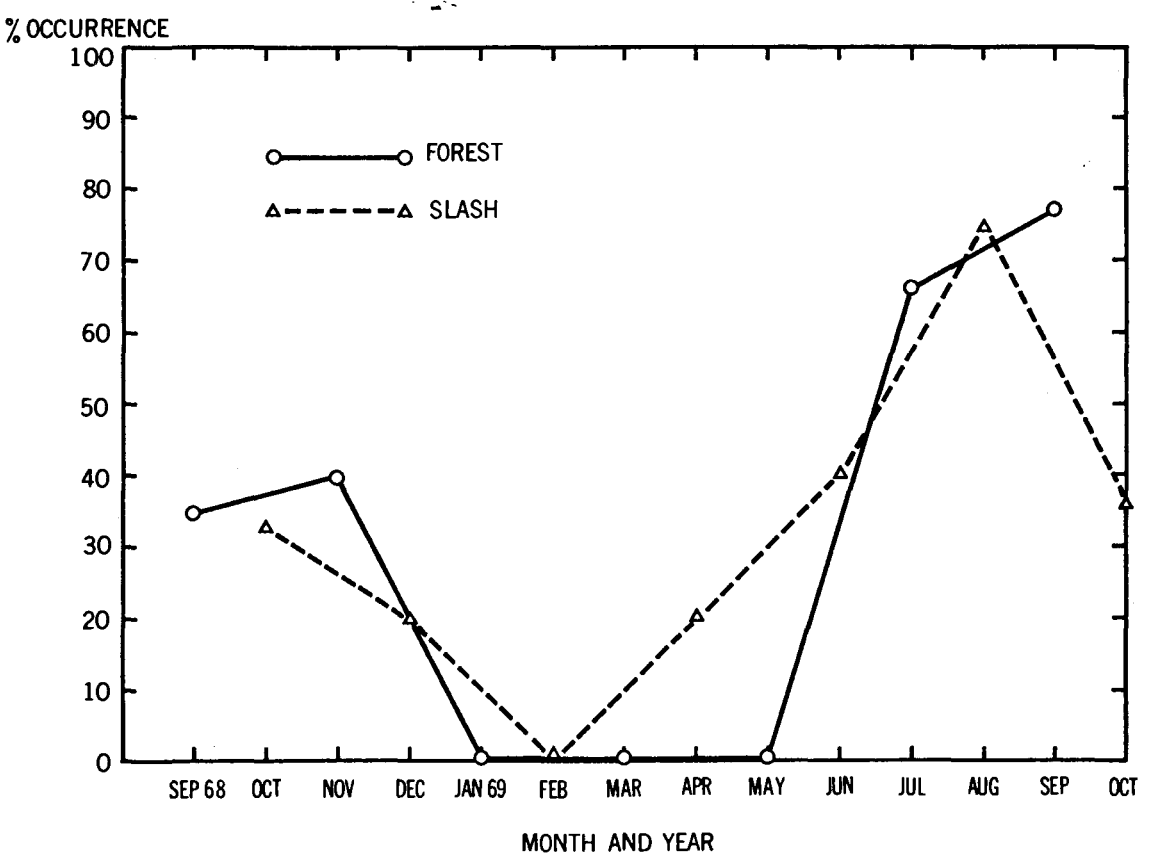


FIGURE 5. Percentage occurrence of *Endogone* in stomach contents of *Peromyscus maniculatus* trapped in forest and slash areas, University of British Columbia Research Forest, Haney, British Columbia.

during the spring and summer of 1969 (Fig. 5). *Endogone* was found with approximately equal frequency in the stomachs of males and females.

The walls of chlamydospores of *Endogone macrocarpa* ranged in thickness from 5 to 10 μ. The chlamydospores most often appeared to be intact, even though they were among other plant and animal material which had obviously been macerated during feeding. Occasional chlamydospores were found in which the wall was ruptured (Fig. 4). In these instances the spores appeared empty of their normal granular cytoplasm. No correlation was observed between the occurrence of *Endogone* chlamydospores and the occurrence of other plant or animal remains in the stomach contents. No regular system of quantifying the number of *Endogone* chlamydospores in the stomach contents was employed, but in many instances more than 100 chlamydospores were observed in a single microscope slide mount of material. Attempts to germinate the chlamydospores by plating out stomach contents on malt agar have so far proven unsuccessful.

Discussion

Dowding (1955) reported *Endogone fasiculata* and *E. pulvinata* in the stomach contents of rodents trapped in a wide area of southern Alberta. Similarly, Bakerspigel (1956) reported *E. fasiculata* chlamydospores and zygospores in the stomach contents of rodents trapped from May to September in Saskatchewan and northwestern Manitoba. Although *E. fasiculata* would appear to be the most commonly encountered species in the stomachs of rodents in these provinces, our material seems to be entirely of *E. macrocarpa*. Thaxter (1922) commented that *E. macrocarpa* is one of the most frequently observed and variable members of the genus. Godfrey (1957) also observed wide variations in chlamydospore size, colour, and wall thickness in *E. macrocarpa*. She concluded that this species contained overlapping " strains " which could occur in the same area. Our material showed a range in chlamydospore colouration from golden to brown, and a variation in spore size and wall thickness. However, Thaxter also noted that this species had been found rarely in North America before that date (1922). Additional material, collected from mice and other rodents over a larger area of southern British Columbia might reveal the presence of *E. fasiculata*, and other species, particularly in the stomachs of rodents from eastern British Columbia.

It is difficult to account for the seasonal changes in frequency of occurrence of *Endogone macrocarpa* during the period of the survey. The winter of 1968–69 was particularly severe in southwestern British Columbia and the number of mice trapped was low. The absence of *Endogone* spores in the stomach contents of mice trapped during January–March 1969, may have been due either to non occurrence of *Endogone* sporocarps in the area or to an inability of the mice to forage widely for food because of the heavy snow cover during these months. Other studies (Dowding, 1955; Bakerspigel, 1956, 1958; Williams and Finney, 1964) have not attempted to survey the occurrence of *Endogone* during the winter. Williams and Finney (1964), moreover, reported that *Endogone* occurred in the stomachs of mice only in August in Colorado and Wyoming. They attributed this to the fact that the sporocarps of the fungus were only produced in that region during the late summer and early fall. In our survey, *Endogone macrocarpa* chlamydospores were found in stomach contents in April 1969, not in May of that year, and with generally increasing frequency of occurrence as the year progressed.

The value of *Endogone* as food material for rodents is at present unknown. The chlamydospores observed in the stomach contents of *Peromyscus maniculatus* were generally intact, and did not appear to have been physically or chemically degraded. However, the hyphæ making up the remainder of the sporocarp which contains the chlamydospores of *E. macrocarpa* appeared to have been broken up into short fragments, and they were generally uncommon in the stomach contents.

It has been suggested (Diehl, 1931; Dowding, 1955) that *Endogone* sporocarps might be eaten by insects or other arthropods or by earthworms, which might then be eaten by rodents. In this way, the presence of *Endogone* spores in the stomach contents of rodents might be entirely fortuitous. Although we noted

arthropod remains among the stomach contents of some of the mice examined, there did not appear to be any necessary correlation between the occurrence of the animal remains and the presence of *E. macrocarpa* chlamydospores. In fact, in the total survey *Endogone* chlamydospores were more commonly encountered than arthropod remains. It would appear unlikely, therefore, that the deermice eat *Endogone* secondarily only through arthropod consumption.

Conclusion

Endogone macrocarpa occurs regularly in the stomach contents of deermice in both slash and forested areas in southwestern British Columbia. The occurrence of the fungus varies with the season, but no exact correlation can yet be made between the occurrence of the fungus in nature and its presence in the stomach contents of mice. The nutrient value of *Endogone macrocarpa* is unknown.

Acknowledgments

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Personal History:

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Academic Qualifications:

Teachers' Certificate. Wing Course in Science. Durham (England) 1965.
B.Sc. (Honours) Zoology. Durham (England) 1968.

Awards:

Local Education Authority (Carlisle, England) Grants to attend Bede College, Durham University 1962-1965.
County Major Awards (Carlisle, England) to attend Durham University 1966-1968.
Westbury Preston Travel Grant (English-Speaking Union of the Commonwealth, London, England). Travel Scholarship to undertake research in Canada - Simon Fraser University 1968.
National Research Council Graduate Bursary. Simon Fraser University 1969-1970.
President's Research Stipend, Simon Fraser University, Spring Semester, 1972.

Teaching and Related Experience:

Harraby Secondary Modern School (ages 11-18), Carlisle, England. Teaching Science subjects, mainly biology 1965-1966.
Outward Bound Mountain School, Eskdale, England (ages 17-21). Visiting Instructor 1963-1968.

Department of Biological Sciences, Simon Fraser University, Teaching Assistant. Involved in planning and teaching of 409 (Field Ecology) and 410 (Ethology) courses. Guest lectures in 101 and 102 (Introductory Biology) and Kinesiology courses. 1968-1972.

Simon Fraser University, Television Ecology Project. Assistant to Project Director. 1971.

Notre Dame University, Nelson, B.C. Assistant Professor. 1972 to date.

Membership in Professional Organizations:

Canadian Society of Zoologists
British Ecological Society
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Publications:

Harling, J. 1968. The effect of wind direction on the index of diversity of night flying Lepidoptera in a particular area. Entomologist's Rec. J. Var. 80: 32-35.

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Papers Read:

Activity and feeding patterns of water voles in Old Durham Beck, Durham. British Mammal Society Conference, Nottingham University, England, Easter, 1968.

Intake and requirements of energy and protein in wild deermice (Peromyscus maniculatus) relative to breeding duration. British Society of Reproduction and Fertility Symposium, Edinburgh University, Scotland, March, 1972.