

THE UNIVERSITY OF MANITOBA

CHANGES IN BODY WEIGHT AND ACTIVITY OF JUVENILE  
RICHARDSON'S GROUND SQUIRRELS, SPERMOPHILUS RICHARDSONI,  
UNDER CONTROLLED LABORATORY CONDITIONS.

BY

DEBORAH HELEN HARDING

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES  
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS OF  
THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

WINNIPEG, MANITOBA

JUNE, 1980

CHANGES IN BODY WEIGHT AND ACTIVITY OF JUVENILE  
RICHARDSON'S GROUND SQUIRRELS, SPERMOPHILUS RICHARDSONI,  
UNDER CONTROLLED LABORATORY CONDITIONS

BY

DEBORAH HELEN HARDING

A thesis submitted to the Faculty of Graduate Studies of  
the University of Manitoba in partial fulfillment of the requirements  
of the degree of

MASTER OF SCIENCE

© 1980

Permission has been granted to the LIBRARY OF THE UNIVER-  
SITY OF MANITOBA to lend or sell copies of this thesis, to  
the NATIONAL LIBRARY OF CANADA to microfilm this  
thesis and to lend or sell copies of the film, and UNIVERSITY  
MICROFILMS to publish an abstract of this thesis.

The author reserves other publication rights, and neither the  
thesis nor extensive extracts from it may be printed or other-  
wise reproduced without the author's written permission.

## ABSTRACT

Body weight, food consumption, and activity of juvenile Richardson's ground squirrels (Spermophilus richardsoni) were determined for one year in two different year groups of animals under controlled conditions of photoperiod, temperature, and food availability. Standard metabolic rate for these two groups and lean body weight for a third group of animals were determined also for one active season. Body weights of free-ranging juveniles were obtained for comparison.

Mean body weight of juvenile Richardson's ground squirrels increased rapidly as a result of growth and fat deposition during initial captivity. Maximum weights were attained in late summer and remained relatively constant as long as animals had free access to food. Stabilization of body weight was accompanied by a reduction in food consumption and in metabolism. Reduced food consumption, metabolic rate and activity, moulting, nest building and docility in autumn occurred under constant conditions of ambient temperature and photoperiod, and indicated physiological and behavioral adjustments in preparation for hibernation. Hibernation occurred under laboratory conditions in most animals deprived of food but not in those with food ad libitum. Weight loss after food deprivation was

regained rapidly upon reprovision of food. All animals gained weight in the early spring and food consumption and activity increased to levels similar to those in autumn. Activity and food intake subsequently declined while body weight continued to increase.

Mean body weight changes of juvenile female ground squirrels in the field paralleled those of ground squirrels in the laboratory. The former, however, gained weight at a slower rate and to a lesser extent. Mean body weight of free-ranging juvenile males increased steadily throughout the season. Data obtained indicate that most free-ranging juvenile females obtain maximum body weights prior to hibernation at an earlier time than do juvenile males.

Possible causes for differences in body weight changes, and factors involved in the triggering of hibernation of Richardson's ground squirrels have been discussed.

## ACKNOWLEDGMENTS

I would like to thank Dr. J.C. Rauch for her guidance and supervision during this study, for her careful criticism of this manuscript, and for her help in the collection of animals.

I am grateful to Drs. K.W. Stewart and J.M. Stewart for their evaluation of this thesis.

I thank Mr. Van Wynnberg of the Brockville Farm, Winnipeg, for allowing me to trap on his property and Mr. W. Grassler and Mr. J. Gould of Central Instruments, University of Manitoba, for designing and building the activity recording device.

My thanks go also to my parents, Dr. and Mrs. F.H. Brown, for their financial assistance and encouragement, and to my husband, Warren, for his assistance in the trapping of animals.

This study was supported by a grant (A6790) to Dr. J.C. Rauch from the National Research Council of Canada (NRC) and by an NRC scholarship.

TABLE OF CONTENTS

	Page
ABSTRACT . . . . .	i
ACKNOWLEDGMENTS . . . . .	iii
LIST OF TABLES . . . . .	vi
LIST OF FIGURES . . . . .	vii
INTRODUCTION . . . . .	1
MATERIALS AND METHODS . . . . .	4
Source of Animals . . . . .	4
Grouping of Animals . . . . .	4
Care of Animals . . . . .	5
Experimental Conditions . . . . .	6
Body Weight Measurements . . . . .	9
Lean Body Weight Determinations . . . . .	10
Metabolic Rate Determination . . . . .	11
Determination of Respiratory Quotient . . . . .	13
Activity Measurements . . . . .	14
Food Consumption Measurement . . . . .	17
Treatment of Data . . . . .	17
Statistical Analysis . . . . .	18

TABLE OF CONTENTS Continued...

	Page
RESULTS . . . . .	20
Body Weights . . . . .	20
Growth and Fat Deposition . . . . .	26
Metabolic Rate . . . . .	28
Activity . . . . .	31
Food Consumption . . . . .	40
Interrelationships of Activity, Food Consumption, Standard Metabolic Rate and Weight . . . . .	42
DISCUSSION . . . . .	46
LITERATURE CITED . . . . .	63
APPENDICES . . . . .	71

LIST OF TABLES

Table		Page
1	Summary of experimental conditions . . . . .	7
2	Effect of light and food deprivation on hibernation of juvenile <u>S. richardsoni</u> . . . . .	36

LIST OF FIGURES

Figures		Page
1	Two-way swinging door and microswitch triggering system . . . . .	15
2	Mean body weights of Group I and II juvenile <u>S. richardsoni</u> maintained at different photoperiods . . . . .	21
3	Mean body weights of Group I male and Group I and II female juvenile <u>S. richardsoni</u> . . . . .	22
4	Mean body weights of female and male juvenile <u>S. richardsoni</u> in their natural habitat during their first active season . . . . .	24
5	Individual body weights of five female and four male juvenile <u>S. richardsoni</u> in their natural habitat during their first active season . . . . .	25
6	Mean lean and total body weights of Group III juvenile <u>S. richardsoni</u> . . . . .	27
7	Mean body weights and oxygen consumption of Group I and II female juvenile <u>S. richardsoni</u> . . . . .	29
8	Mean body weights and oxygen consumption of Group I male juvenile <u>S. richardsoni</u> . . . . .	30
9	Mean daily activity of Group I and II juvenile <u>S. richardsoni</u> maintained at different photoperiods . . . . .	32
10	Activity of paired juvenile <u>S. richardsoni</u> during the 24 h cycle . . . . .	34
11	Monthly changes in daily distribution of activity of Group I A <sub>1</sub> juvenile <u>S. richardsoni</u> . . . . .	37
12	Hibernation bouts of Group II juvenile <u>S. richardsoni</u> . . . . .	38

LIST OF FIGURES Continued...

Figures		Page
13	Mean daily activity of two pairs of Group II juvenile <u>S. richardsoni</u> held ing food deprivation . . . . .	39
14	Mean weekly food consumption of Group I and II juvenile <u>S. richardsoni</u> maintained at different photoperiods . . . . .	41
15	Daily activity, weekly food consumption, oxygen consumption and body weight of a Group II juvenile <u>S. richardsoni</u> held at LD 00:24 during winter . . . . .	43
16	Daily activity, weekly food consumption, oxygen consumption and body weight of a Group II juvenile <u>S. richardsoni</u> held at LD 12:12 . . . . .	44

## INTRODUCTION

Hibernation is a periodic state of depressed metabolism. The lower energy expenditure it permits, as compared with the non-hibernating state (Lyman and Chatfield 1955; Bailey and Davis 1965; Wang 1979), allows survival in environments with extended periods of cold and concomitant food shortage.

Ground squirrels of the genus Spermophilus (Cuvier) may spend six to eight months of the year in a torpid state (Davis 1976). Their active life is confined, therefore, to a relatively short period during which changes take place for reproduction, growth, and fat deposition (Kalabukhov 1960). To meet this seasonal restriction, some species of ground squirrels have developed annual endogenous rhythms (Pengelley and Asmundson 1971, 1974) reflected by such changes as body weight, activity, and food consumption. These may be expressed over long periods under laboratory conditions, i.e. in the absence of environmental cues (Pengelley and Fisher 1963, 1966; Pengelley and Kelly 1966; Heller and Poulson 1970; Pengelley and Asmundson 1974). Endogenously rather than exogenously-regulated rhythms ensure the preparation of animals for environmental events before their occurrence (Heller and Poulson 1970; Immelman 1973), buffer animals from unseasonable weather (Enright

1970), and allow for physiological changes in animals divorced from environmental cues (Heller and Poulson 1970). The rigidity of endogenous control, however, is apparently species-dependent and related to the ecology of the animal (Pengelley and Kelly 1966; Heller and Poulson 1970).

The type of control initiating hibernation in ground squirrels also appears to depend upon the species. Under laboratory conditions, at least, some species enter hibernation at a given time of the year regardless of environmental conditions (Pengelley and Fisher 1957, 1961, 1963). Other species, however, do not readily enter hibernation in the laboratory, presumably because of the absence of appropriate environmental cues (Pengelley and Fisher 1961; Pengelley and Kelly 1966).

Richardson's ground squirrel, Spermophilus richardsoni, a relatively abundant hibernator in the central plains of North America, is annually subjected to long periods of cold weather and food shortage in the more northern reaches of its distribution. Although the annual cycle of this species in its natural habitat has been well documented (Quanstrom 1968; Yeaton 1969; Clark 1970a; Michener 1968, 1974; Dorrance 1974; Zegers and Williams 1977; Michener 1977a, 1978, 1979a), many factors underlying this cycle have not yet been established. In addition, there are conflicting results regarding the conditions under which this animal will hibernate (Pengelley and Fisher 1961; Scott and Fisher 1970; Hudson and Deavers 1976). For these

reasons, this study has been designed to investigate possible changes in body weight and activity in Richardson's ground squirrels under different conditions of photoperiod and food availability. Metabolic rate and food consumption were determined because of their relationship to body weight. For comparative purposes, body weight of free-ranging ground squirrels of similar age and the same population were recorded in the field. The study has been confined to juvenile animals to minimize the effect of reproductive activity and previous experience of hibernation.

In accordance with the decision of the International Commission on Zoological Nomenclature (Hemming 1958), the generic name Spermophilus (Cuvier) has been used in this thesis for reasons given by Hershkovitz (1949).

## MATERIALS AND METHODS

### Source of Animals

Juvenile Spermophilus richardsoni were trapped from a colony inhabiting a cow pasture in southwest Winnipeg (49°54'N; 97°14'W), Manitoba. Collapsible live traps, No. 3 (Tomahawk, Wisconsin, USA), were baited with a peanut butter oatmeal mixture and placed upwind of burrows. Since S. richardsoni are not distributed randomly within the colony (Yeaton 1969), and juveniles were of particular interest, traps were set in an area which contained mainly adult females and young.

### Grouping of Animals

Animals were grouped as follows:

Group I consisted of 12 juvenile males and 12 juvenile females trapped in the middle of July, 1976, and transferred to the University of Manitoba for study in the laboratory for a one-year period (1976-77).

Group II consisted of 16 juvenile females trapped in early July, 1977, and transferred to the University of Manitoba for study in the laboratory for a one-year period (1977-78).

Group III consisted of 10 juvenile females trapped in early July, 1977, and transferred to the laboratory for lean body weight determinations.

Group IV consisted initially of 40 juvenile males and 40 juvenile females used for weekly weight determinations conducted in the field between June and November, 1978. The study was performed until above-ground activity ceased.

Group IV animals were marked by toe clipping using the technique of Baumgartner (1940). They were restrained in gloved hands and the first joint of the required toe was removed with nail clippers. In no animal were more than two toes clipped and only one toe per foot. Animals appeared not to be grossly disturbed as some were recaptured within a half hour of marking.

During each trapping session, all juveniles caught were sexed, weighed on a triple beam balance and dyed with vegetable dye to ensure the weight of animals recaptured during a given trapping session would not be recorded twice.

#### Care of Animals

Animals were held in wire mesh cages (0.5 m x 0.6 m x 0.3 m) with one or two animals per cage, depending on experimental conditions. Each cage was partitioned by a central wall with a vertically-suspended two-way swinging door allowing free movement between the two halves of the cage. This door was required for activity measurements. Attached to the exit of each cage was a runway consisting of

a wooden frame (0.9 m x 0.3 m x 0.3 m) enclosed in a double-layered, meshed cooping wire except for the bottom which was wood. This permitted the animals to move from the cage to the food placed at the end of the runway.

Cages were covered with black cloth to minimize light in nesting areas. Wood shavings served as nesting material. Cages were cleaned every four to five days except during the expected hibernation period when cleaning was discontinued to minimize disturbance of animals.

Lab Chow, Wayne Blox F6 (Allied Mills, Inc., Chicago, Illinois, USA), 24% protein, 6% fat, 4.5% fibre, was provided ad libitum except when food was withdrawn for experimental purposes.

#### Experimental Conditions

Group I animals were paired as outlined in Table 1. From the time of capture until the middle of September, these animals were kept at an ambient temperature ( $T_a$ ) of 23°C and a photoperiod of LD 12:12. In the middle of September they were transferred to a controlled environmental chamber (CE room) and  $T_a$  was gradually lowered from approximately 23°C to 7°C. A  $T_a$  of 7°C was chosen for the hibernation season as Quanstrom (1968) measured comparable temperatures in ground squirrel burrows during the middle of winter.

Commencing the beginning of December, half of the animals were subjected to continuous darkness (Group I B<sub>1</sub>),

Table 1. Experimental conditions to which juvenile <u>S. richardsoni</u> were exposed during 1976-77 and 1977-78				
EXPERIMENTAL CONDITIONS	TREATMENT A <sub>1</sub>	TREATMENT B <sub>1</sub>	TREATMENT A <sub>2</sub>	TREATMENT B <sub>2</sub>
YEAR OF STUDY	1976-77	1976-77	1977-78	1977-78
LIGHT REGIME	LD 12:12	LD 12:12 JUL 15 - NOV 30 LD 00:24 DEC 1 - APR 30 LD 12:12 MAY 1 - JUN 24	LD 12:12	LD 12:12 JUL 1 - NOV 22 LD 00:24 NOV 23 - APR 30 LD 12:12 MAY 1 - JUN 22
TEMPERATURE	23°C JUL 15 - SEPT 15 7°C OCT 1 - APR 1 20°C MAY 1 - JUN 24	Similar to 1	20°C JUL 1 - SEPT 15 7°C OCT 1 - APR 1 20°C MAY 1 - JUN 22	Similar to 3
FEEDING REGIME	Food <u>ad libitum</u>	Similar to 1	Food <u>ad libitum</u> JUL 1 - NOV 22 JAN 15 - JUN 22 Withdrawl NOV 23 - JAN 14	Similar to 3
TOTAL NUMBER OF ANIMALS	8	8	6	6
SOCIAL ENVIRONMENT <sup>ab</sup>	2 pr male-female 1 pr male-male 1 pr female-female	Similar to 1	1 pr females 4 single females	Similar to 3

<sup>a</sup> Prior to its division into treatments 1 and 2, Group I animals consisted of 6 pr male-female, 3 pr male-male and 3 pr female-female

<sup>b</sup> Prior to the hibernation season, Group II animals consisted of 4 pr female-female and 8 single females

the other half were retained at LD 12:12 (Group I A<sub>1</sub>). Animals were subjected to these conditions until April when T<sub>a</sub> was gradually increased to 20°C, and animals which had been kept at LD 00:24 were re-exposed to LD 12:12. Group I animals had free access to food and water.

Four deaths occurred in Group I. These consisted of one male from a male-female pair, one female from a female-female pair, and both males from a male-male pair.

One CE room broke down in late March, the other in early April. Animals were then exposed to T<sub>a</sub> as high as 27°C for 3 to 4 h, and to approximately 20°C for several days. Subsequently, previous experimental conditions were resumed.

Group II, consisting of females only, were held under similar conditions of photoperiod and temperature as Group I animals; Group II A<sub>2</sub> were held at LD 12:12, Group II B<sub>2</sub> were transferred to LD 00:24 in late November (Table 1). Two major changes in experimental design were made as compared to that for Group I. Half of the animals were held one per cage, the other half were kept in pairs, and food was withheld from late November until the middle of January (Table 1). The reason for keeping some animals individually was that during the previous year, paired animals did not hibernate. This might have been caused by disturbance or aggression (Carl 1971). Some Group II animals were paired, however, for comparison with animals from the year before, and with individually-caged animals of the same year.

Food was withheld commencing late November when none of the animals had gone into hibernation and because availability of food might influence hibernation in this species (Davis 1976). Because of the continued activity of some animals despite food withdrawal, body weights were measured in the middle of January and, due to considerable weight decline, food was again supplied.

Four deaths occurred within Group II. Two animals, one from a pair held at LD 12:12, the other from a pair held at LD 00:24 died between late November and the middle of January. Two further deaths, again one from each photoperiodic treatment, occurred after animals had free access to food.

A light failure during January exposed animals of Group II A<sub>2</sub> to darkness for several days. Since most animals remained in hibernation, as indicated by their activity record, they were probably not adversely affected by the change in photoperiod.

#### Body Weight Measurements

Captive animals of Groups I and II were weighed once a week between July and November whereupon measurements were discontinued to minimize disturbance during the hibernation season. Weight measurements of Group I animals were resumed at the beginning of March, and of Group II animals in the middle of January.

### Lean Body Weight Determinations

To estimate to what extent body weight changes in captive animals were due to growth and to fat deposition, lean body weight determinations were made on Group III animals. They were kept in pairs at 20°C and LD 12:12 with food ad libitum. Four of the 10 animals were used in early July and three animals each in the middle of August and in early September.

Animals were fasted for 12 h and killed in a desiccator with excess ether. The 12 h fasting period was to provide information on the amount and distribution of chyme in the gut, and consequently, on whether or not this period of food deprivation indicates a post-absorptive state, a requirement for standard metabolic rate (SMR) studies.

Immediately after death, specimens were weighed to obtain total body weight. Their thoracic cavity was cut open and approximately 8 ml of heparin (1000 I.U./ $\ell$ ) was injected into the heart to prevent coagulation of blood. Heart and lungs were excised, and blood, which drained into the chest cavity, was removed with the aid of a syringe. White adipose tissue was excised and placed in a pre-weighed jar containing mineral oil to prevent desiccation of tissue. Reweighing to obtain tissue weight occurred at a later time. Gut contents were removed and their weight determined. Specimens were kept on saline-soaked paper towels to minimize desiccation during dissection.

Quantification of white fat deposits enabled a comparison between lean body weight (total body weight minus white fat and gut contents) and total body weight (minus gut contents).

#### Metabolic Rate Determination

Standard metabolic rate (SMR) was measured in eight males and 23 females twice a month between the middle of July and the middle of November at a  $T_a$  of approximately 23°C. An open circuit system was employed in conjunction with a Beckman paramagnetic oxygen analyser, model F<sub>3</sub> (Beckman Instruments Inc., Fullerton, California, USA).

The metabolism chamber consisted of a 5 l glass desiccator sprayed with black paint except for a narrow slit through which the animal could be observed. Influent and effluent air tubes passed through a rubber stopper at the apex of the lid. The influent air tube was connected to a copper tube which extended to the bottom of the chamber. It had a series of holes along its length to allow even distribution of incoming air in the chamber. Shredded paper was placed at the bottom of the chamber as animals were more settled when nesting material was present.

Influent air was passed through a desiccant, drierite (CaSO<sub>4</sub>), and into the chamber at a flow rate of 825 ml min<sup>-1</sup>, measured by a Gilmont flowmeter (Roger Gilmont Instruments, Great Neck, New York, USA). Effluent air was similarly dried before the sample reached the analyser.

Animals used for metabolic rate studies were fasted for a minimum of 12 h to ascertain that they were in a post-absorptive state. This appeared to be the case since fasted animals, dissected for lean body weight determinations, had no chyme in the upper gastro-intestinal tract.

Animals were weighed before and after each experiment performed between 0900-1200. After placing them in the metabolism chamber, the lid was sealed with stop-cock grease and at least 25 min were allowed for the system to equilibrate before taking measurements. Equilibration time had been previously determined by flushing the system with a standard gas (16% O<sub>2</sub>) and measuring the time required for the recorder to indicate 95% of this value. During oxygen consumption measurements, the lowest value recorded over a 2 min interval, when the animal was known to be well settled, was used in calculations. Oxygen consumption determinations also required knowing the respiratory quotient (RQ), i.e., the ratio of CO<sub>2</sub> produced to O<sub>2</sub> consumed. This ratio is an indicator of the major food type being metabolized; it was obtained experimentally as outlined on page 13. The following equation by Withers (1977) served in MR determinations:

$$\dot{V}O_2 = \frac{V_i (F_iO_2 - F_eO_2)}{1 - F_eO_2 (1 - RQ)}$$

where  $\dot{V}O_2$  = rate of  $O_2$  consumption at STP  
 $\dot{V}CO_2$  = rate of  $CO_2$  production at STP  
 $\dot{V}_i$  = rate of air flow into the chamber  
 $F_iO_2$  = fractional conc. of  $O_2$  in the influent air  
 $F_eO_2$  = fractional conc. of  $O_2$  in the effluent air  
 $RQ$  =  $\dot{V}CO_2 / \dot{V}O_2$

#### Determination of Respiratory Quotient

To obtain RQ, the amount of  $CO_2$  expired by animals was determined during oxygen consumption measurements. Both  $CO_2$  and  $H_2O$  were removed from air flowing into and out of the metabolism chamber. Of three plexiglass chambers along the inflow air system, the first contained drierite, the remaining two soda lime, a  $CO_2$  absorbant. The outflow system had a similar arrangement except it contained two drierite chambers, one in front of and one behind the three  $CO_2$  traps.

The amount of  $CO_2$  expired during the experiment was obtained by weight differences in the three downstream  $CO_2$  traps and the drierite trap in front of the analyser. Data were converted to ml  $CO_2$  expired  $h^{-1}$ .

Oxygen consumption was determined at 12 sec intervals from continuous measurements, averaged for the period of the determinations, and expressed as ml  $O_2$  consumed  $h^{-1}$ . The equation by Depocas and Hart (1957) served in these determinations:

$$\dot{V}O_2 = \frac{FiO_2 - FeO_2}{1 - FeO_2}$$

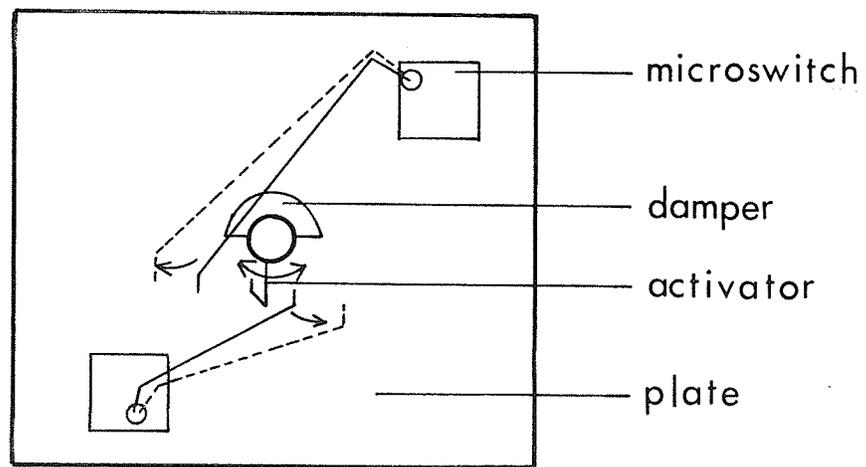
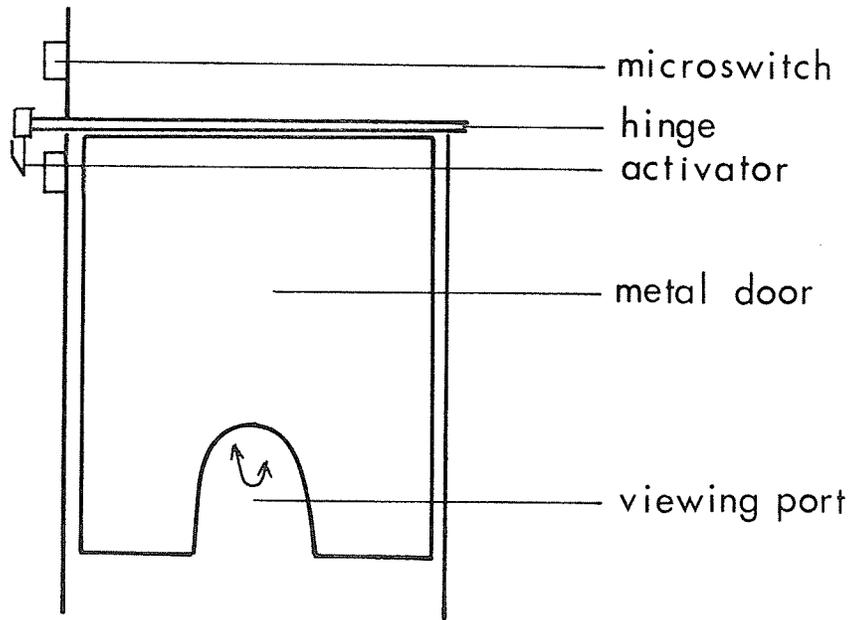
where  $\dot{V}O_2$  = rate of  $O_2$  consumption at STP  
 $FiO_2$  = fractional conc. of  $O_2$  in the influent air  
 $FeO_2$  = fractional conc. of  $O_2$  in the effluent air

### Activity Measurements

Activity of Group I and II animals was monitored over approximately a one-year period, the duration animals were kept in the laboratory. Prior to, and following the hibernation season, monitoring occurred for two 24 h periods every week. Activity during the hibernation season was recorded for 10 days during each half month period.

The equipment for recording activity consisted of a two-way swinging door suspended vertically in the metal partition of the cage and two microswitches in the vicinity of the door hinge. These microswitches were connected to an Esterline Angus event recorder, Model 620X (Esterline Angus, Indianapolis, Indiana, USA), located outside the CE room. When an animal passed either in or out of the door, an activator on the door hinge made contact with one of the two microswitches (Fig. 1). The consequent triggering of a microswitch resulted in a mark on the recording paper, run at a speed of  $2 \text{ cm h}^{-1}$ . At this speed, a maximum of 50 marks  $\text{h}^{-1}$  could be resolved. Whenever two or more marks were not clearly distinguishable, an estimate of the number of marks was made.

Figure 1. Two-way swinging door and microswitch triggering system for measuring activity.



Activity has been expressed in arbitrary units. One unit of activity relates to a single mark on the event recorder and is due to the activity of an animal causing a single doorswing in either direction.

Daily activity refers to the total number of doorswings per animal in a 24 h period of continuous recording.

Distribution of daily activity refers to the pattern of activity per day. To obtain this pattern, each 24 h activity tracing of 10 days within each half month from October until March was divided into bihourly periods (0000-0200 . . . 2200-2400). These 2 h intervals were subdivided into 8 min periods. If an animal was active once or more during an 8 min interval, it was considered to have been active and allotted one activity count. The maximum count for any animal within this 2 h interval was 15. The mean activity for each bihourly period for each half month was determined.

To compare the daily distribution of activity between Group I and II animals, data from paired animals held at LD 00:24 were excluded because the activity of two of these pairs went out of phase with pairs held at LD 12:12 and with the two remaining pairs held at LD 00:24 (App. 3E, 3F).

Hibernation was considered to occur only after an animal had been inactive for a minimum of 24 h, as not to confuse torpor with sleep. Hibernation bout was taken as the period between the cessation and onset of activity.

### Food Consumption Measurement

Prior to and following the hibernation season, food consumption was determined from the weekly sum of the weight differences of the lab chow provided at the beginning of a 24 h period and that remaining at the end of it. For Group I animals during the hibernation season and Group II animals following the reprovision of food at the middle of January, food consumption was determined from the weekly weight differences of lab chow provided at the beginning and that remaining at the end of each week.

Group II animals were food-deprived from late November until the middle of January. This period corresponded in time with that when the activity of Group I animals reached minimal levels the year before.

Food consumption has been expressed as weekly intake of food per animal and is a gross measure of food intake as that wasted as powder has not been taken into consideration. The assumption has been that all individuals wasted similar amounts of food. Therefore, a consistent error has been introduced with reported values higher than actual values.

### Treatment of Data

To enable comparison between Groups I and II, data have been expressed on a per animal basis. Corrected values for paired animals fell within the range of variation for single animals.

Data from certain animals (Table 1) were omitted from comparisons of weight, activity, and food consumption between subgroups within each year. The reason for this was that some animals died during the course of investigation and comparison required equal sample sizes with regard to sex (Group I) and with regard to individually-caged and paired animals (Group II).

Within Group II, one animal from a pair in each subgroup died during food deprivation. Since two further deaths occurred following the reprovision of food, and since sample sizes were small, data from the surviving animal of the pairs were used for replacement. Justification for this was that these animals were held under similar conditions as the animals they replaced. Also, their initial data were similar.

The activity of two animals, one from each subgroup of Group II, was considerably higher than that of other animals investigated. To prevent masking the trends observed in the majority of animals, data from the animals with very high activity were excluded. A comparison between the two animals and their respective treatment groups is shown in Appendix 3D.

#### Statistical Analysis

Means of data from animals at different photoperiods within each year group were tested for statistically-significant differences by the Student's t-test. Equality of

variance was tested using the variance ratio test, and if found to be significantly different, Cochran's approximation of the Behren's-Fisher solution was employed and  $t$  was replaced by  $t'$ . Cochran's approximation is more conservative than the Behren's-Fisher solution in that slightly higher values of  $t'$  are required for significance (Snedecor and Cochran 1967).

When sample sizes are equal or nearly equal, as in the present study, the Student's  $t$ -test is robust enough to withstand a marked departure from its underlying assumption that samples were obtained at random from a normal population with equal variance (Zar 1974). The requirement that samples be independent of each other was not met in studies with laboratory animals since the same animals were used throughout a year. Since the effect of non-independent samples is weakened with time, the comparisons were made at monthly intervals.

The lowest acceptable level of significance tested for in this study was  $p < 0.05$ .

## RESULTS

### Body Weights

Body weights of juvenile S. richardsoni increased rapidly during the first month of captivity, stabilized, and then remained fairly stable until early winter when experimental conditions were altered (Fig. 2). There was a marked weight loss of Group II over the two months of food deprivation in winter. Whether weight loss occurred in Group I animals during winter cannot be determined from data available. Body weights increased again rapidly in the spring (Group I) and with reprovision of food (Group II). Both groups had higher mean body weights in their second than in their first summer.

Both Group I and II animals showed a similar pattern of change in weight (Fig. 2); the higher mean body weights of Group I (males and females) as compared to Group II (females only) can be accounted for by the generally higher weight of males (Fig. 3; App. 1E).

For comparing body weights of females from Groups I and II, data from animals under different light regimes were pooled as these did not differ significantly between animals in each subgroup (App. 1B, 1C, 5). Mean body weights between Group I and II females were not significantly different for periods when comparison could be made

Figure 2. (Upper graph) Mean body weights of juvenile S.  
richardsoni maintained at LD 12:12.

(Lower graph) Mean body weights of juvenile S.  
richardsoni maintained at LD 00:24 (Dec. - May).

○ Group I; n = 8

● Group II; n = 6

---Period of food deprivation

Vertical lines: ± SE

n = Sample size

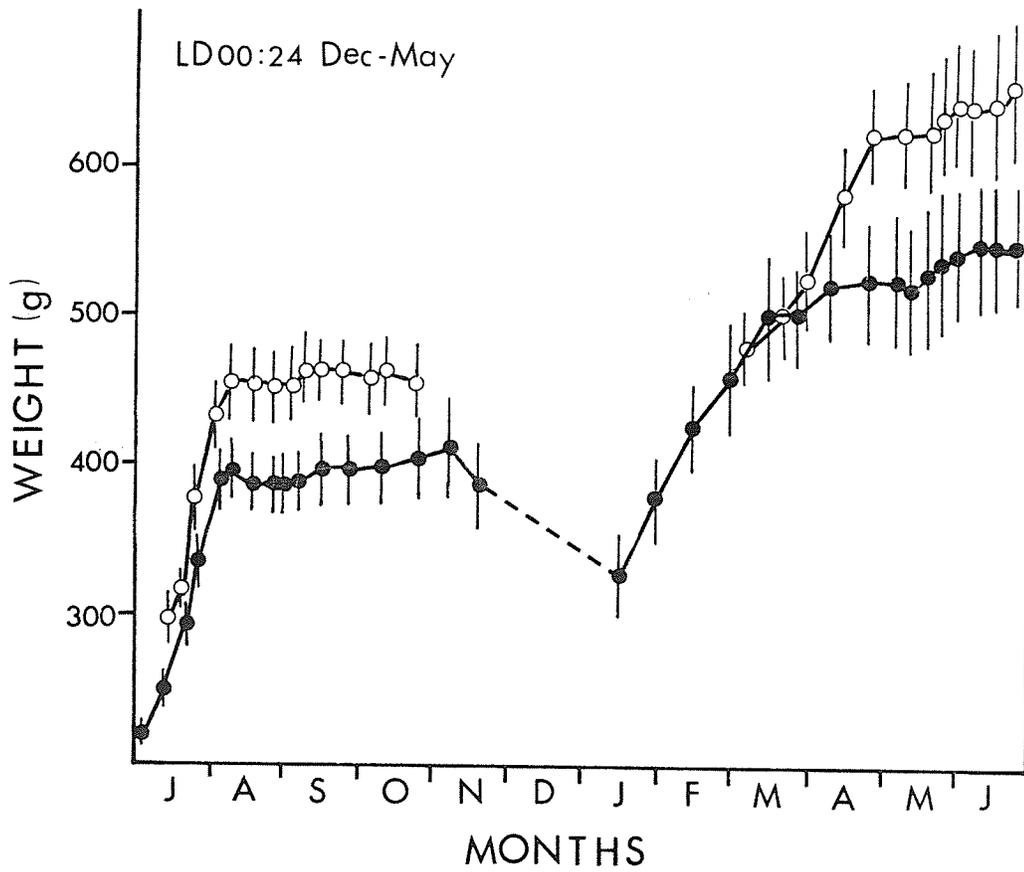
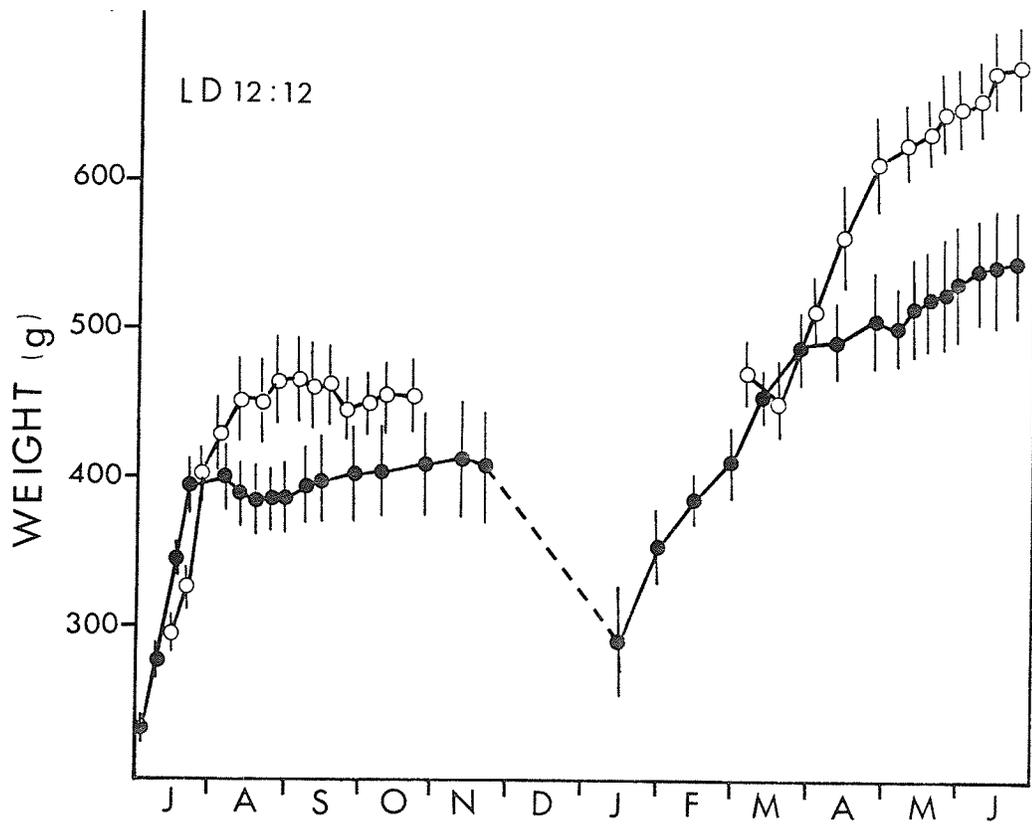


Figure 3. (Upper graph) Mean body weights of Group I male juvenile S. richardsoni. Data from animals held at different photoperiods have been pooled; n = 9-12.

(Lower graph) Mean body weights of Group I and II female juvenile S. richardsoni. Data from animals held at different photoperiods have been pooled; n = 11-16.

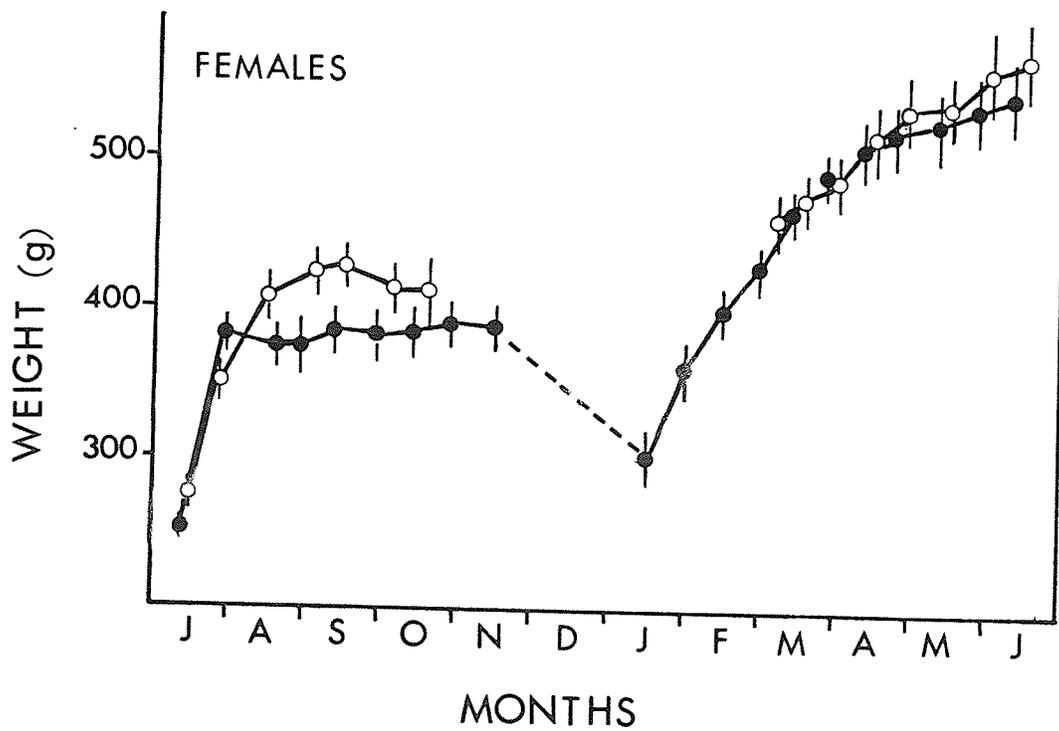
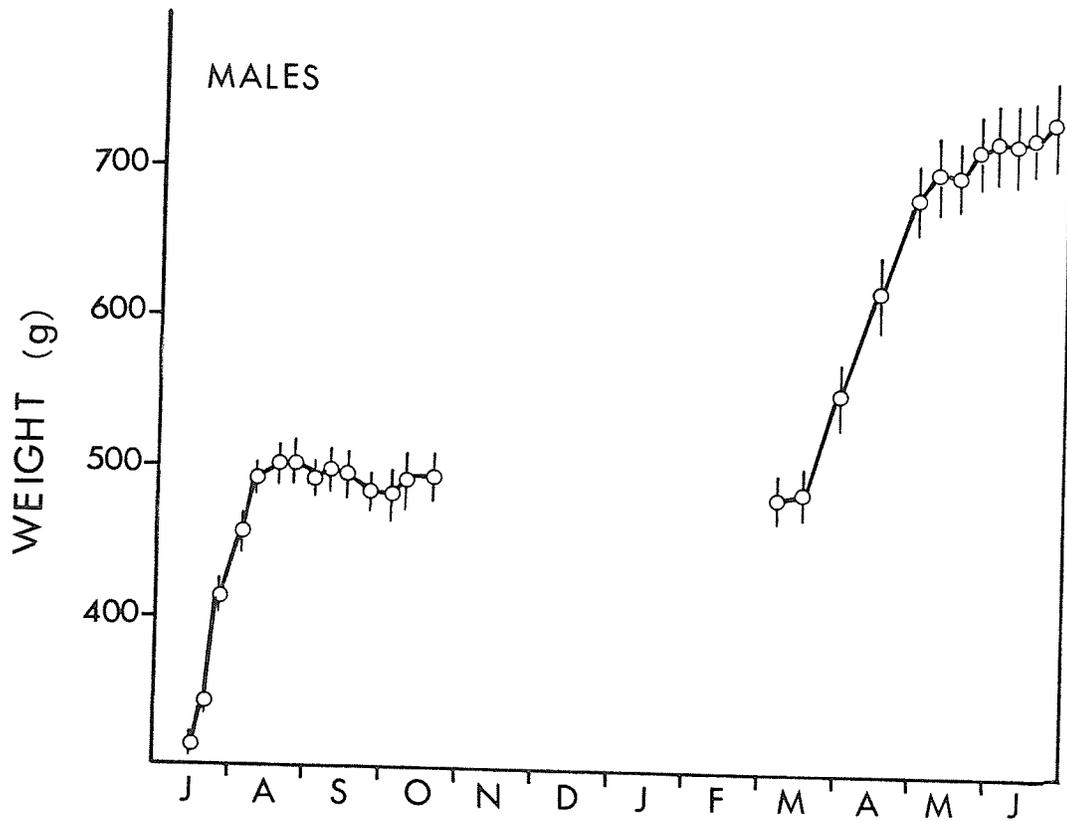
○ Group I

● Group II

---Period of food deprivation

Vertical lines: ± SE

n = Sample size



(Fig. 3); the one exception in late August (App. 1F) can be explained by weight gain being slightly out of phase between the two groups of animals.

Juvenile S. richardsoni underwent marked body weight changes also in their natural habitat (Fig. 4). Mean weights of males and females were similar in late May when they first emerged, and both sexes gained weight rapidly throughout June and July. As the season progressed, males became significantly heavier than females (App. 1G). Also, whereas mean weight gain in juvenile males continued throughout the season, the mean weight of juvenile females began to plateau as early as August and remained at a fairly stable level until the end of the season. Weight change throughout the active season was similar between a randomly sampled group of animals (untagged) (Fig. 4) and a selected group (tagged) (App. 1J).

Figure 5 illustrates seasonal weight changes of tagged individuals selected on the basis of highest recapture success. Weight changes of individual males correspond to the pattern manifest in the population as a whole. The pattern for individual females differs from that of the population (Fig. 4) in that weight gain of individuals continued throughout the season (Fig. 5). However, not all females were trapped until the end of the season.

A comparison between male ground squirrels in the laboratory (Fig. 3) and those in their natural habitat (Fig. 4) shows that captive males gained weight rapidly in

Figure 4. (Upper graph) Mean body weights of female juvenile S. richardsoni in their natural habitat.

(Lower graph) Mean body weights of male juvenile S. richardsoni in their natural habitat.

Vertical lines:  $\pm$  SE

Numbers = Sample size

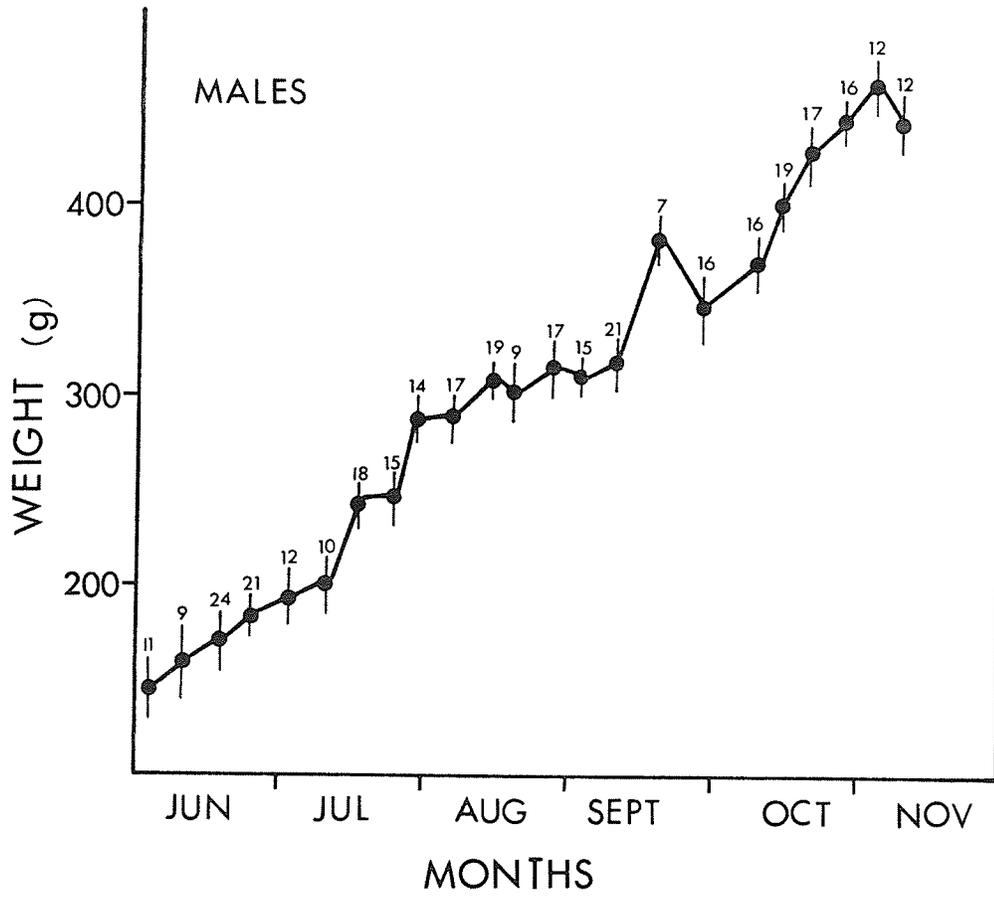
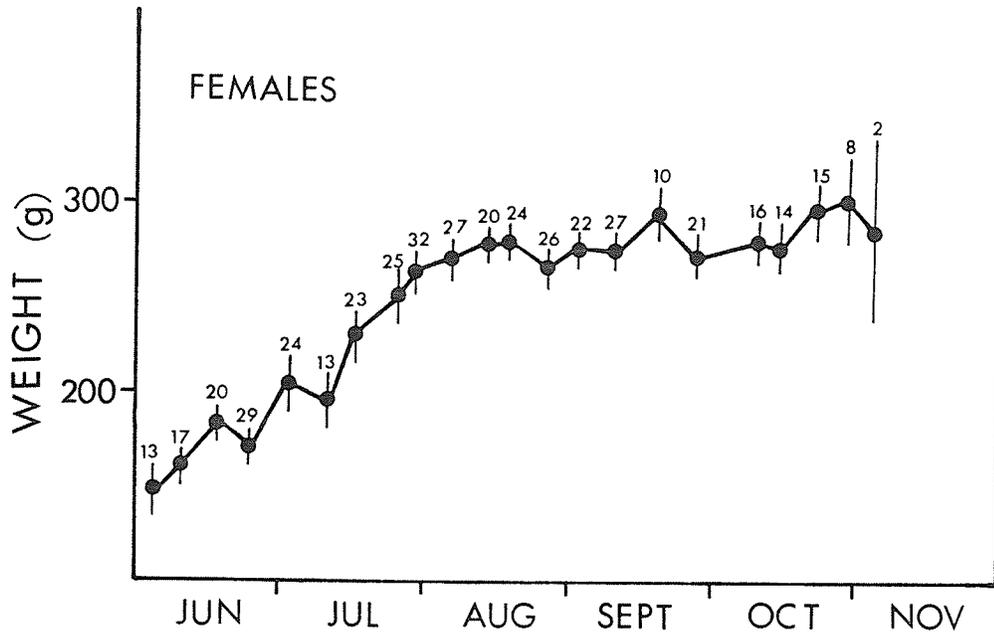
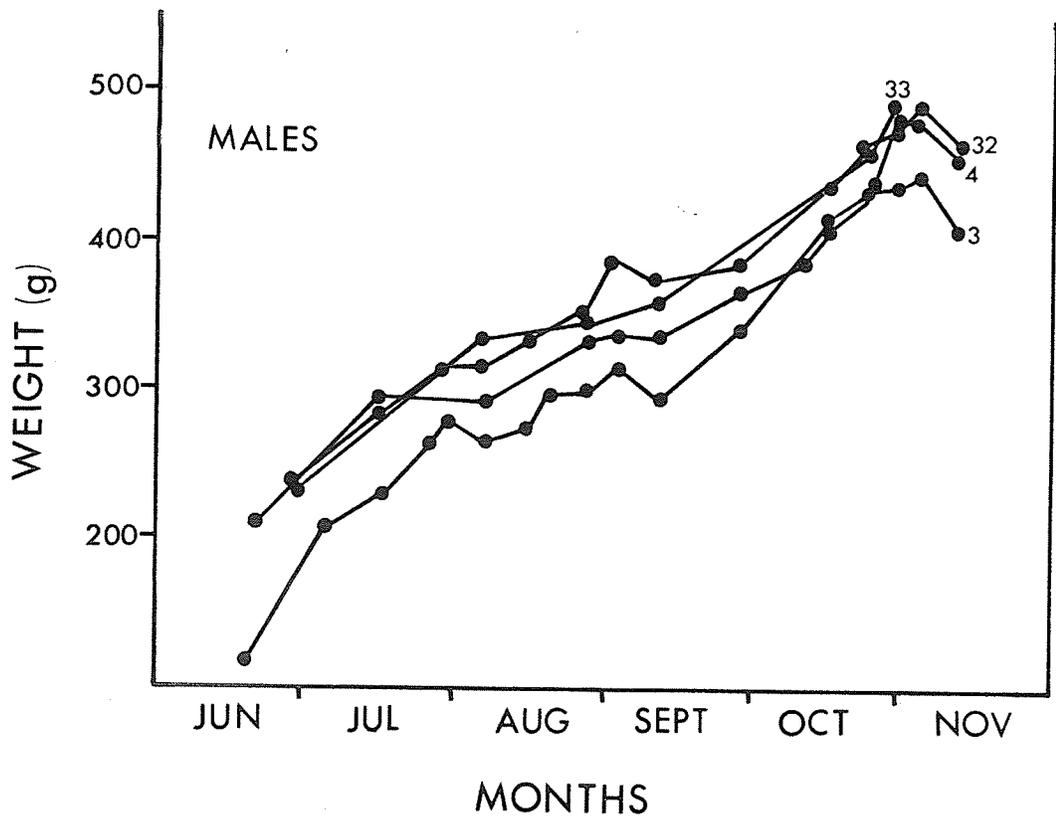
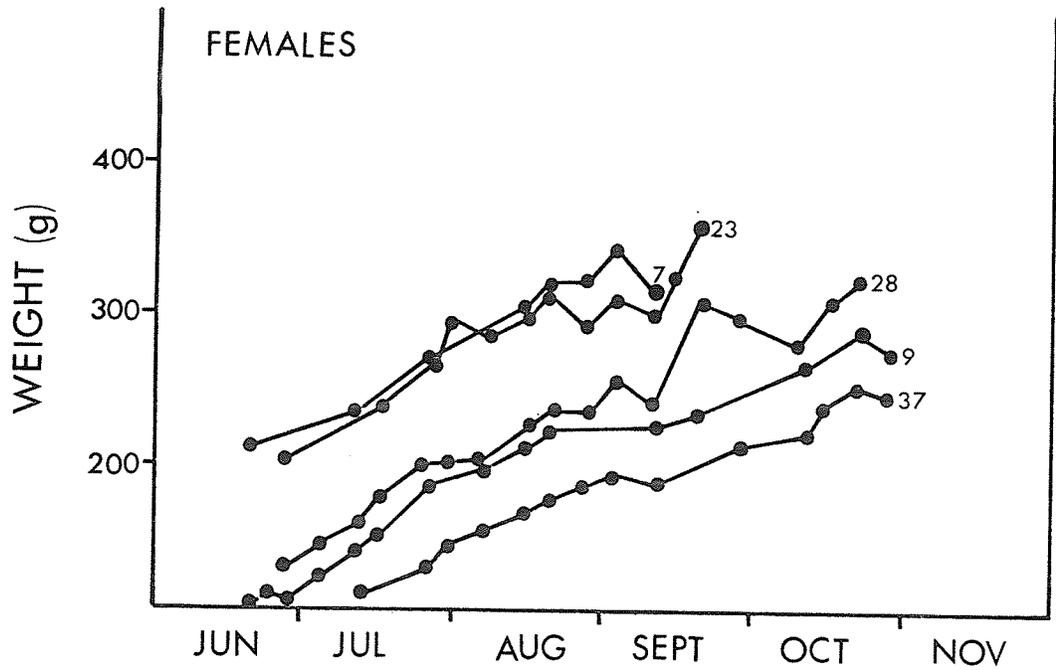


Figure 5. (Upper graph) Body weights of five female juvenile S. richardsoni in their natural habitat.

(Lower graph) Body weights of four male juvenile S. richardsoni in their natural habitat.

Numbers indicate identification numbers.



early summer and maintained a fairly steady level for several months; free-ranging males, in contrast, gained weight throughout the season. Mean weight gain was similar between captive females (Fig. 3) and that of females in their natural habitat (Fig. 4). However, whereas free-ranging individual females gained weight throughout the season (Fig. 5), individual females in the laboratory gained weight rapidly during early captivity and then maintained relatively high body weights for several months (App. 1I). Both sexes in the laboratory had higher body weights than their free-ranging counterparts.

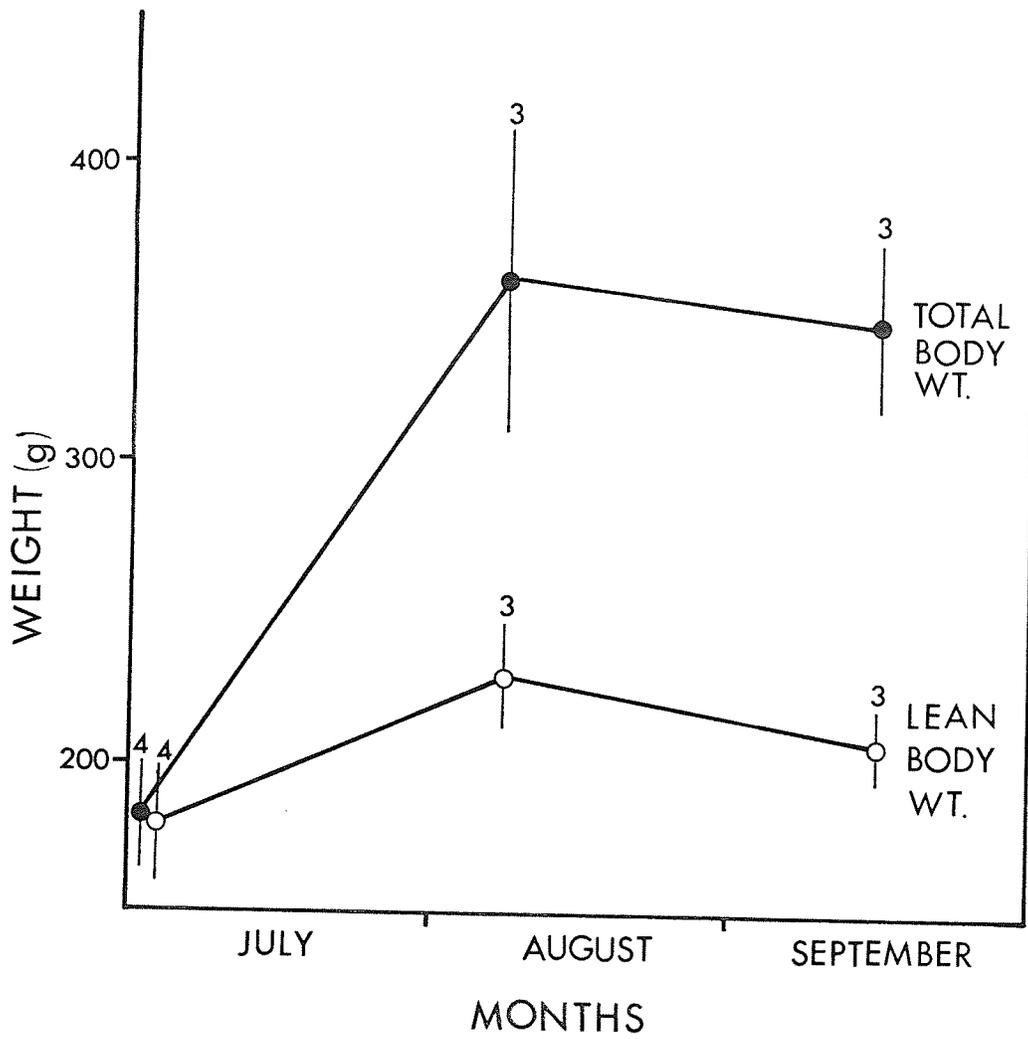
#### Growth and Fat Deposition

The marked increase in weight of Group I and II animals in July (Fig. 2) was associated with an increase in both lean weight (growth) and fat deposition; this is indicated by lean body weight determinations of Group III animals (Fig. 6). The steeper slope for total body weight than for lean body weight infers that the greater proportion of weight gain was due to deposition of white fat which increased as summer progressed. Moreover, it appears juvenile ground squirrels attained a given body mass due to growth and any additional increase in weight resulted from fat deposition (App. 1K).

Figure 6. Mean total body weight and mean lean body weight of Group III juvenile S. richardsoni.

Vertical lines:  $\pm$  SE

Numbers = Sample size



### Metabolic Rate

Standard metabolic rate, expressed on an hourly basis per animal ( $\dot{V}O_2 \text{ h}^{-1}$ ), of both Group I and II females increased until early August, declined until early September, and from then on remained relatively low until the termination of measurements (Fig. 7; centre graph). The initial increase in total oxygen consumption accompanied an increase in body weight (Fig. 7; upper graph) but as body weight began to stabilize during the middle of August, SMR declined markedly and continued to decline until late August, apparently for a short time after the stabilization of weight. Subsequently, a relatively high body weight was associated with a relatively low SMR. The higher  $\dot{V}O_2 \text{ h}^{-1}$  of Group I females is believed to relate to their relatively higher body weights.

When standard oxygen consumption is expressed on a unit weight basis (Fig. 7; lower graph), it can be seen that  $\dot{V}O_2$  declined with increasing body weight and continued to decline for a brief period after the stabilization of body weight. Commencing late August, a relatively low level of metabolic rate was reached and maintained until the termination of measurements. No statistically-significant differences were detected in weight-specific SMR between Group I and II females (App. 2E).

Both total SMR (Fig. 8; centre graph) and SMR per unit weight (Fig. 8; lower graph) of juvenile males declined between late July and early September when measurements were

Figure 7. Interrelationship between mean body weight (upper graph), and mean standard metabolic rate expressed on an hourly basis per animal (centre graph) and per unit weight (lower graph), in female juvenile S. richardsoni held at LD 12:12 with food ad libitum.

○ Group I

● Group II

Vertical lines:  $\pm$  SE

Numbers = Sample size

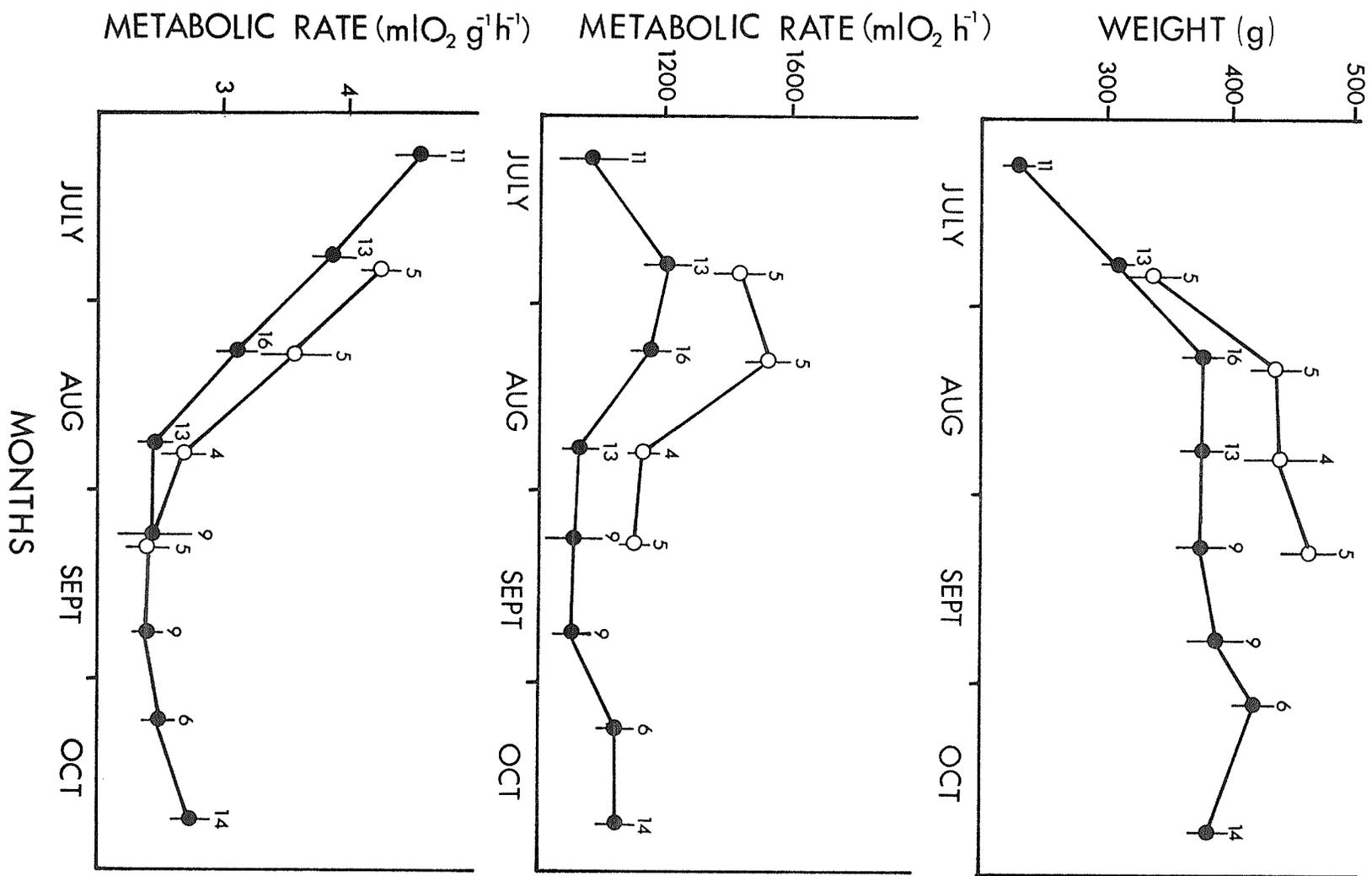
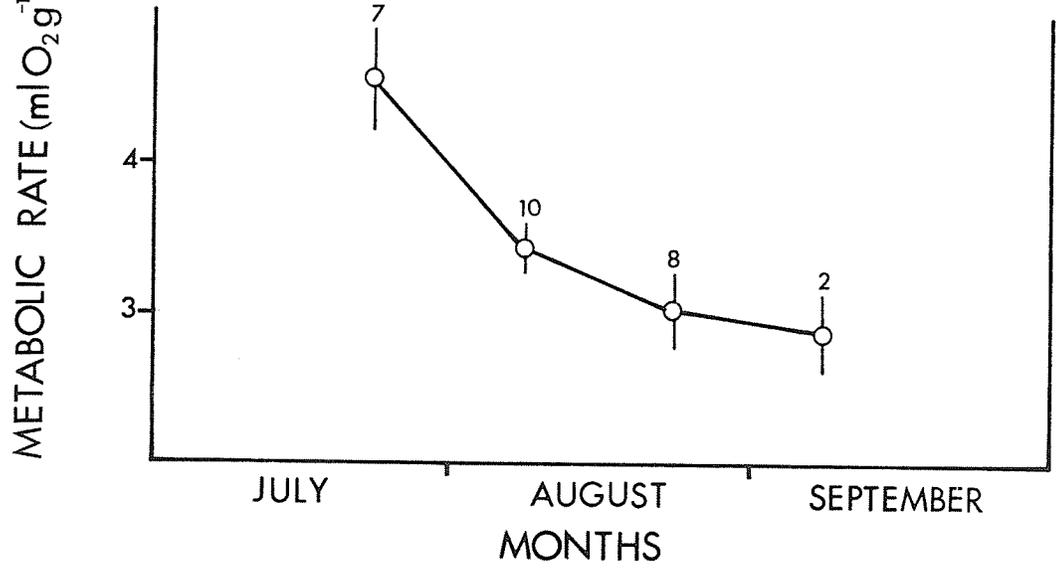
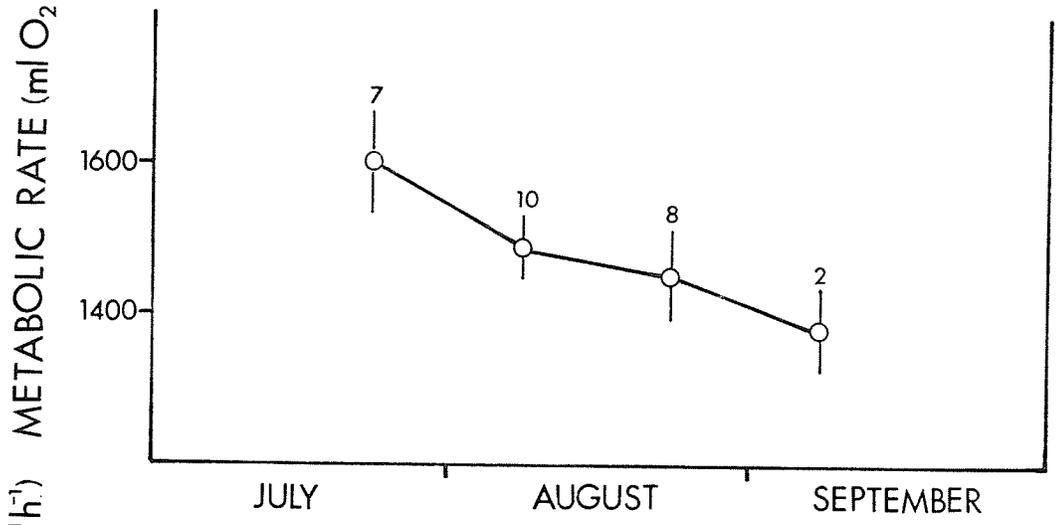
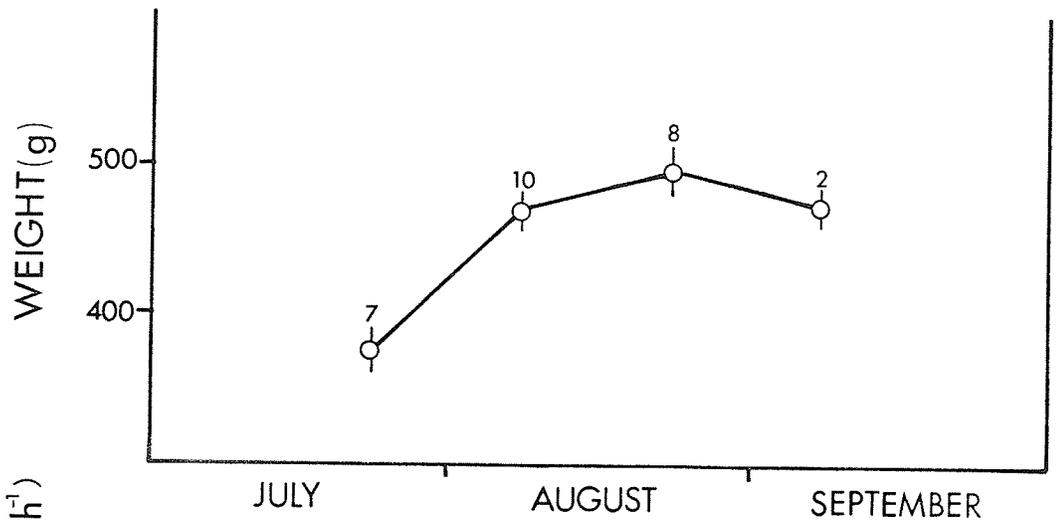


Figure 8. Interrelationship between mean body weight (upper graph) and mean standard metabolic rate, expressed on an hourly basis per animal (centre graph) and per unit weight (lower graph), in male juvenile S. richardsoni held at LD 12:12 with food ad libitum.

Vertical lines:  $\pm$  SE

Numbers = Sample size



made. The body weight of these animals increased until early August and subsequently stabilized (Fig. 8; upper graph). It appears total SMR of Group I males started to decline several weeks earlier than that of Group I females. However, because of small sample sizes and because measurements did not begin until late July, this cannot be said with certainty. No statistically-significant differences in weight-specific SMR were detected between Group I males and females (App. 2C).

#### Activity

Daily activity of juvenile S. richardsoni was relatively high in summer and declined during autumn to a minimum in December (Fig. 9). Activity increased again during January and February and high levels of activity were maintained from then on until the end of the study. The increase in activity of one group of animals (Group II A<sub>2</sub>) in late October (Fig. 9; upper graph) can be explained by the unusually high activity of two individuals during this period (App. 3G).

A comparison between Groups I and II (Fig. 9) shows that changes in activity were similar in the two groups although there was a difference in the degree of activity. The generally lower activity of Group I was a consequence of paired animals having been less active than individual ones (App. 3H). The decline to zero or near zero activity in December of Group II animals related to torpor in these

Figure 9. (Upper graph) Mean daily activity of juvenile S. richardsoni maintained at LD 12:12.

(Lower graph) Mean daily activity of juvenile S. richardsoni maintained at LD 00:24 (Dec. - May).

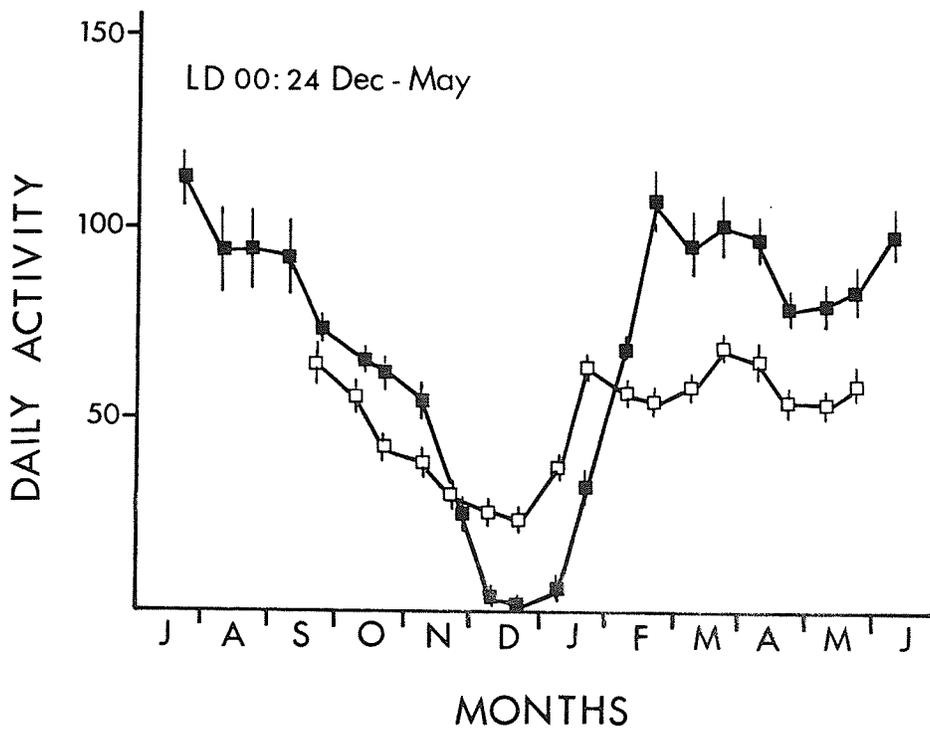
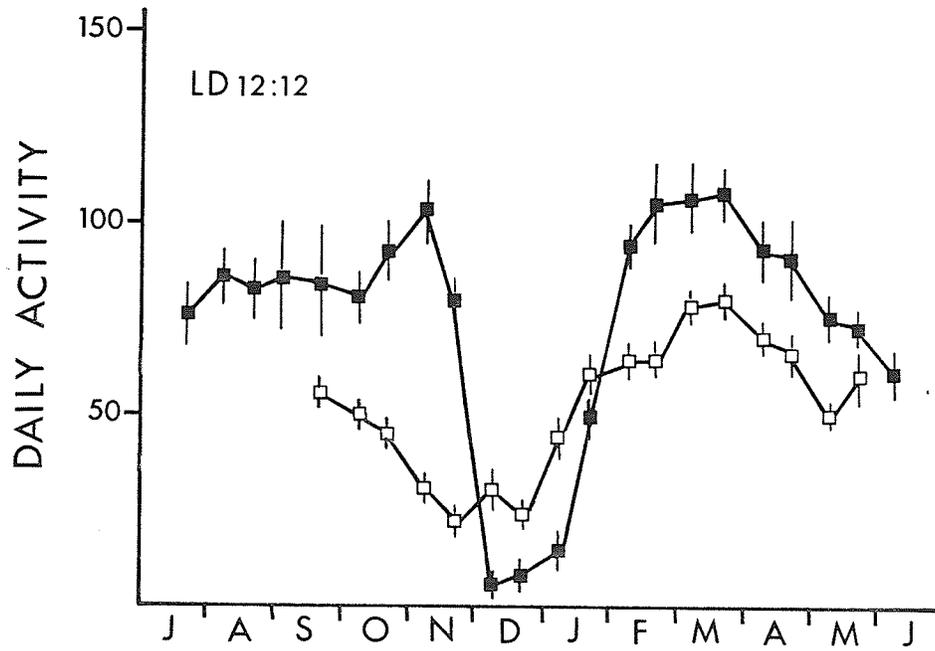
Units of activity are arbitrary (Page 16).

□ Group I

■ Group II

Vertical lines:  $\pm$  SE

Sample size: The majority of means consist of 30 - 40 24 h measurements; some consist of 16 - 21 24 h measurements.



animals.

The decline in activity during autumn does not appear to relate to either food deprivation or to a lowering of  $T_a$  since, except for Group II A<sub>2</sub> with two unusually active animals, activity declined well before food withdrawal and continued to decline at a  $T_a$  of 7°C. Furthermore, activity changes cannot be accounted for by a change in photoperiod. In two subgroups (Groups I B<sub>1</sub>, II B<sub>2</sub>) changes occurred before exposure of animals to LD 00:24; in the other subgroups (Groups I A<sub>1</sub>, II A<sub>2</sub>) changes took place even though photoperiod remained unchanged. Statistically-significant differences in daily activity between subgroups were detected both prior to and following the alteration of photoperiod (App. 3A, 3B). These might be explained by the relatively large differences in activity levels among individuals and the small number of animals within each treatment group.

Distribution of daily activity was similar in paired animals of Group I A<sub>1</sub> and II A<sub>2</sub>, though the change was larger in food-deprived animals (Fig. 10). Activity during the dark phase of the light cycle was minimal and relatively low between October and March; during the light phase, activity declined between October and December and increased between January and March. These changes occurred about the same time of day whether animals were provided with food or not. Also, with decreasing activity in autumn and winter, there appeared to be a shift in maximum

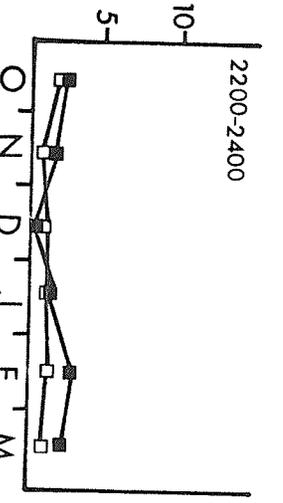
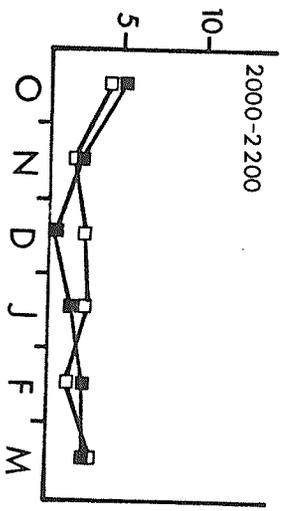
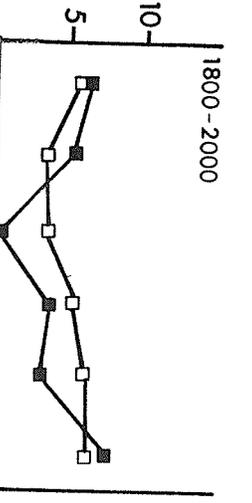
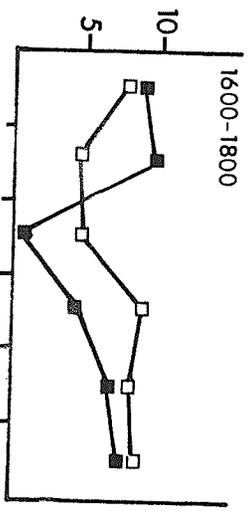
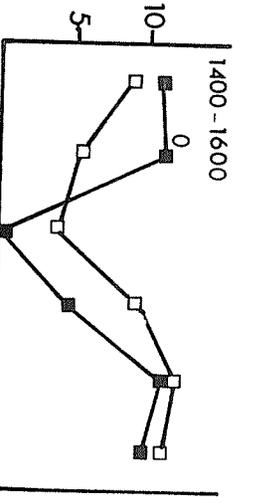
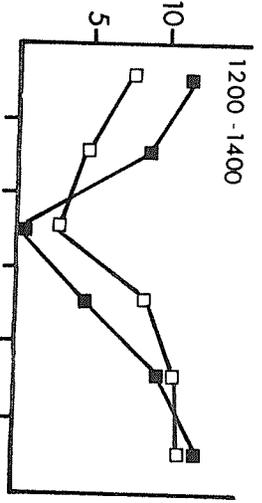
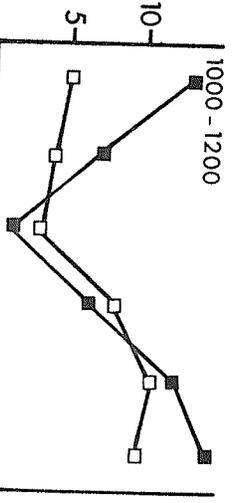
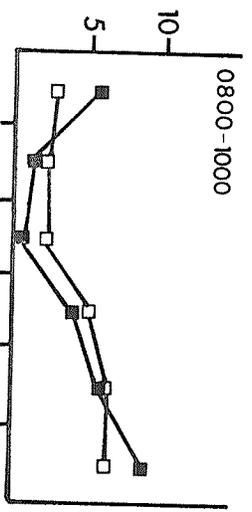
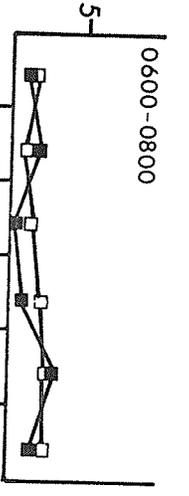
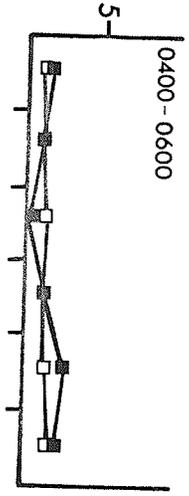
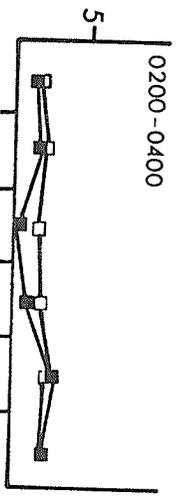
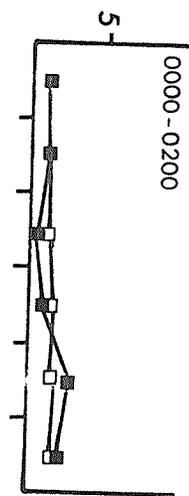
Figure 10. Activity of paired juvenile S. richardsoni during the 24 h cycle (Oct. - March). Animals were held at LD 12:12.

Units of activity are arbitrary (Page 16).

□ Group I

■ Group II

# BI-HOURLY ACTIVITY



MONTHS

MONTHS

activity toward the central part of the day (Fig. 11).

Observations indicated that all animals investigated underwent physiological changes at the onset of the hibernation season but hibernation occurred in food-deprived animals only. Thus, all animals underwent moult, built well-constructed nests and became noticeably docile even before the lowering of  $T_a$ . Of the food-deprived animals all singly-housed animals and two of four sets of paired animals hibernated (Table 2); this was indicated by the lack of measurable activity.

Hibernation bouts lasted from 1 - 11 days (App. 3C) and occurred between late November and January (Fig. 12). Hibernation terminated during the middle of January when food was resupplied. Some animals aroused permanently before this time. No further hibernation was observed following the restoration of food except for one obese female which became torpid in June.

There was no apparent difference in the ability to hibernate in the laboratory between animals held under different photoperiods. Entrance into hibernation, however, seemed hindered in paired animals as two of the four pairs did not hibernate. Cannibalism or death and subsequent consumption occurred in these pairs. These non-hibernating Group II animals showed a marked temporary increase in activity when food was initially withdrawn. A temporary increase was not observed in pairs which hibernated (Fig. 13). Also, in contrast to pairs which hibernated,

Table 2. Effect of light and food deprivation on hibernation in juvenile Spermophilus richardsoni  
 n = sample size

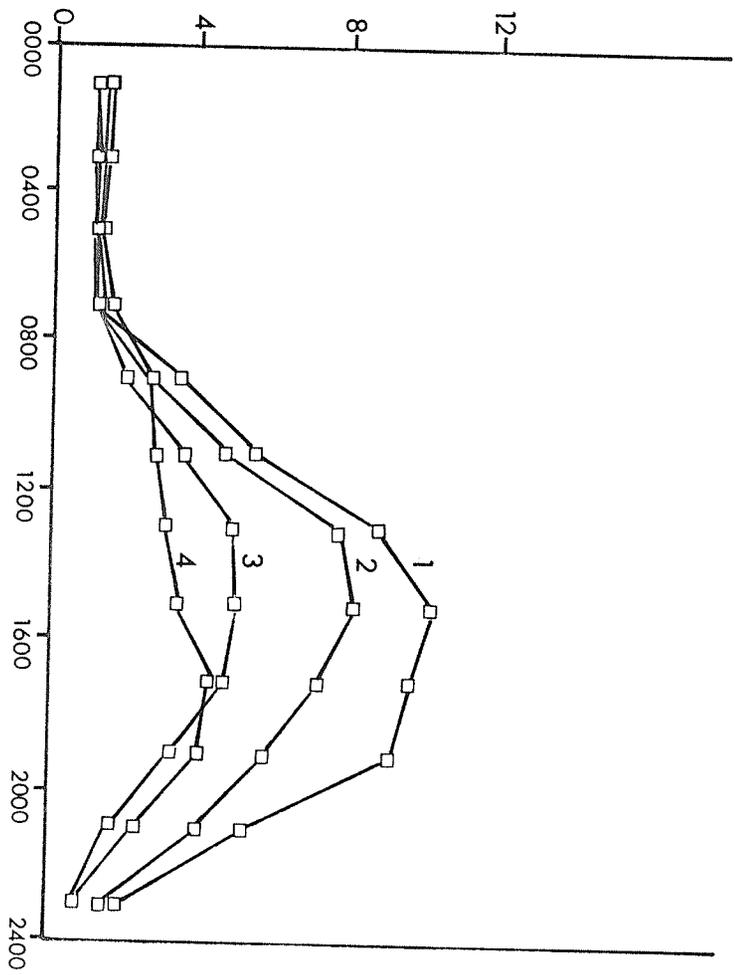
Social Environment	LD 12:12 7°C.		LD 00:24 7°C	
	Food Deprivation	Food <u>Ad Libitum</u>	Food Deprivation	Food <u>Ad Libitum</u>
Single Animals	ALL ANIMALS HIBERNATED  (n=4)	Before food deprivation, all single animals were exposed to these conditions from Oct.1-Nov 22.  No hibernation occurred in this period.  (n=8)	ALL ANIMALS HIBERNATED  (n=4)	Following the reprov- ision of food on Jan 15 to food deprived animals, 4 individuals were exposed to these conditions until April 1.  No hibernation occurred in this period.  (n=4)
Paired Animals	2 ANIMALS HIBERNATED <sup>†</sup>  (n=4)	NONE OF THE ANIMALS HIBERNATED  (n=8)	2 ANIMALS HIBERNATED <sup>†</sup>  (n=4)	NONE OF THE ANIMALS HIBERNATED  (n=8)
<sup>†</sup> Cannibalism occurred in those pairs which did not hibernate.				

Figure 11. Monthly changes in daily distribution of activity of Group I A<sub>1</sub> juvenile S. richardsoni.

Units of activity are arbitrary (Page 16).

- 1 September
- 2 October
- 3 November
- 4 December
- 5 January
- 6 February
- 7 March

BI-HOURLY ACTIVITY



BI-HOURLY ACTIVITY

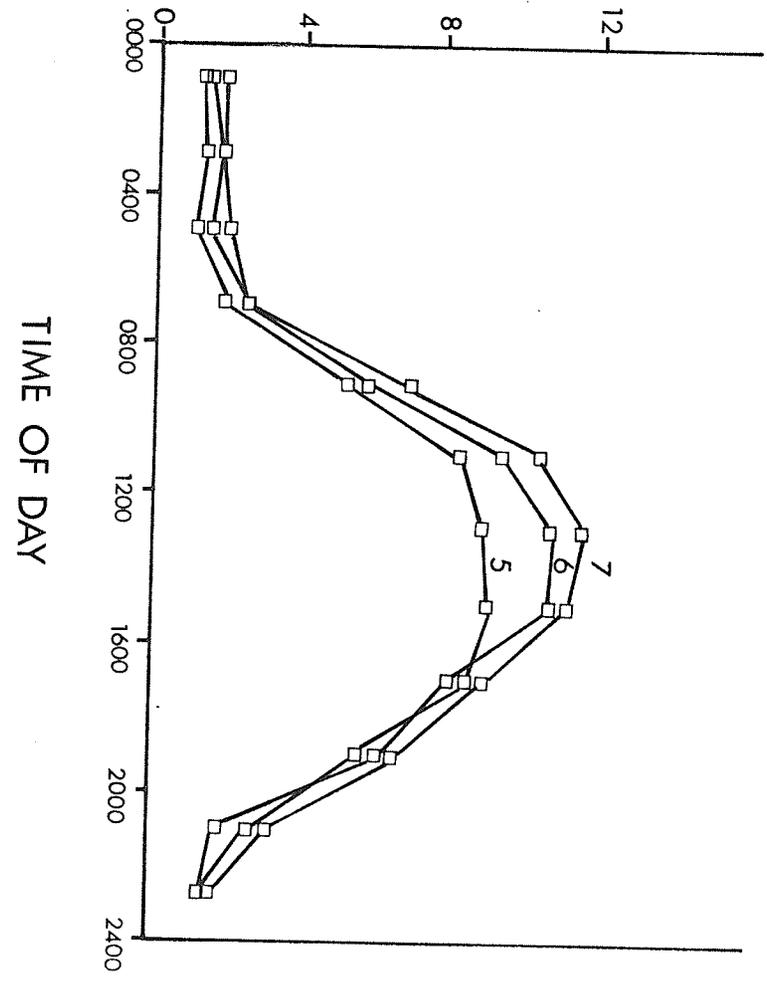


Figure 12. Hibernation bouts of Group II juvenile S.  
richardsoni following food deprivation between  
late November and the middle of January.

X Animals which aroused permanently.

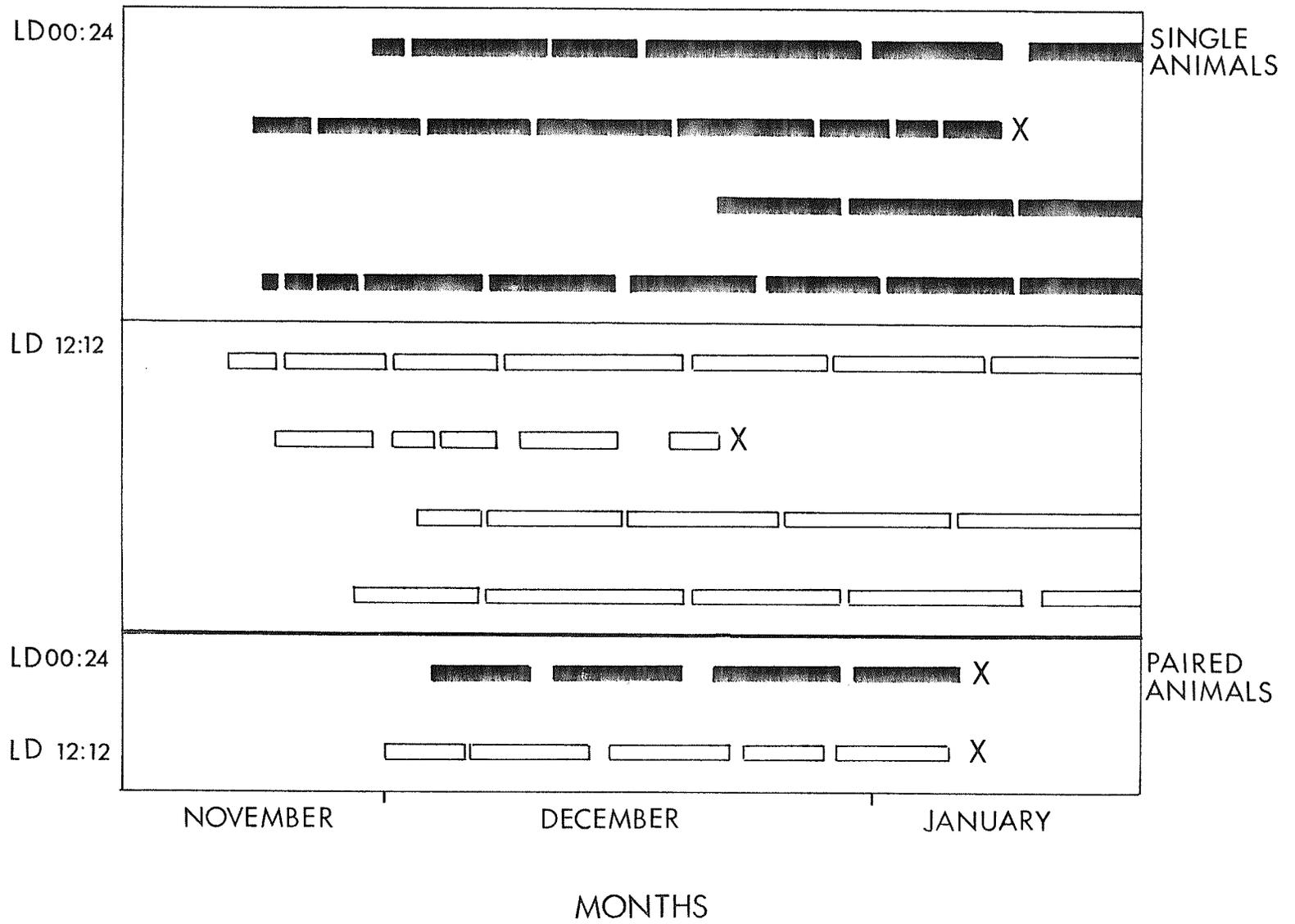
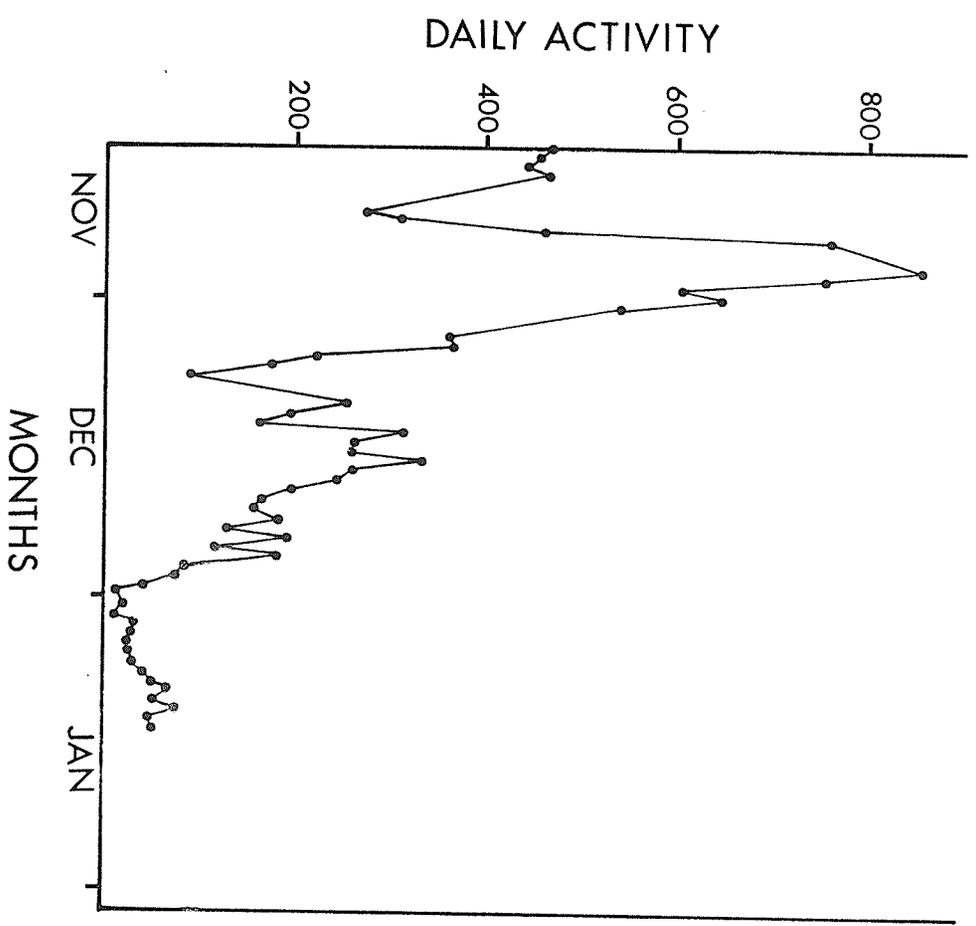
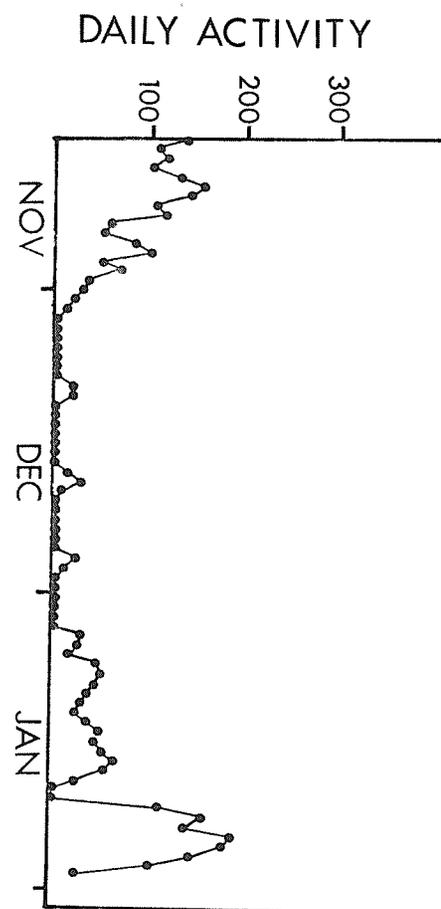


Figure 13. (Upper graph) Daily activity of one pair of food-deprived female juvenile S. richardsoni.  
(Lower graph) Daily activity of one pair of food-deprived female juvenile S. richardsoni.  
One animal was found to be consumed.



the activity of the non-hibernating paired animals was comparatively high from the time of capture. Flesh-eating was not confined to food-deprived animals but occurred also in Group I which had food ad libitum.

#### Food Consumption

Food consumption of juvenile S. richardsoni increased rapidly during the first month of captivity (Fig. 14). After becoming maximal in late July, it declined and reached a relatively low level by early September. A low food consumption was maintained until November when measurements were terminated. Reprovision of food was followed by a rapid increase of food intake in Group II and was associated with a rapid recovery in weight following hibernation. Food consumption was again high throughout March and declined during April to levels similar to those attained before the hibernation season. Changes in food consumption were similar between Groups I and II for periods when comparison could be made and occurred in both groups while animals were provided with food ad libitum.

Mean weekly food consumption was generally not significantly different between subgroups (App. 4A, 4B, 5). An exception in Group II was associated with a high food consumption of all members of one group at this time when food consumption of corresponding animals in the other group had already started to decline. The second exception in early March was the result of food intake of members of

Figure 14. (Upper graph) Mean weekly food consumption of juvenile S. richardsoni held at LD 12:12; n = 4-5.

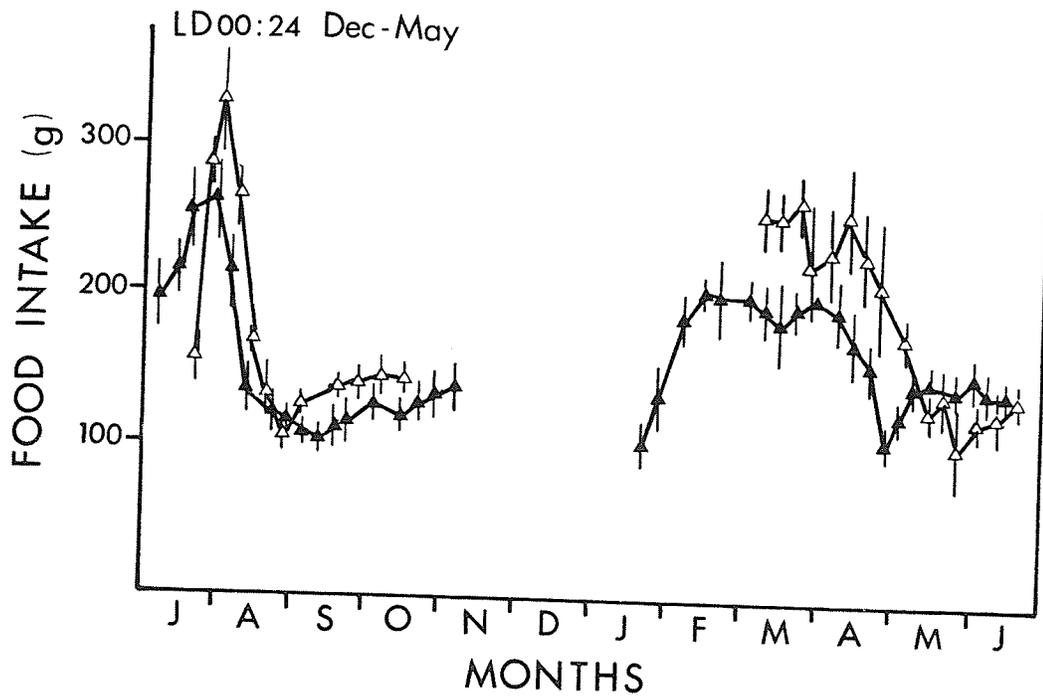
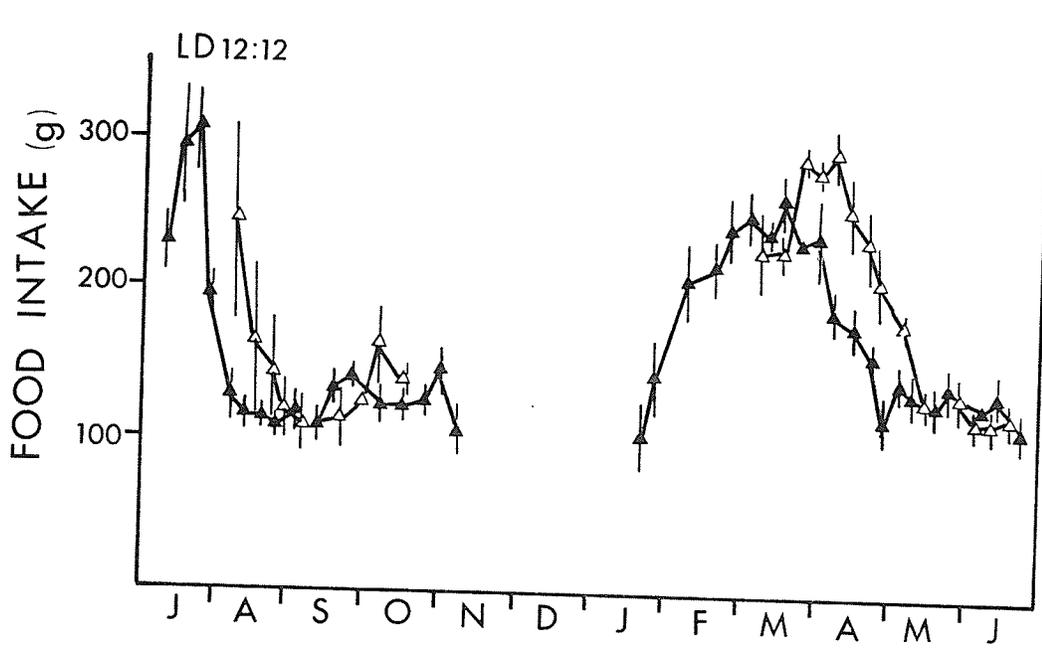
(Lower graph) Mean weekly food consumption of juvenile S. richardsoni held at LD 00:24; n = 4-5.

△ Group I

▲ Group II

Vertical lines: ± SE

n = Sample size



one group having been consistently higher than that of animals in the other group during this period (App. 4C).

Interrelationships of Activity, Food Consumption, Standard Metabolic Rate and Weight

The interrelationships of activity, food consumption, SMR, and body weight are depicted in Figs. 15 and 16 for two animals representative of Group II. Additional data are provided in App. 6 to demonstrate the trends in Figs. 15 and 16 are characteristic of animals of this group.

The rapid increase in food consumption during early captivity related to a rapid gain in body weight and a relatively high weight-specific SMR. Activity, although varying among individuals, was also fairly high at this time. The subsequent decline in food consumption and SMR began shortly before the stabilization of weight; both food consumption and SMR became relatively low by early September. From then on until the termination of measurements in late November, fairly constant and comparatively low levels of food intake and  $O_2$  consumption were associated with relatively high and stable body weights. During this period, activity declined in some individuals (Fig. 15; App. 6A, 6B) but remained fairly constant in others until such time when food was withdrawn (Fig. 16).

Food deprivation in late November coincided with the absence of measurable activity, an indication of hiber-

Figure 15. Daily activity, weekly food consumption, weight-specific metabolic rate and body weight of a female S. richardsoni representative of Group II B<sub>2</sub> animals held at LD 00:24 (Dec. - May).

- Daily activity
- ▲ Food consumption
- Metabolic rate
- Body weight
- Period of food deprivation

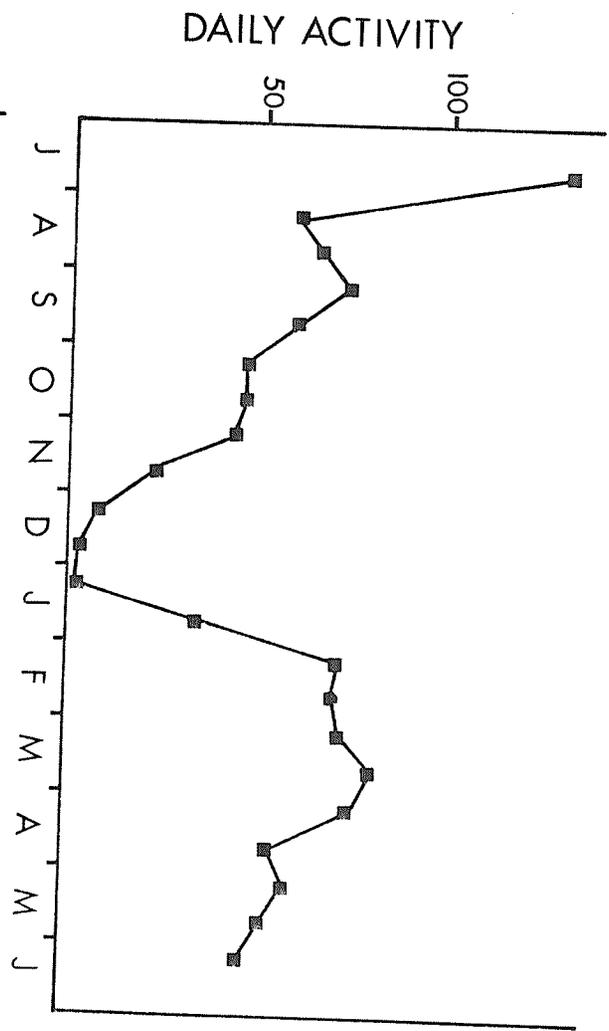
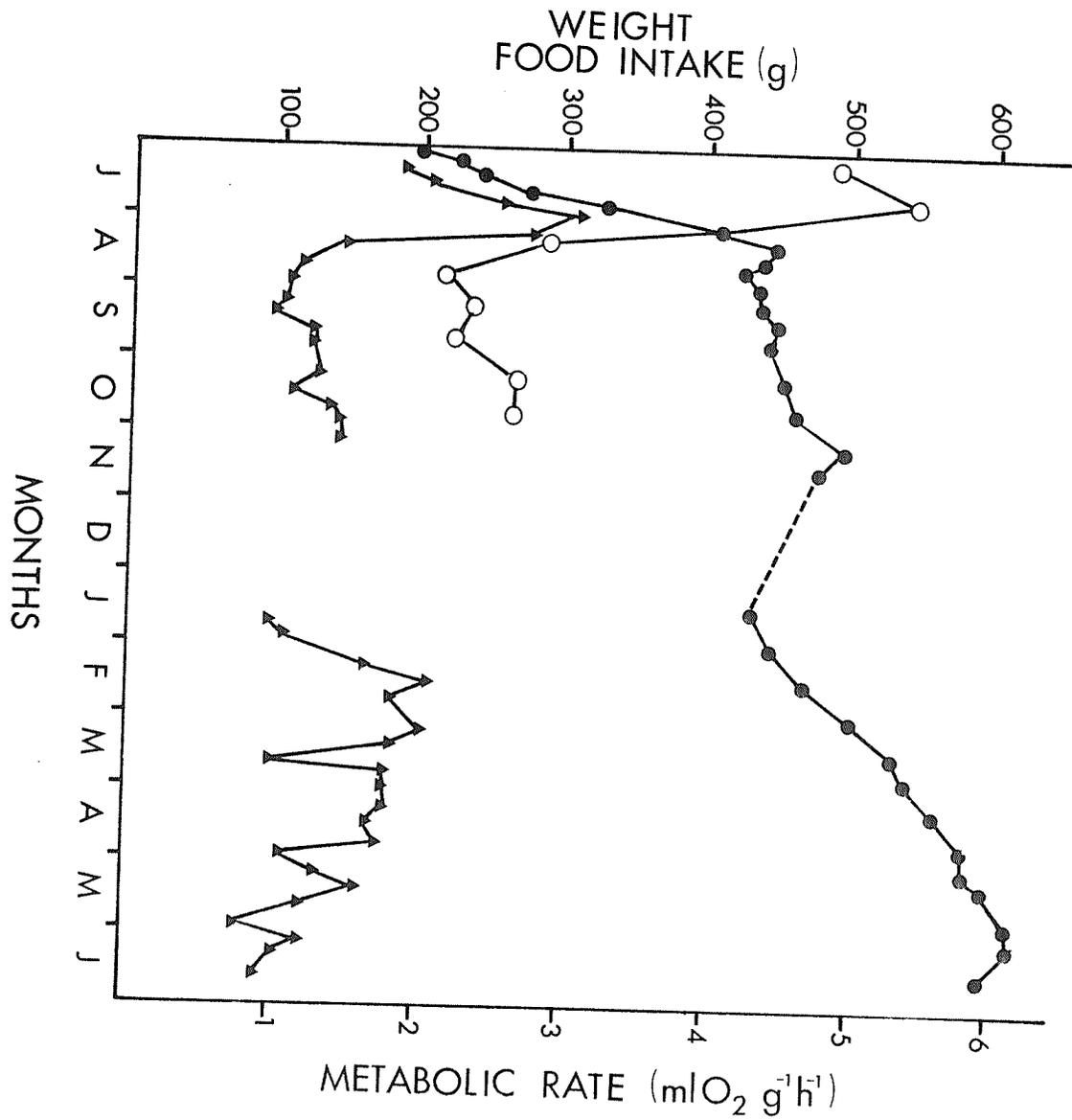
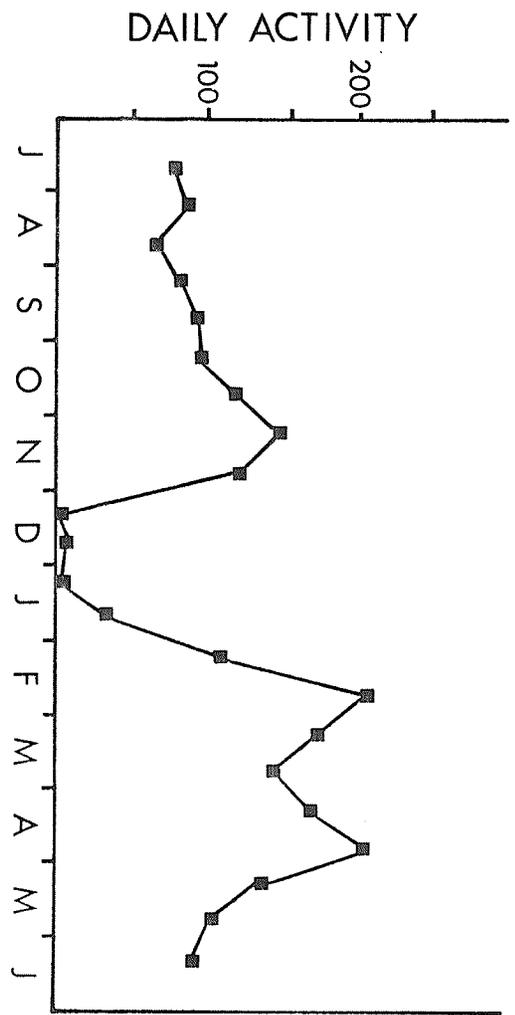
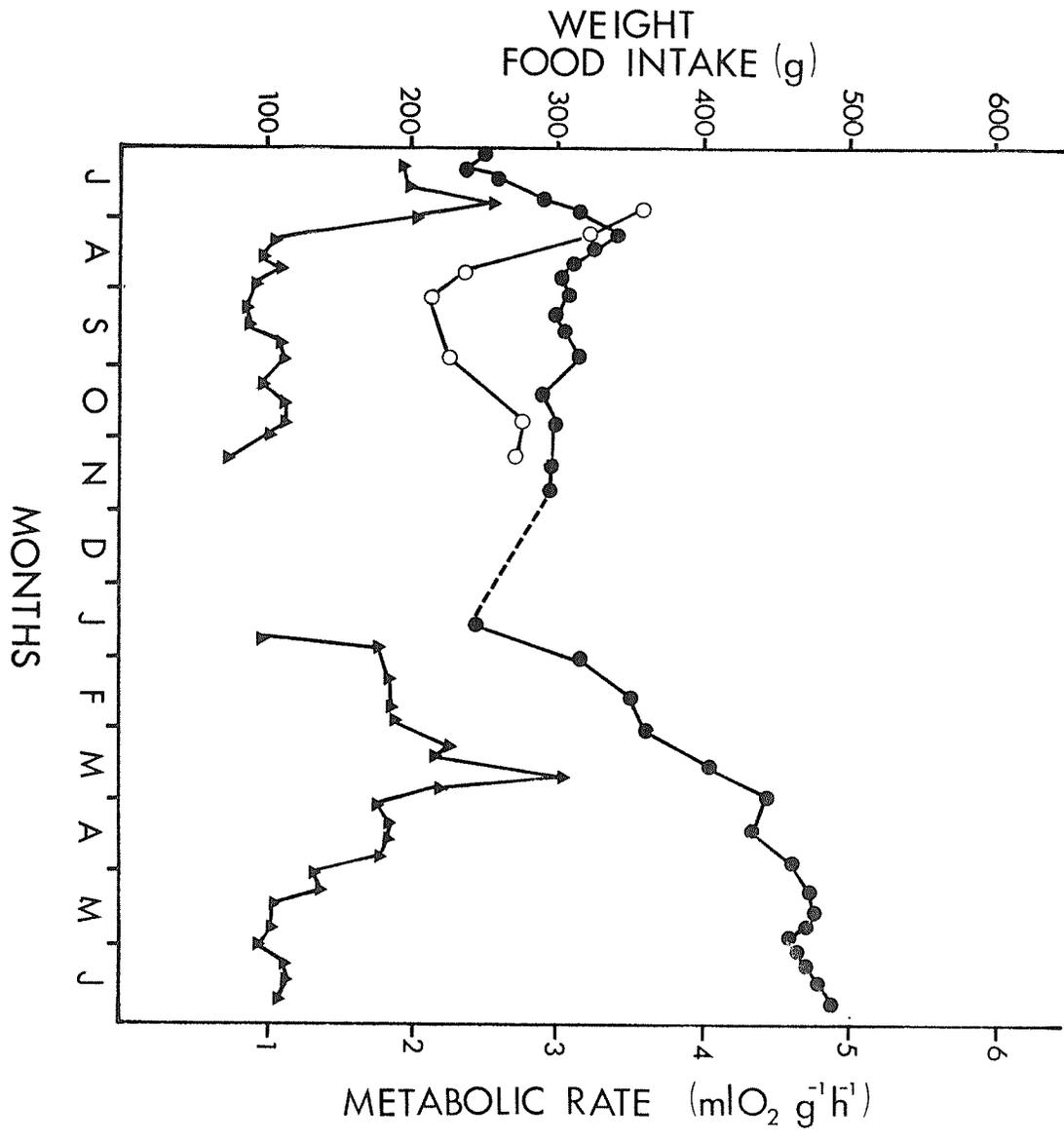


Figure 16. Daily activity, weekly food consumption, weight-specific metabolic rate and body weight of a female S. richardsoni representative of Group II A<sub>2</sub> animals held at LD 12:12.

- Daily activity
- ▲ Food consumption
- Metabolic rate
- Body weight
- Period of food deprivation



nation. When animals again had access to food in January, food consumption and body weight increased rapidly after a marked decline during hibernation. However, whereas body weight continued to increase until termination of the study in late June, both activity and food consumption declined after attainment of maximal levels in spring.

## DISCUSSION

Under conditions of this study captive juvenile Richardson's ground squirrels show marked changes in body weight, SMR, food consumption, and activity. Except for body weight, it is difficult to assess to what extent the changes observed in animals in the laboratory compare with those in animals in the field. However, since two different year groups of animals showed similar patterns of change one is lead to believe that, although duration and magnitude of changes may differ, changes in captive animals probably parallel those in free-ranging ones.

The occurrence of marked changes in body weight is well documented for a variety of ground squirrels in their natural habitat (Evans and Holdenreid 1943; Fitch 1948; Wade 1948; Jameson and Mead 1964; Hohn and Marshall 1966; Clark 1970a; Skryja and Clark 1970; Morton and Tung 1971a; Iverson and Turner 1972; Murie 1973; Dorrance 1974; Michener 1974; Morton et al. 1974; Morton 1975; Morton and Parmer 1975; Zegers and Williams 1977; Michener 1978). In general, ground squirrels attain maximal weights just before the hibernation season; they then lose weight, and by the beginning of the next active season, their body weight is minimal. This pattern exists also under laboratory conditions in the golden-mantled ground squirrel, S. lateralis

(Pengelley 1967; Blake 1972; review: Pengelley and Asmundson 1974), the arctic ground squirrel, S. undulatis (Galster and Morrison 1976), the thirteen-lined ground squirrel, S. tridecemlineatus (Mrosovsky and Fisher 1970), and in S. lateralis at least, occurs in both captive juveniles (Pengelley and Asmundson 1969) and young born and weaned under constant conditions of temperature and photoperiod (Heller and Poulson 1970; Pengelley and Asmundson 1970). Also, a typical pattern of weight change occurred in the same S. lateralis each year for four years (Pengelley and Asmundson 1970; Pengelley et al. 1979), and existed in animals which failed to hibernate (Pengelley and Fisher 1963).

Juvenile Richardson's ground squirrels in the laboratory differ from their free-ranging counterparts in the pattern of their body weight change in that the former gain weight more rapidly and to a greater extent than the latter (Figs. 2, 4). This can largely be explained by nutritious food in addition to reduced activity due to confinement in the laboratory. Since neither quality nor quantity of food in the laboratory was limiting, and since in spite of runways the activity of captive animals was more restricted than that of animals in the field, conditions for fat deposition were more favourable in the laboratory.

Abundance of food and reduced activity may account also for the weight plateau demonstrated for the animals in captivity (Fig. 2). Growth and fat deposition in preparation for hibernation appear to be limited to a particular

maximum level because when females attained a body weight of about 400 g during their first active season, they reduced food intake even though food was readily available, and their body weight stabilized. In fact, once a lean body weight of approximately 220 g was attained no more growth occurred and further weight gain resulted mainly from fat deposition (App. 1K). Thus, under favourable conditions for growth and fat deposition in the laboratory, animals could acquire their maximal weight at a relatively early time of year and then maintain this weight, presumably until some yet undetermined cue(s) triggers entrance into hibernation.

There is also a difference in the pattern of mean body weight change between free-ranging females and males (Fig. 4). This is related not only to differences in total body weight due to sex but probably also to the apparent disappearance from the population of animals that have completed fat deposition in preparation for hibernation. That a weight plateau is apparent for the female population as a whole but not for individuals that were trapped throughout the season (Fig. 5) suggests that commencing in August, animals which attain maximal weights disappear from the population. If it can be assumed that individual animals attain their maximal weight at different times, and that this weight is similar for different individuals, as indicated by the weight plateau in the laboratory, and that upon attainment of maximal weight individuals disappear from the population, then a plot of mean body weight would reveal a

period of apparent stability as seen in Fig. 4. The assumption that maximal weights are attained at different times is tenable considering conception may be from two to three weeks apart (Nellis 1969; Sheppard 1972; Michener 1973) and also considering that the growth rate of large litters may be comparatively slow (Bridgewater 1966). Another possible explanation for the plateau in mean body weight is that free-ranging animals, like captive ones, reduce food intake upon attainment of maximal weights and no longer enter traps readily. This possibility does not contradict the aforementioned assumption since other species of ground squirrels in the laboratory start to hibernate immediately following the attainment of maximal body weight and reduced food consumption (review: Pengelley and Asmundson 1974). If this is what occurs in Richardson's ground squirrels in the field, then those animals which do not enter traps may disappear underground to hibernate. Alternatively, the majority of females may complete growth and fat deposition at about the same time and remain in the population until the onset of hibernation in late autumn. This does not appear to happen as tagged individuals, that were trapped repeatedly, gained weight progressively throughout the season (Fig. 5). However, the sample size was too small to eliminate the aforementioned possibility.

Growth and fat deposition in preparation for hibernation is probably limited to a particular level also in juvenile male Richardson's ground squirrels even though,

unlike for the female population, a weight plateau could not be demonstrated for males in the field (Fig. 4). One explanation for this difference is that males attain a greater body mass than females and this is probably associated with a prolonged period of weight gain. Thus, juvenile males may not be able to attain prehibernation weights until late in the season and this would account for their continuous increase in body weight and their relatively late disappearance from above ground (App. 7).

Disappearance of animals upon becoming fat could explain not only the difference in time of disappearance between juvenile males and females but also that between adult males and females. The order of disappearance from a given population has been demonstrated to be: adult males, adult females, juvenile females, juvenile males (Yeaton 1969; Michener 1974; Davis 1976; Michener 1977a, 1979a). Since adults are fully grown, males, following mating, could complete fat deposition relatively early in the season. On the other hand, females have to produce and suckle young which is energetically-costly as indicated in some species by a weight loss at this time (Hohn and Marshall 1966). They would, therefore, deposit fat at a later time than do males. Reduced weight gain and delayed attainment of prehibernation weights could also explain the later disappearance of females which undergo gestation and lactation as compared to those which do not (Barash 1976; Michener 1978), and the later onset of hibernation in the laboratory of the former

group of females (Pengelley and Asmundson 1975).

Based on the recapture of animals in the same area the following spring, Michener (1974) and Michener (1979a, b) have attributed the disappearance of animals upon becoming fat to hibernation rather than to dispersal. Furthermore, the tendency to trap comparatively small animals late in the season suggested that lean animals go into hibernation at a later date than do fat ones (Murie 1973; Dorrance 1974; Morton et al. 1974). These suggestions have been supported by the studies of Wang (1973, 1979) who observed late hibernation with delayed fattening in juvenile Richardson's ground squirrels and who, by means of radio-telemetry, obtained evidence of torpor in animals that disappeared underground.

Differences in time have been reported for the disappearance underground of juvenile Richardson's ground squirrels from different localities of similar latitudes. These differences do not seem to result from differences in breeding dates. In Winnipeg ( $49^{\circ}54'N$ ;  $97^{\circ}14'W$ ), Manitoba, juvenile Richardson's ground squirrels were first observed above ground on May 21. Assuming that gestation in this species takes about 25 days and that young spend their first 30 days underground (Michener 1977b), conception of ground squirrels in southern Manitoba can be estimated to occur between the end of March and the beginning of April. This corresponds with breeding dates reported by Michener (1973, 1977a) for Richardson's ground squirrels in Kayville

(49°40'N; 105°10'W), Saskatchewan, and Longview (50°34'N; 114°18'W), Alberta, and is slightly earlier for the same species in Rochester (approx. 54°30'N; 113°10'W), Alberta, and near Regina (approx. 50°30'N; 104°30'W), Saskatchewan (Nellis 1969; Sheppard 1972). Despite that breeding in these areas occurs at similar times, juvenile Richardson's ground squirrels in Winnipeg remain active much later in the year than do juveniles of this species in other localities. Unlike elsewhere, juvenile males were trapped in Winnipeg until November 11; several females were also trapped at this late a date, although most of them had disappeared by October 28. These dates differ by up to two months from those reported by Yeaton (1969) and Michener (1977a) for juvenile Richardson's ground squirrels in Bogy Creek (approx. 50°35'N), Saskatchewan, and Longview (50°34'N; 114°18'W), Alberta, and by almost three months for this species in Mapleton County (approx. 46°50'N; 97°15'W), North Dakota (Quanstrom 1968).

The relatively late disappearance of juvenile Richardson's ground squirrels in southern Manitoba is difficult to explain particularly since general weather patterns are similar to those in southern Saskatchewan and North Dakota. Abnormally high rainfall may cause weight loss and late disappearance (Michener 1979a); however, weather reports from the local Winnipeg airport for the period of the study showed no marked departures from normal mean monthly temperatures or precipitation. Nonetheless,

this does not eliminate the possibility that local climatic conditions in Winnipeg were less favourable for growth and fat deposition during the period of the study than those in the other localities at similar latitude but during different years, and that juvenile Richardson's ground squirrels in southern Manitoba take longer to attain a particular body weight before their disappearance underground. That juvenile Richardson's ground squirrels trapped in late August in Rochester (approx.  $54^{\circ}20'N$ ;  $113^{\circ}10'W$ ), Alberta (Dorrance 1974) were considerably heavier than ground squirrels trapped at a similar time of the year in southern Manitoba would support this suggestion. Unfortunately, Dorrance (1974) discontinued trapping before aboveground activity ceased so that maximum weights of Richardson's ground squirrels in Alberta are not available for comparison. Body weights of juvenile Richardson's ground squirrels in Kayville ( $49^{\circ}40'N$ ;  $105^{\circ}10'W$ ), Saskatchewan are comparable to those of juveniles in Winnipeg at similar times throughout the season (Michener 1974), but a comparison of the dates of disappearance cannot be made since Michener (1974) has not stated if trapping occurred until all animals disappeared.

Although on the basis of body weight differences there is insufficient information to explain the relatively late disappearance of juvenile Richardson's ground squirrels locally, a study conducted on two populations of adult Belding ground squirrels, *S. beldingi*, at different altitudes in Mono County (approx.  $37^{\circ}58'N$ ;  $119^{\circ}40'W$ ), California

shows such an effect. The comparatively late disappearance of one of the populations could be related to their delayed fattening as a consequence of unfavourable weather which had delayed appearance above ground in the spring (Morton 1975).

Differences apparently exist in the rapidity with which prehibernation weights are attained in different species. Franklin's ground squirrels, S. franklini, S. undulatis, and S. richardsoni, all inhabiting environments with a short growing season, attain different ontogenetic stages relatively quickly. This indicates a comparatively rapid rate of development and growth (Clark 1970b; Morton and Tung 1971b; Turner et al. 1976; Kiell and Millar 1978) and thus, prehibernation weights can be attained in a short time in animals in northern temperate zones.

Standard metabolic rate in juvenile Richardson's ground squirrels requires consideration of both changes in body weight due to growth and those due to deposition of fat. Thus, the comparatively high total SMR in late July and early August is probably a consequence mainly of growth, and its reduction throughout August a reflection of lower energy requirements after cessation of growth (Figs. 7, 8). However, cessation of growth does not account entirely for the reduction in total SMR which continued to decline for almost a month after stabilization of body weight. The declining total SMR may be, therefore, an indication of metabolic adjustments in preparation for hibernation as

suggested for other species which undergo similar changes in autumn (Hoffman 1964a, b; Bailey 1965). That during August weight-specific SMR shows a decline similar to that of total SMR is to be expected since total body weight remained relatively stable at this time.

A gradual decline in metabolic rate in autumn has been observed in other hibernators (Kayser 1940, cited by Lachiver 1969; Popovic 1959; Hock 1960; Kalabukhov 1960; Bailey 1965; review: Kayser 1965; Armitage and Shulenberg 1972; Scott et al. 1974; Ward and Armitage 1977) but as yet, investigations concerning possible shifts in metabolic processes have not been performed. It has been suggested that an early depression in metabolism may facilitate fat deposition (Bailey 1965; Mrosovsky 1976). This could be the case in juvenile Richardson's ground squirrels since weight-specific SMR began to decrease while food consumption was still relatively high and before body weight had stabilized.

Within limits, body weight depends on the amount and type of food available to an animal. Hibernators, even in the presence of food, reduce food consumption in autumn under laboratory conditions (Pengelley and Fisher 1963; Jameson 1965; Lachiver 1969; Davis 1967; Armitage and Shulenberg 1972), and probably also in their natural habitat as suggested by a reduced foraging time (Barash 1976). Individual records of the present study indicate that reduction in food consumption of juvenile Richardson's ground squirrels starts prior to the stabilization of apparent

maximum body weight and approximately parallels the decline in weight-specific SMR (Figs. 15, 16; App. 6A, 6b). At least some of the reduction in food consumption and SMR will be the result of lower energy requirements during the period of cessation of growth; any further reduction, particularly after the completion of fat deposition, may relate to a decrease in energy requirement with a possible change in metabolic processes in preparation for hibernation. The low food consumption after cessation of growth and fat deposition implies food intake was such as to retain body fat accumulated for hibernation.

Following hibernation and the reprovision of food, juvenile Richardson's ground squirrels quickly regained weight through increased food consumption. They compensated for the weight loss during hibernation only until weights were similar to those of animals provided with food ad libitum at a similar time the year before (Fig. 3). From then on, body weights and food consumption were similar in the two year groups of animals (Figs. 3, 14). That hibernators upon recovery from absence of food regain weights appropriate for the particular time of year (Canguilhem and Marx 1973) and that corresponding food intake reaches a level it would have been had no deprivation occurred, has been observed also by Heller and Poulson (1970), and by Mrosovsky and Fisher (1970). These investigators postulated a changing hypothalamic set point for body weight which would ensure the return of animals to a

'programmed' level of weight at any given time of the year.

Changes of activity in hibernators indirectly relate to changes in body weight (Pengelley and Fisher 1966; Richter unpubl., cited by Pengelley 1967). Fat animals are relatively inactive before hibernation in the autumn; the same animals may be very active after emergence from hibernation when they are lean. Generally, juvenile Richardson's ground squirrels showed such a relationship between activity and body weight though the relationship between body weight and activity was more pronounced in some animals than in others (Figs. 15, 16; App. 6A, 6B). Also, this relationship did not persist throughout the year since, in the autumn when body weight stabilized for several months, activity generally continued to decline, and in the early spring, when body weight increased rapidly, activity increased rapidly also. Nonetheless, activity changes of Richardson's ground squirrels are comparable to the annual changes that have been reported for S. lateralis (Pengelley and Fisher 1966).

Richardson's ground squirrels generally decreased their activity in autumn regardless of whether or not they entered hibernation (Figs. 9, 10). That activity became very low in ground squirrels that did not hibernate probably relates to the animals' readiness for hibernation. A decline in activity with the approach of hibernation has been reported also for S. tridecemlineatus (McCarley 1966; Wistrand 1974) and for S. richardsoni (Michener 1972) in

their natural habitat. A low activity in winter occurs also in the chipmunk, Eutamias amoenus, under semi-natural conditions (Stebbins and Orich 1977), in S. tridecemlineatus (Landau and Dawe 1960), and in S. lateralis (Pengelley and Fisher 1966) in the laboratory.

For captive Richardson's ground squirrels the rate of decline in activity during autumn was more pronounced in animals deprived of food as a result of these animals entering hibernation (Fig. 9); the exception was paired animals which exhibited carnivorous behavior (Fig. 13). Apparently, a decline, or stable levels of activity are typical of dormice, Glis glis (Mrosovsky 1964; Cornish and Mrosovsky 1965), the Townsend ground squirrel, S. townsendi, and chipmunks, E. minimus (Cornish and Mrosovsky 1965), when deprived of food. This is unlike the response of such nonhibernators as rats, Rattus norvegicus, and guinea pigs, Cavia porcellus, which tend to increase their activity when food is withdrawn (Cornish and Mrosovsky 1965).

Changes observed in Richardson's ground squirrels during late summer suggest that animals were ready for hibernation even though hibernation did not occur unless food was withdrawn. Occurrences associated with preparation for hibernation included cessation of growth and fat deposition, reductions in SMR, food consumption, and activity, moult, building of deep nests, and noticeable docility. All these events occurred prior to changes in either photoperiod or temperature and, therefore, they are probably endogenously-

controlled, inherent events that occur periodically. This suggestion is supported by the observation that similar changes took place in two different year groups of animals and with no apparent correspondence to changes in experimental conditions.

That, unlike other species (Pengelley and Kelly 1966; Heller and Poulson 1970; Mrosovsky and Fisher 1970; review: Pengelley and Asmundson 1974), Richardson's ground squirrels did not hibernate unless food-deprived agrees with previous observations of species differences in the ability to hibernate under laboratory conditions. Thus, captive S. lateralis (Heller and Poulson 1970; Scott and Fisher 1970; review: Pengelley and Asmundson 1974), S. tridecemlineatus (Mrosovsky and Fisher 1970; Mrosovsky and Lang 1971), and the Mohave ground squirrel, S. mohavensis (Pengelley and Kelly 1966), hibernate readily during their first autumn in the presence of food. On the other hand, the round-tailed ground squirrel, S. tereticaudis, the rock squirrel, S. variegatus, and the California ground squirrel, S. beecheyi, exhibit shorter, less regular hibernation bouts than do S. lateralis and S. mohavensis when food is supplied ad libitum, and under this condition, S. beecheyi may not hibernate at all (Pengelley and Kelly 1966).

Present findings support those of Pengelley and Fisher (1961) who reported that hibernation does not occur in Richardson's ground squirrels held at LD 12:12, 0°C, and supplied with food ad libitum. Under similar conditions in

subsequent years, Scott and Fisher (1970) did observe hibernation in this species; animals held at 18°C hibernated also. However, the animals did not hibernate as well as S. lateralis (Scott and Fisher 1970). In some animals, hibernation did not occur until their second and third year in the laboratory and others had two hibernation periods per year. Present findings are in contrast to those of Hudson and Deavers (1976) who reported that prolonged food deprivation does not elicit hibernation in Richardson's ground squirrels held at LD 12:12 and at either room temperature or 15°C. Nonetheless, the animals underwent two periods of reduced metabolism per year (Hudson and Deavers 1976), a probable reflection of an inherent change related to dormancy.

Since Richardson's ground squirrels do occasionally hibernate in the presence of food (Scott and Fisher 1970), food availability per se may not be the sole factor in preventing hibernation. The availability of food, though, may have caused animals to retain some activity and hence, social interaction among animals may have hindered hibernation in the laboratory. Social interaction did impede hibernation in several pairs of Richardson's ground squirrels though this occurred after food was withdrawn. Carnivorous behavior ensued in the presence and absence of food in some of these animals, but this is apparently not unusual for ground squirrels (Cade 1951; Mayer 1953; Musacchia 1954; Steiner 1972; Holmes 1977; Michener and Michener 1977;

Morton and Sherman 1978). One of the initially paired animals entered hibernation after the death of its partner, indicating that this animal was capable of hibernating under present laboratory conditions and that the influence of the other animal probably prevented an earlier entrance into hibernation. There is suggestive evidence that some species of ground squirrels are not likely to hibernate if they have access to activity wheels (Pengelley and Fisher 1966; Heller and Poulson 1970). Richardson's ground squirrels in this study were relatively unconfined and this may have been a factor contributing to the prevention of hibernation.

The occurrence or complete manifestation of certain biological phenomena at a particular time of year depends on the interaction between an internal rhythm of an organism and physical changes in the environment. Such interaction requires readiness for physiological and/or behavioral events triggered by changes in the environment. Hibernation depends to a greater or lesser degree on the interaction between endogenous and exogenous events. Thus, the changes observed in body weight, metabolism, food consumption and activity, moulting and nest building, probably reflect internal rhythms, their occurrence being independent of changes in ambient temperature and photoperiod. Despite these internal changes, hibernation did not occur in animals provided with food. Therefore, the presence of food and/or the lack of some other environmental stimulus prevented hibernation of animals in this study.

Lack of food might be a factor that triggers entrance into hibernation. Indeed, most animals hibernated when food was withdrawn. It is doubtful, though, that in nature food availability is the dominant factor, or the only factor required to stimulate entrance into hibernation. Both adult and juvenile Richardson's ground squirrels disappear from the population upon attainment of maximum body weights even though this might occur relatively early in the season when food is still readily available. However, fat animals may be too lethargic to forage and stay in burrows where food is not available and temperatures are comparatively low. In the case of juveniles active late in the season, confinement to burrows is probably the result of snowfall and/or severe cold. Consequently, the dark, quiet environment, restricted activity in burrows, comparatively low temperatures and lack of food superimposed on maximum body weight, decreased energy requirements, and the ability to lower body temperature result in hibernation of Spermophilus richardsoni in their natural habitat.

#### LITERATURE CITED

- Armitage, K.B., and E. Shulenberger. 1972. Evidence for a circannual metabolic cycle in Citellus tridecemlineatus, a hibernator. *Comp. Biochem. Physiol.* 42A:667-688.
- Bailey, E.D. 1965. Seasonal changes in metabolic activity of non-hibernating woodchucks. *Can. J. Zool.* 43:905-909.
- Bailey, E.D., and D.E. Davis. 1965. The utilization of body fat during hibernation in woodchucks. *Can. J. Zool.* 43:701-707.
- Barash, D.P. 1976. Pre-hibernation behavior of free-living hoary marmots, Marmota caligata. *J. Mammal.* 57:182-185.
- Baumgartner, L.L. 1940. Trapping, handling and marking fox squirrels. *J. Wildl. Manage.* 4:444-450.
- Blake, B.H. 1972. The annual cycle and fat storage in two populations of golden-mantled ground squirrels. *J. Mammal.* 53:157-167.
- Bridgewater, D.D. 1966. Laboratory breeding, early growth development and behaviour of Citellus tridecemlineatus (Rodentia). *Southwestern Nat.* 11:325-337.
- Cade, T. 1951. Carnivorous ground squirrels on St. Lawrence Island, Alaska. *J. Mammal.* 32:358-360.
- Canguilhem, B., and Ch Marx. 1973. Regulation of the body weight of the European hamster during the annual cycle. *Pflügers Arch.* 338:169-175.
- Carl, E.A. 1971. Population control in arctic ground squirrels. *Ecology* 52:396-413.
- Clark, T.W. 1970a. Richardson's ground squirrel (Spermophilus richardsonii) in the Laramie Basin, Wyoming. *Great Basin Nat.* 30:55-70.
- Clark, T.W. 1970b. Early growth development, and behavior of the Richardson ground squirrel (Spermophilus richardsonii elegans). *Am. Midl. Nat.* 83:197-205.

- Cornish, E.R., and N. Mrosovsky. 1975. Food deprivation and satiation of six species of rodent. *Anim. Behav.* 13:242-248.
- Davis, D.E. 1967. The annual rhythm of fat deposition in woodchucks Marmota monax. *Physiol. Zool.* 40:391-402.
- Davis, D.E. 1976. Hibernation and circannual rhythms of food consumption in marmots and ground squirrels. *Quart. Rev. Biol.* 51:477-514.
- Depocas, F., and J.S. Hart. 1957. Use of the Pauling oxygen analyser for measurements of oxygen consumption of animals in open circuit systems and in a short-lag, closed-circuit apparatus. *J. Appl. Physiol.* 10:388-392.
- Dorrance, M. 1974. The annual cycle and population dynamics of Richardson's ground squirrel. Ph.D. Thesis. University of Wisconsin.
- Enright, J.T. 1970. Ecological aspects of endogenous rhythmicity. *Ann. Rev. Ecol. Syst.* 1:221-237.
- Evans, F.C., and R. Holdenreid. 1943. A population study of the Beechey ground squirrel in central California. *J. Mammal.* 24:231-260.
- Fitch, H.S. 1948. Ecology of the California ground squirrel in grazing lands. *Am. Midl. Nat.* 39:513-596.
- Galster, W., and P. Morrison. 1976. Seasonal changes in body composition of the arctic ground squirrel, Citellus undulatus. *Can. J. Zool.* 54:74-78.
- Heller, H.C., and T.L. Poulson. 1970. Circadian rhythms II. Endogenous and exogenous factors controlling reproduction and hibernation in chipmunks Eutamias, and ground squirrels, Spermophilus. *Comp. Biochem. Physiol.* 33:357-383.
- Hemming, F. (ed.) 1958. Official Index of Rejected and Invalid Works in Zoological Nomenclature. London: Printed by order of the International Trust for Zoological Nomenclature. p. 8.
- HersHKovitz, P. 1949. Status of names credited to Oken, 1816. *J. Mammal.* 30:289-301.
- Hock, R.J. 1960. Seasonal variations in physiologic functions of arctic ground squirrels and black bears. *Bull. Mus. Comp. Zool.* 124:155-171.

- Hoffman, R.A. 1964a. Terrestrial animals in cold: hibernators. In: Dill, D.B. (ed.), Handbook of Physiology: Adaption to the Environment. Am. Physiol. Soc., Washington, D.C.
- Hoffman, R.A. 1964b. Speculations on the regulation of hibernation. *Ann. Acad. Scient. Fennicae A IV.* 71/14: 199-214.
- Hohn, B.M., and W.H. Marshall. 1966. Annual and seasonal weight changes in a thirteen-lined ground squirrel population, Itasca State Park, Minnesota. *Minnesota Acad. Sci.* 33:102-106.
- Holmes, W.G. 1977. Cannibalism in the arctic ground squirrel (Spermophilus parryi). *J. Mammal.* 58:437-438.
- Hudson, J.W., and D.R. Deavers. 1976. Thyroid function and basal metabolism in the ground squirrels Ammospermophilus leucurus and Spermophilus spp. *Physiol. Zool.* 49:425-444.
- Immelman, K. 1973. Role of the environment in reproduction as a source of predictive information. In: Farner, D.S. (ed.), Breeding Biology of Birds. Natl. Acad. Sci., Washington.
- Iverson, S.L., and B.N. Turner. 1972. Natural history of a Manitoba population of Franklin's ground squirrels. *Can. Field-Nat.* 86:145-149.
- Jameson, E.W. 1965. Food consumption of hibernating and non-hibernating Citellus lateralis. *J. Mammal.* 46: 634-640.
- Jameson, E.W., and R.A. Mead. 1964. Seasonal changes in body fat, water and basic weight in Citellus lateralis, Eutamias speciosus and E. amoenus. *J. Mammal.* 45:359-365.
- Kalabukhov, N.I. 1960. Comparative ecology of hibernating mammals. *Bull. Mus. Comp. Zool.* 124:45-74.
- Kayser, C. 1965. Hibernation. In: Mayer, W.V., and R.G. Van Gelder (eds.), Physiological Mammalogy Vol. II: Mammalian Reactions to Stressful Environments. Academic Press, N.Y.
- Kiell, D.J., and J.S. Millar. 1978. Growth of juvenile arctic ground squirrels (Spermophilus parryii) at McConnell River, N.W.T. *Can. J. Zool.* 56:1475-1478.

- Lachiver, F. 1969. Seasonal hormonal effect of states of depressed metabolism. In: Musacchia, X.J., and J.F. Saunders (eds.), Depressed Metabolism. Am. Elsevier Pub. Co. Inc., N.Y.
- Landau, B.R., and A.R. Dawe. 1960. Observations on a colony of captive ground squirrels throughout the year. *Bull. Mus. Comp. Zool.* 124:173-191.
- Lyman, C.P., and P.O. Chatfield. 1965. Physiology of hibernation in mammals. *Physiol. Rev.* 35:403-425.
- Mayer, M.V. 1953. A preliminary study of the Barrow ground squirrel, Citellus parryi barrowensis. *J. Mammal.* 34:334-345.
- McCarley, H. 1966. Annual cycle, population dynamics and adaptive behaviour of Citellus tridecemlineatus. *J. Mammal.* 47:294-315.
- Michener, D.R. 1968. A study of the ecology of Richardson's ground squirrel, Citellus richardsoni richardsoni with special reference to the effects of meteorological variables on activity. M.Sc. Thesis. University of Waterloo.
- Michener, D.R. 1972. Notes on home range and social behavior in adult Richardson's ground squirrels, Spermophilus richardsonii. *Can. Field-Nat.* 86:77-79.
- Michener, D.R. 1974. Annual cycle of activity and weight changes in Richardson's ground squirrels, Spermophilus richardsonii. *Can. Field-Nat.* 88:409-413.
- Michener, G.R. 1973. Climatic conditions and breeding in Richardson's ground squirrel. *J. Mammal.* 54:499-503.
- Michener, G.R. 1977a. Effect of climatic conditions on the annual activity and hibernation cycle of Richardson's ground squirrels and Columbian ground squirrels. *Can. J. Zool.* 55:693-703.
- Michener, G.R. 1977b. Gestation period and juvenile age at emergence in Richardson's ground squirrel. *Can. Field-Nat.* 91:410-413.
- Michener, G.R. 1978. Effect of age and parity on weight gain and entry into hibernation in Richardson's ground squirrels. *Can. J. Zool.* 56:2573-2577.
- Michener, G.R. 1979a. The circannual cycle of Richardson's ground squirrels in Southern Alberta. *J. Mammal.* 60:760-768.

- Michener, G.R. 1979b. Yearly variations in the population dynamics of Richardson's ground squirrels. *Can. Field-Nat.* 93:363-370.
- Michener, G.R., and D.R. Michener. 1977. Population structure and dispersal in Richardson's ground squirrels. *Ecology* 58:359-368.
- Morton, M.L. 1975. Seasonal cycles of body weights and lipids in Belding ground squirrels. *South. Calif. Acad. Sci.* 74:128-143.
- Morton, M.L., C.S. Maxwell, and C.E. Wade. 1974. Body size, body composition, and behaviour of juvenile Belding ground squirrels. *Great Basin Nat.* 34:121-134.
- Morton, M.L., and R.J. Parmer. 1975. Body size, organ size and sex ratios in adult and yearling Belding ground squirrels. *Great Basin Nat.* 35:305-309.
- Morton, M.L., and P.W. Sherman. 1978. Effects of a spring snow storm on behaviour, reproduction, and survival of Belding's ground squirrels. *Can. J. Zool.* 56:2578-2590.
- Morton, M.L., and H.L. Tung. 1971a. The relationship of total body lipid to fat depot weight and body weight in the Belding ground squirrel. *J. Mammal.* 52:839-842.
- Morton, M.L., and H.L. Tung. 1971b. Growth and development in the Belding ground squirrel (*Spermophilus beldingi beldingi*). *J. Mammal.* 52:611-616.
- Mrosovsky, N. 1964. The performance of dormice and other hibernators on tests of hunger motivation. *Anim. Behav.* 12:454-469.
- Mrosovsky, N. 1976. Lipid programmes and life strategies in hibernators. *Am. Zool.* 16:685-697.
- Mrosovsky, N., and K.C. Fisher. 1970. Sliding set points for body weight in ground squirrels during the hibernation season. *Can. J. Zool.* 48:241-247.
- Mrosovsky, N., and K. Lang. 1971. Disturbances in the annual weight and hibernation cycles of thirteen-lined ground squirrels kept in constant conditions and the effects of temperature changes. *Interdiscipl. Cycle. Res.* 2:79-90.

- Murie, J.O. 1973. Population characteristics and phenology of a Franklin ground squirrel (Spermophilus franklinii) colony in Alberta, Canada. Am. Midl. Nat. 90: 334-340.
- Musacchia, X.J. 1954. Cannibalism and other observations of captive ground squirrels. J. Mammal. 35:445-447.
- Nellis, C.H. 1969. Productivity of Richardson's ground squirrels near Rochester, Alberta. Can. Field-Nat. 83:246-250.
- Pengelley, E.T. 1967. The relation of external conditions to the onset and termination of hibernation and estivation. In: Fisher, K.C., A.R. Dawe, C.P. Lyman, E. Schonbaum, and F.E. South (eds.), Mammalian Hibernation III: Proc. Third Intl. Symp. on Natural Mammalian Hibernation (1965). Am. Elsevier Pub. Co. Inc., N.Y.
- Pengelley, E.T., R.C. Aloia, B.M. Barnes, and D. Whitson. 1979. Differential temporal behaviour between males and females in the hibernating ground squirrel, Citellus lateralis. Comp. Biochem. Physiol. 64A:593-596.
- Pengelley, E.T., and S.J. Asmundson. 1969. Free-running periods of endogenous rhythms in the golden-mantled ground squirrel, Citellus lateralis. Comp. Biochem. Physiol. 30:177-183.
- Pengelley, E.T., and S.J. Asmundson. 1970. The effect of light on the free-running circannual rhythm of the golden-mantled ground squirrel, Citellus lateralis. Comp. Biochem. Physiol. 32:155-160.
- Pengelley, E.T., and S.J. Asmundson. 1971. Annual biological clocks. Sci. Am. 224:72-79.
- Pengelley, E.T., and S.J. Asmundson. 1974. Circannual rhythmicity in hibernating animals. In: Pengelley, E.T. (ed.), Circannual Clocks: Annual Biological Rhythms. Academic Press, N.Y.
- Pengelley, E.T., and S.J. Asmundson. 1975. Female gestation and lactation as Zeitgebers for circannual rhythmicity in the hibernating ground squirrel, Citellus lateralis. Comp. Biochem. Physiol. 50A:621-625.
- Pengelley, E.T., and K.C. Fisher. 1957. Onset and cessation of hibernation under constant temperature and light in the golden-mantled ground squirrel (Citellus lateralis). Nature 180:1371-1372.

- Pengelley, E.T., and K.C. Fisher. 1961. Rhythmical arousal from hibernation in the golden-mantled ground squirrel, Citellus lateralis tescorum. Can. J. Zool. 39:105-120.
- Pengelley, E.T., and K.C. Fisher. 1963. The effect of temperature and photoperiod on the yearly hibernating behaviour of captive golden-mantled ground squirrels Citellus lateralis tescorum. Can. J. Zool. 41:1103-1120.
- Pengelley, E.T., and K.C. Fisher. 1966. Locomotor activity patterns and their relation to hibernation in the golden-mantled ground squirrel. J. Mammal. 47:63-73.
- Pengelley, E.T., and K.H. Kelly. 1966. A 'circannian' rhythm in hibernating species of the genus Citellus with observations on their physiological evolution. Comp. Biochem. Physiol. 19:603-617.
- Popovic, V. 1959. Lethargic hypothermia in hibernators and nonhibernators. Ann. N.Y. Acad. Sci. 80:320-331.
- Quanstrom, W. 1968. Some aspects of the ethoecology of Richardson's ground squirrel in Eastern North Dakota. Ph.D. Thesis. University of Oklahoma.
- Scott, G.W., and K.C. Fisher. 1970. The lengths of hibernation cycles in mammalian hibernators living under controlled conditions. Penn. Acad. Sci. 44:180-183.
- Scott, G.W., K.C. Fisher, and J.A. Love. 1974. A telemetric study of the abdominal temperature of a hibernator, Spermophilus richardsonii, maintained under constant conditions of temperature and light during the active season. Can. J. Zool. 52:653-658.
- Sheppard, D.H. 1972. Reproduction of Richardson's ground squirrel (Spermophilus richardsonii) in southern Saskatchewan. Can. J. Zool. 50:1577-1581.
- Skryja, D.D., and T.W. Clark. 1970. Reproduction, seasonal changes in body weight, fat deposition, spleen and adrenal gland weight of the golden-mantled ground squirrel, Spermophilus lateralis lateralis, (Sciuridae) in the Laramie mountains, Wyoming. Southwestern Nat. 15:201-208.
- Snedecor, G.W., and W.G. Cochran. 1967. Statistical Methods. Iowa State University Press, Iowa. 593 pp.
- Stebbins, L.L., and R. Orich. 1977. Some aspects of overwintering in the chipmunk Eutamias amoenus. Can. J. Zool. 55:1139-1146.

- Steiner, A.L. 1972. Mortality resulting from intraspecific fighting in some ground squirrel populations. *J. Mammal.* 53:601-603.
- Turner, B.N., S.L. Iverson, and K.L. Severson. 1976. Postnatal growth and development of captive Franklin's ground squirrels (*Spermophilus franklinii*). *Am. Midl. Nat.* 95:93-102.
- Wade, O. 1948. Rapid fat production by ground squirrels preceding hibernation. *Nat. Hist. Misc.*, Chicago Acad. Sci. 28:1-3.
- Wang, L.C.H. 1973. Radiotelemetric study of hibernation under natural and laboratory conditions. *Am. J. Physiol.* 224:673-677.
- Wang, L.C.H. 1979. Time patterns and metabolic rate of natural torpor in Richardson's ground squirrels. *Can. J. Zool.* 57:149-155.
- Ward, J.M., and K.B. Armitage. 1977. Metabolism of the yellow-bellied marmot (*Marmota flaviventris*). Abstr. In: Strategies in Cold: Natural Torpidity and Thermogenesis. International Hibernation Conference, Jasper Park Lodge, Canada.
- Wistrand, H. 1974. Individual, social and seasonal behavior of the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). *J. Mammal.* 55:329-347.
- Withers, P.C. 1977. Measurement of  $VO_2$ ,  $VCO_2$  and evaporative water loss with a flow through mask. *J. Appl. Physiol. Respirat. Environ. Exercise Physiol.* 42:120-123.
- Yeaton, R.I. 1969. Social behaviour, social organization and daily activity patterns in the Richardson's ground squirrel. M.Sc. Thesis. University of Saskatchewan.
- Zar, J.H. 1974. Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs, N.J. 620 pp.
- Zegers, D.A., and O. Williams. 1977. Seasonal cycles of body weight and lipids in Richardson's ground squirrel, *Spermophilus richardsonii elegans*. *Acta Theriol.* 22, 29:380-383.

APPENDICES

APPENDIX 1

Body Weights of Juvenile S. richardsoni

Appendix 1A. Mean body weights of Group I juvenile *S. richardsoni* held at different photoperiods but otherwise similar experimental conditions.

BODY WEIGHT (g)								
Date	Group I A <sub>1</sub> <u>LD 12:12</u>			Group I B <sub>1</sub> <u>LD 12:12</u>			t-value	
	$\bar{X}$	$\pm$ SD	n	$\bar{X}$	$\pm$ SD	n		
July 16	297	(31.4)	8	294	(34.3)	8	0.21	
Aug. 4	431	(66.3)	8	434	(61.4)	8	-0.09	
Sept. 2	465	(81.8)	8	454	(60.7)	8	0.31	
Oct. 2	450	(64.8)	8	460	(66.9)	8	-0.30	
Oct. 20	457	(75.0)	8	456	(83.1)	8	0.03	
Dec. 1				<u>LD 00:24</u>				
March 5	471	(58.5)	8	478	(79.5)	8	-0.22	
April 1	517	(51.4)	8	525	(94.3)	8	-0.21	
April 29	613	(82.1)	8	623	(95.3)	8	-0.23	
May 1				<u>LD 12:12</u>				
June 1	643	(90.6)	8	643	(121.5)	8	0.17	
June 24	680	(76.8)	8	654	(118.4)	8	0.52	

There were no significant differences in mean body weights between animals held at different photoperiods.

Appendix 1B. Mean body weights of Group II juvenile S. richardsoni held at different photoperiods but otherwise similar experimental conditions.

BODY WEIGHT (g)								
Date	Group II A <sub>2</sub>			Group II B <sub>2</sub>			t-value	
	<u>LD 12:12</u>			<u>LD 12:12</u>				
	$\bar{X}$	$\pm$ SD	n	$\bar{X}$	$\pm$ SD	n		
July 1	214	(21.1)	6	195	(16.2)	6	1.74	
Aug. 3	400	(49.3)	6	388	(61.8)	6	0.37	
Aug. 30	386	(63.4)	6	383	(56.0)	6	0.11	
Sept. 28	407	(74.8)	6	396	(56.0)	6	0.30	
Oct. 26	409	(84.1)	6	404	(51.3)	6	0.11	
Nov. 17	410	(84.7)	6	389	(65.9)	6	0.48	
Dec. 1				<u>LD 00:24</u>				
Jan. 16	290	(89.4)	6	328	(63.1)	6	-0.86	
Feb. 1	354	(52.5)	6	382	(60.0)	6	-0.85	
March 1	412	(44.7)	6	460	(81.7)	6	-1.26	
March 28	490	(46.2)	6	504	(76.8)	6	-0.38	
May 1				<u>LD 12:12</u>				
May 3	501	(64.4)	6	528	(101.6)	6	-0.55	
May 31	530	(93.3)	6	545	(101.9)	6	-0.26	
June 14	544	(99.2)	6	545	(102.9)	6	0.02	

There were no significant differences in mean body weights between animals held at different photoperiods.

Appendix 1C. Mean body weights of Group I female S. richardsoni held at different photoperiods but otherwise similar experimental conditions.

BODY WEIGHT (g)							
Date	Group I A <sub>1</sub>			Group I B <sub>1</sub>			t-value
	$\bar{X}$	$\pm$ SD	n	$\bar{X}$	$\pm$ SD	n	
July 16	288	(32.9)	4	277	(42.0)	4	0.40
Aug. 4	409	(57.4)	4	411	(83.1)	4	-0.04
Sept. 2	435	(78.8)	4	439	(80.1)	4	-0.09
Oct. 2	415	(73.1)	4	442	(85.1)	4	-0.48
Oct. 20	424	(74.9)	4	435	(99.2)	4	-0.18
Dec. 1				<u>LD 00:24</u>			
March 5	466	(76.1)	4	455	(103.1)	4	0.16
April 1	508	(69.0)	4	469	(75.8)	4	0.76
April 29	528	(79.6)	4	556	(72.8)	4	-0.50
May 1				<u>LD 12:12</u>			
June 1	559	(96.1)	4	557	(91.8)	4	0.02
June 24	608	(128.1)	4	577	(92.5)	4	0.40

There were no significant differences in mean body weights between females held at different photoperiods.

Appendix 1D. Mean body weights of Group I male S. richardsoni held at different photoperiods but otherwise similar experimental conditions.

BODY WEIGHT (g)							
Date	Group I A <sub>1</sub>			Group I B <sub>1</sub>			t-value
	<u>LD 12:12</u>			<u>LD 12:12</u>			
	$\bar{X}$	$\pm$ SD	n	$\bar{X}$	$\pm$ SD	n	
July 16	310	(20.7)	4	310	(15.8)	4	-0.04
Aug. 4	469	(42.1)	4	458	(20.7)	4	0.49
Sept. 2	500	(77.1)	4	469	(39.8)	4	0.71
Oct. 2	481	(46.1)	4	477	(48.6)	4	0.10
Oct. 20	492	(63.7)	4	476	(71.9)	4	0.33
Dec. 1				<u>LD 00:24</u>			
March 5	475	(46.1)	4	501	(52.3)	4	0.74
April 1	526	(35.9)	4	581	(81.0)	4	-1.24
April 29	672	(45.1)	4	691	(60.9)	4	-0.48
May 1				<u>LD 12:12</u>			
June 1	705	(55.3)	4	734	(99.1)	4	-0.50
June 24	725	(72.7)	4	732	(90.5)	4	-0.11

There were no significant differences in mean body weights between males held at different photoperiods.

Appendix 1E. Mean body weights of Group I juvenile S. richardsoni held under similar experimental conditions.

BODY WEIGHT (g)							
Date	Females			Males			t-value
	$\bar{X}$	$\pm$ SD	n	$\bar{X}$	$\pm$ SD	n	
July 16	273	(32.4)	12	316	(26.4)	12	-4.10**
Aug. 4	387	(63.4)	12	459	(32.6)	12	-3.52** (t')
Sept. 2	425	(61.8)	12	493	(56.9)	11	-2.88**
Oct. 2	416	(63.7)	12	486	(45.0)	11	-2.95**
Oct. 20	417	(70.4)	12	496	(61.3)	11	-0.90
March 5	462	(73.1)	11	487	(44.7)	9	-0.55
April 1	490	(61.6)	11	554	(61.2)	9	-3.44**
April 29	539	(69.1)	11	692	(56.5)	9	-4.73**
June 1	562	(82.0)	11	723	(64.4)	9	-4.64**
June 24	585	(33.5)	11	738	(76.7)	9	-4.23**

Since there were no significant differences in the mean body weights of females (Appendix 1C) or of males (Appendix 1D) held at different photoperiods, the above data have been pooled for males and for females.

\*\* Statistically significant;  $p < 0.01$ .

Appendix 1F. Mean body weights of Group I and Group II female juvenile S. richardsoni.

BODY WEIGHT (g)									
Date	Group I			Group II			t-value		
	$\bar{X}$	$\pm$ SD	n	$\bar{X}$	$\pm$ SD	n			
July 16	273	(32.4)	12	July 13	254	31.4	16	1.54	
Aug. 4	387	(63.4)	12	Aug. 3	383	51.7	16	0.18	
Sept. 2	425	(61.8)	12	Aug. 30	374	54.9	16	2.30*	
Oct. 2	416	(63.7)	12	Sept. 28	384	64.6	16	1.30	
March 5	462	(73.1)	11	March 1	432	65.7	12	1.02	
April 1	490	(61.6)	11	March 28	497	60.9	12	-0.27	
April 29	539	(69.1)	11	April 26	518	82.9	12	0.66	
June 1	562	(82.0)	11	May 31	537	93.5	12	0.68	
June 24	585	(33.5)	11	June 21	545	93.7	12	1.35	

Since there were no significant differences between females held at different photo-periods (Appendices 1B and 1C), data from each group have been pooled.

\* Statistically significant;  $p < 0.05$

Appendix 1G. Mean body weights of male and female juvenile S. richardsoni in their natural habitat.

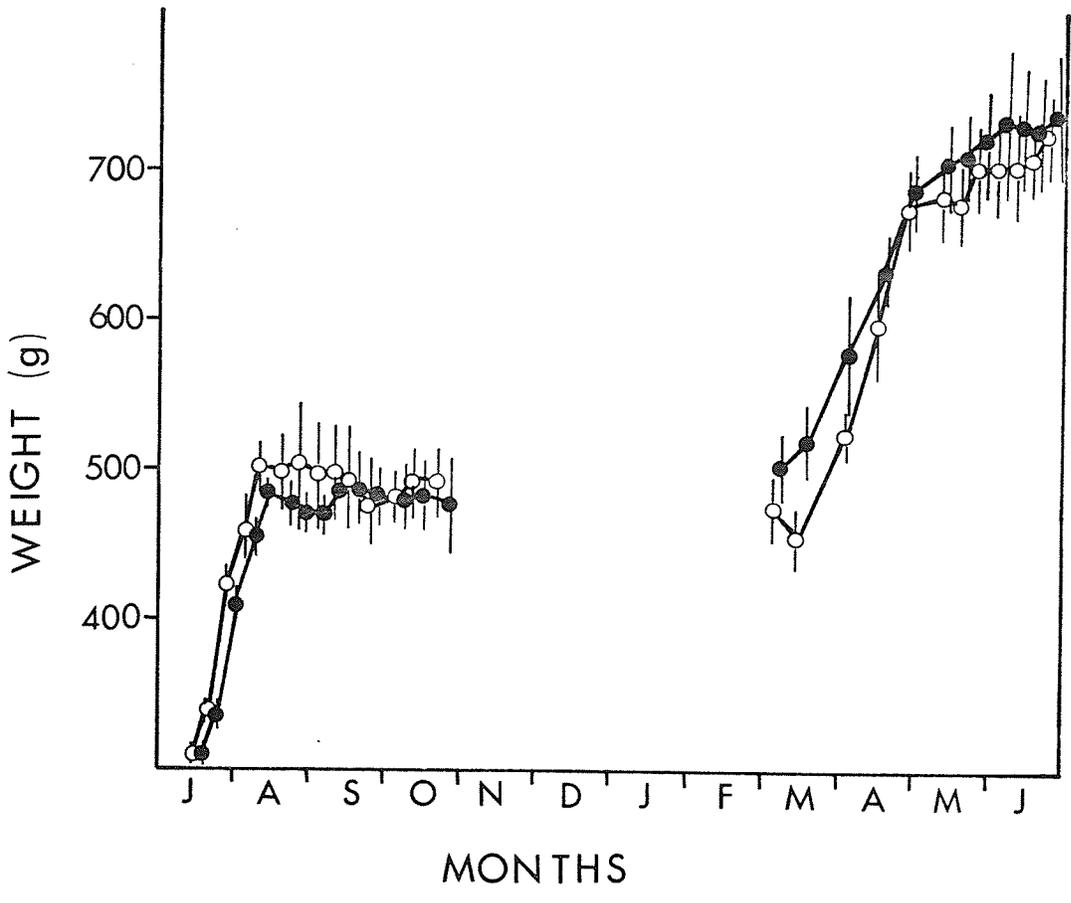
		BODY WEIGHT (g)						
		<u>Males</u>			<u>Females</u>			
Date		$\bar{X}$	$\pm$ SD	n	$\bar{X}$	$\pm$ SD	n	t-value
May	29-30	137	(29.5)	6	139	(28.4)	3	-0.10
June	4	143	(48.3)	11	148	(37.3)	13	-0.29
June	11	158	(55.1)	9	161	(41.6)	17	-0.14
June	18-22	171	(63.2)	24	185	(52.5)	20	-0.82
June	25-26	185	(55.2)	21	169	(46.9)	29	1.11
July	3	193	(53.6)	12	208	(67.6)	24	-0.65
July	10-12	203	(51.9)	10	195	(47.9)	13	0.36
July	16	248	(41.9)	18	229	(62.7)	23	1.09
July	24	248	(51.1)	15	251	(57.7)	25	-0.18
July	29	283	(47.1)	14	262	(58.1)	32	1.18
Aug.	6	283	(43.4)	17	272	(60.4)	27	0.66
Aug.	14	310	(39.1)	19	280	(57.4)	20	1.91
Aug.	18	301	(42.1)	9	282	(59.9)	24	0.88
Aug.	27	313	(37.8)	17	267	(49.0)	26	3.32**
Sept.	2	312	(47.4)	15	277	(58.3)	22	1.90
Sept.	10	320	(46.7)	21	274	(54.2)	27	3.16**
Sept.	19	386	(38.7)	7	293	(43.8)	10	4.47**
Sept.	28	349	(52.5)	16	271	(55.2)	21	4.26**
Oct.	11	369	(67.8)	16	278	(50.4)	16	4.30**
Oct.	15	403	(57.3)	19	277	(53.9)	14	6.39**
Oct.	21	431	(54.6)	17	298	(57.2)	15	6.73**
Oct.	28	445	(50.4)	16	302	(68.3)	8	5.83**
Nov.	4	466	(46.0)	12	287	(56.6)	2	26.21**
Nov.	11	440	(45.8)	12				

\*\* Statistically significant;  $p < 0.01$

Appendix 1H. Mean body weights of Group I male S. richardsoni held at different photoperiods but otherwise similar experimental conditions; n = 4.

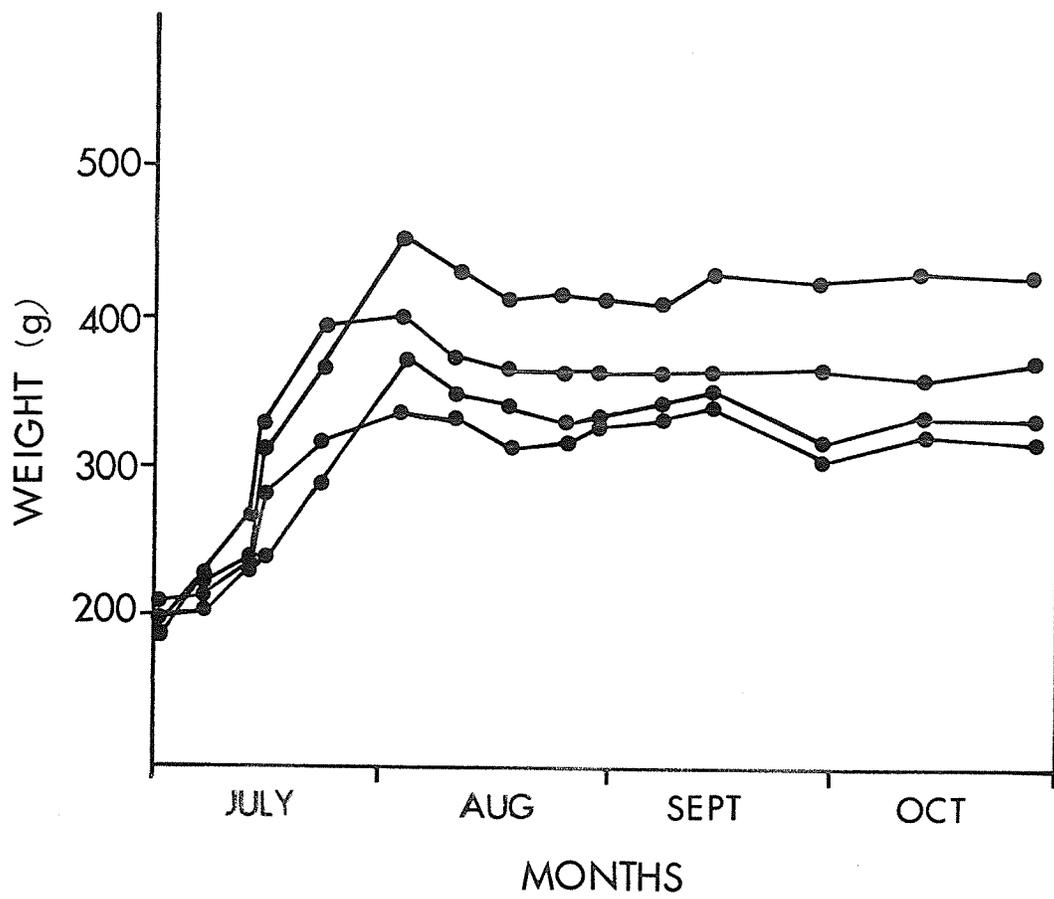
Vertical lines:  $\pm$  SE

n = Sample size



Appendix 1I. Body weights of four female juvenile S.  
richardsoni in the laboratory.

Data from the heaviest and lightest animals  
and from two animals of intermediary weights  
were chosen to represent Group II.

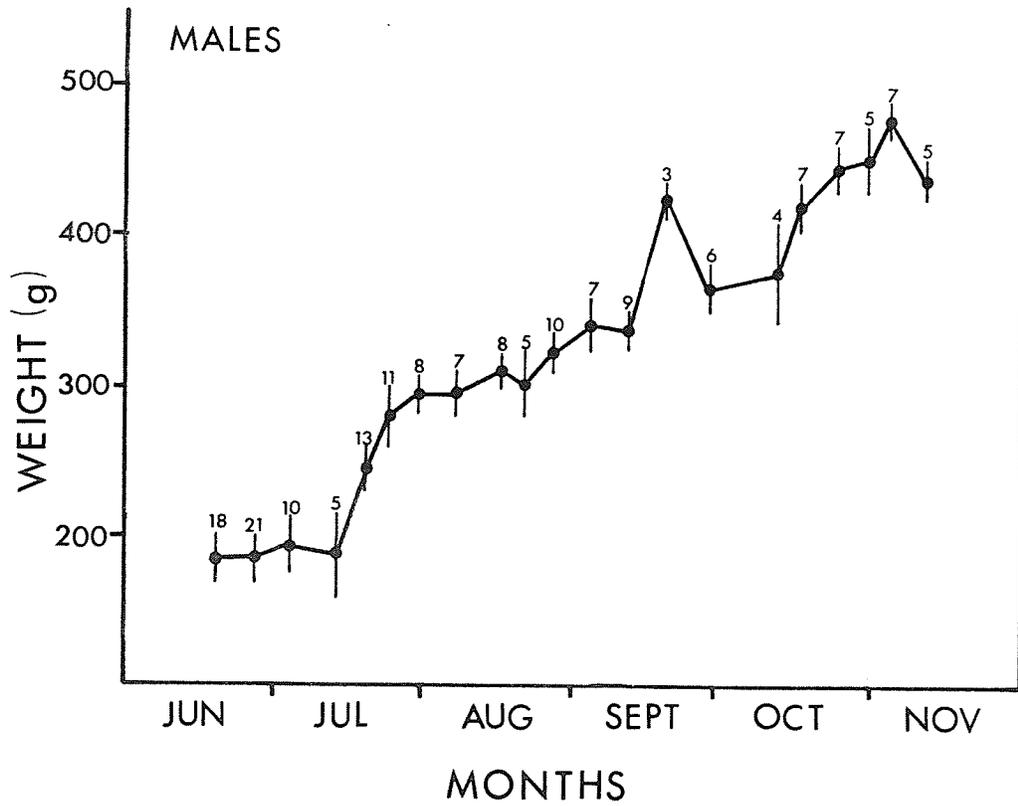
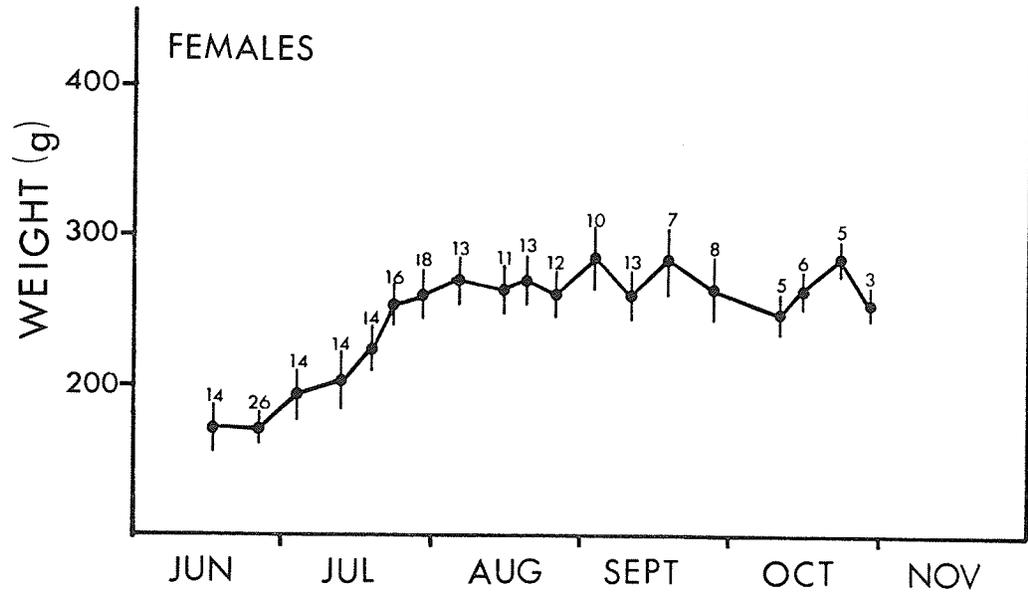


Appendix 1J. (Upper graph) Mean body weights of tagged female juvenile S. richardsoni in their natural habitat.

(Lower graph) Mean body weights of tagged male juvenile S. richardsoni in their natural habitat.

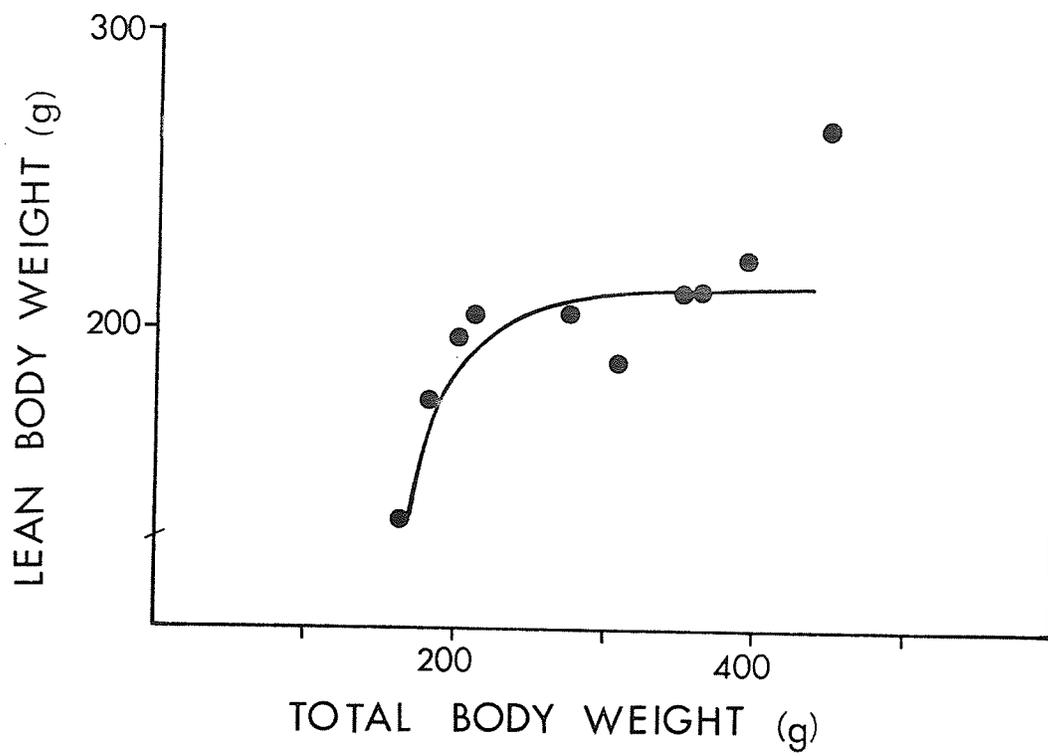
Vertical lines:  $\pm$  SE

n = Sample size



Appendix 1K. Relationship between lean body weight and total body weight in Group III juvenile S. richardsoni.

This graph was obtained by drawing the curve of apparent best fit for all points.



APPENDIX II

Metabolic Rate

Appendix 2A. RQ values determined for 12 h food-deprived female juvenile S. richardsoni.

Animal	$\dot{V}CO_2$ (ml h <sup>-1</sup> )	$\dot{V}O_2$ (ml h <sup>-1</sup> )	RQ
5A.	253.94	414.14	0.618
1A.	338.19	633.53	0.534
6A.U.	361.37	523.75	0.690
3A.	715.84	998.68	0.717
2A.	522.05	687.75	0.759
5A.	204.92	354.76	0.578
2A.	737.61	928.44	0.795
1A.	409.47	499.40	0.820
5A.	267.69	344.99	0.776
3A.	366.55	562.47	0.652
6A.U.	359.48	438.21	0.820
5A.	288.51	341.24	0.846
6A.U.	705.68	1351.89	0.522
			$\bar{X} = 0.702$
			n = 13
			SD = 0.1125

Experimentally-determined RQ (0.702) is not significantly different from expected RQ (0.707);  $p > 0.05$ .

Appendix 2B. Mean standard metabolic rate expressed on an hourly basis per animal and per unit weight, and mean body weight of Group I S. richardsoni.

Date	FEMALES						n
	$\dot{V}O_2$ (ml h <sup>-1</sup> )		$\dot{V}O_2$ (ml g <sup>-1</sup> h <sup>-1</sup> )		Weight (g)		
	$\bar{X}$	±SD	$\bar{X}$	±SD	$\bar{X}$	±SD	
July 15-31	1424.0	(154.6)	4.25	(0.31)	336	(42.5)	5
Aug. 1-15	1536.9	(149.6)	3.57	(0.45)	433	(42.8)	5
Aug. 16-31	1137.9	(62.1)	2.64	(0.44)	437	(57.4)	4
Sept. 1-15	1107.2	(63.3)	2.41	(0.33)	464	(44.9)	5

Date	MALES						n
	$\dot{V}O_2$ (ml h <sup>-1</sup> )		$\dot{V}O_2$ (ml g <sup>-1</sup> h <sup>-1</sup> )		Weight (g)		
	$\bar{X}$	±SD	$\bar{X}$	±SD	$\bar{X}$	±SD	
July 15-31	1801.4	(466.4)	4.83	(1.03)	371	(24.3)	7
Aug. 1-15	1570.1	(212.8)	3.39	(0.40)	464	(36.5)	10
Aug. 16-31	1490.4	(414.8)	3.00	(0.68)	493	(58.7)	8
Sept. 1-15	1347.8	(129.1)	2.87	(0.33)	470	(9.0)	2

Appendix 2C. Weight-specific standard metabolic rate of Group I male and female juvenile S. richardsoni.

Date	$\dot{V}O_2$ (ml g <sup>-1</sup> h <sup>-1</sup> )						
	$\bar{X}$	<u>Males</u> ±SD	n	$\bar{X}$	<u>Females</u> ±SD	n	t-value
July 15-31	4.83	(1.03)	7	4.25	(0.31)	5	1.21
Aug. 1-15	3.39	(0.40)	10	3.57	(0.45)	5	-0.79
Aug. 16-31	3.00	(0.68)	8	2.64	(0.44)	4	0.95
Sept. 1-15	2.87	(0.33)	2	2.41	(0.33)	5	1.66

There were no significant differences in standard metabolic rate between males and females.

Appendix 2D. Mean standard metabolic rate expressed on an hourly basis per animal and per unit weight and mean body weight of Group II S. richardsoni.

Date	$\dot{V}O_2$ (ml h <sup>-1</sup> )		$\dot{V}O_2$ (ml g <sup>-1</sup> h <sup>-1</sup> )		Weight (g)		n
	$\bar{X}$	±SD	$\bar{X}$	±SD	$\bar{X}$	±SD	
July 1-15	962.9	(334.8)	4.55	(0.66)	230	(27.9)	11
July 16-31	1207.5	(229.9)	3.88	(0.83)	312	(40.6)	13
Aug. 1-15	1179.4	(253.5)	3.13	(0.52)	377	(47.5)	16
Aug. 16-31	931.5	(187.3)	2.48	(0.31)	376	(58.2)	13
Sept. 1-15	916.0	(268.2)	2.47	(0.75)	374	(58.1)	9
Sept. 16-30	908.6	(142.1)	2.39	(0.25)	384	(59.9)	9
Oct. 1-15	1049.9	( 92.5)	2.50	(0.13)	421	(33.2)	6
Oct. 16-31	1055.9	(195.5)	2.78	(0.35)	382	(70.5)	14

Appendix 2E. Weight-specific standard metabolic rate of Group I and II female juvenile S. richardsoni.

Date	$\dot{V}O_2$ (ml g <sup>-1</sup> h <sup>-1</sup> )						t-value
	Group I			Group II			
	$\bar{X}$	$\pm$ SD	n	$\bar{X}$	$\pm$ SD	n	
July 15-31	4.25	(0.31)	5	3.88	(0.83)	13	0.95
Aug. 1-15	3.57	(0.45)	5	3.13	(0.52)	16	1.70
Aug. 16-31	2.64	(0.44)	4	2.48	(0.31)	13	0.73
Sept. 1-15	2.41	(0.33)	5	2.47	(0.75)	9	-0.17

There were no significant differences in standard metabolic rate between Group I and II females.

APPENDIX III

Activity

Appendix 3A. Mean daily activity of Group I juvenile S. richardsoni held at different photoperiods but otherwise similar experimental conditions.

MEAN DAILY ACTIVITY							
Date	Group I A <sub>1</sub>			Group I B <sub>1</sub>			t-value
	<u>LD 12:12</u>			<u>LD 12:12</u>			
	$\bar{X}$	SD	n	$\bar{X}$	SD	n	
Sept. 15-30	56.0	(16.7)	40	65.4	(21.5)	40	-2.19*
Oct. 1-15	50.7	(20.1)	40	57.2	(21.0)	40	-1.42
Nov. 1-15	29.8	(22.0)	40	39.2	(14.8)	40	-2.23* (t')
Dec. 1				<u>LD 00:24</u>			
Dec. 1-15	28.9	(32.9)	40	25.7	(12.1)	40	0.59
Jan. 1-15	43.7	(28.4)	40	38.0	(10.5)	40	1.84
Feb. 1-15	63.8	(21.8)	40	57.1	(14.3)	40	1.63
March 1-15	78.2	(30.6)	40	58.2	(6.6)	40	4.04** (t')
April 1-15	68.7	(30.1)	40	66.2	(30.7)	40	0.37
May 1				<u>LD 12:12</u>			
May 1-15	48.5	(10.2)	21	54.8	(13.6)	28	-1.76

Units of activity are arbitrary (Page 16).

\* Statistically significant;  $p < 0.05$

\*\* Statistically significant;  $p < 0.01$

Appendix 3B. Mean daily activity of Group II juvenile *S. richardsoni* held at different photoperiods but otherwise similar experimental conditions.

MEAN DAILY ACTIVITY							
Date	Group II A <sub>2</sub>			Group II B <sub>2</sub>			t-value
	LD 12:12			LD 12:12			
	$\bar{X}$	$\pm$ SD	n	$\bar{X}$	$\pm$ SD	n	
July 15-31	76.8	(26.9)	16	112.5	(37.1)	16	3.11**
Aug. 1-15	87.0	(30.9)	16	92.5	(55.8)	16	0.36
Sept. 1-15	85.8	(54.7)	16	91.9	(45.0)	16	0.34
Oct. 1-15	80.6	(33.7)	40	63.0	(25.4)	40	2.64*
Nov. 1-15	104.0	(57.1)	38	56.2	(20.5)	40	4.97*(t')
Dec. 1				LD 00:24			
Dec. 1-15	5.5	(12.6)	40	3.4	( 6.6)	40	0.95
Jan. 1-15	14.2	(20.1)	40	5.5	( 7.9)	40	2.53*(t')
Feb. 1-15	94.7	(26.6)	40	67.9	(25.1)	40	4.63**
March 1-15	106.9	(45.8)	40	95.4	(49.0)	40	1.08
April 1-15	92.7	(53.6)	40	96.5	(58.5)	40	0.30
May 1				LD 12:12			
May 1-15	75.3	(41.8)	40	80.1	(26.9)	40	0.61
June 1-15	60.0	(25.2)	40	97.4	(46.3)	40	4.48** (t')

Units of activity are arbitrary (Page 16).

\* Statistically significant;  $p < 0.05$

\*\* Statistically significant;  $p < 0.01$

Appendix 3C. Duration and frequency of hibernation bouts of Group II female juvenile S. richardsoni held at different photoperiods.

LD 12:12 (Group II A <sub>2</sub> )					
<u>Days in Hibernation</u>					
<u>Paired Animals</u>		<u>Single Animals</u>			
Pair 1	Pair 2	1	2	3	4
0	4.0	2.7	3.4	3.3	7.7
	8.0	5.8	2.3	9.0	10.5
	6.8	5.8	3.3	9.8	10.1
	5.4	10.7	5.5	11.1	10.5
		8.3	2.1	8.1	3.9
		9.9			
		6.5			
<u>Number of Hibernation Bouts</u>					
0	4	7	5	5	5

LD 00:24 (Group II B <sub>2</sub> )					
<u>Days in Hibernation</u>					
<u>Paired Animals</u>		<u>Single Animals</u>			
Pair 1	Pair 2	1	2	3	4
0	6.7	1.3	7.4	1.2	3.9
	7.7	7.9	10.7	2.6	5.6
	6.9	9.9	4.4	1.7	7.1
	6.2	8.2		8.9	8.3
		8.7		7.4	7.5
		4.8		7.0	4.9
				8.8	2.1
				6.3	3.8
				6.2	
<u>Number of Hibernation Bouts</u>					
0	4	6	3	9	8

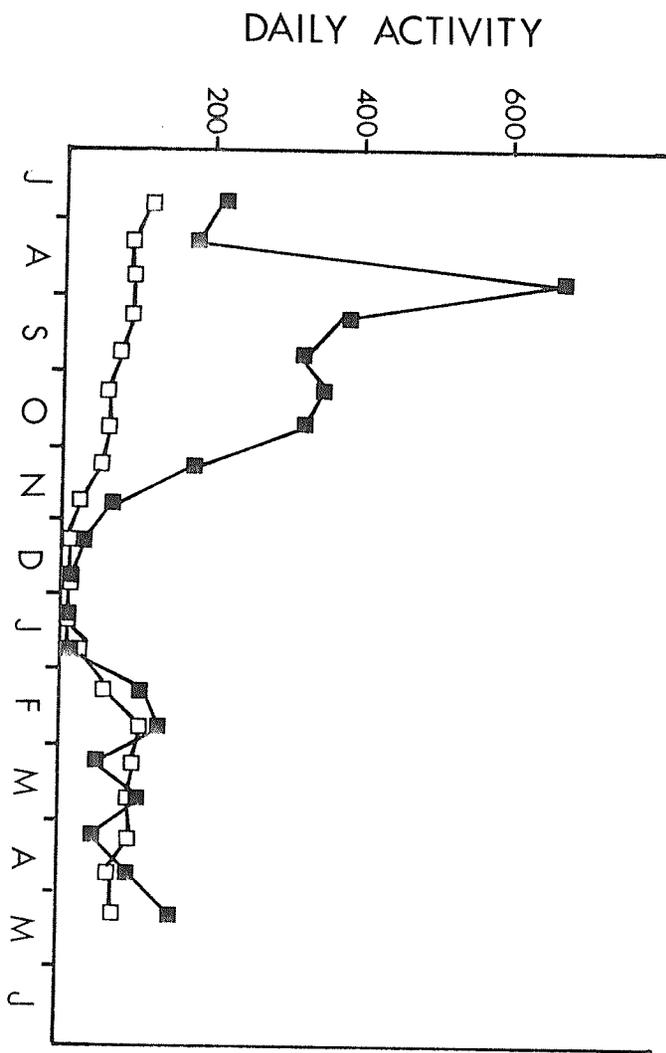
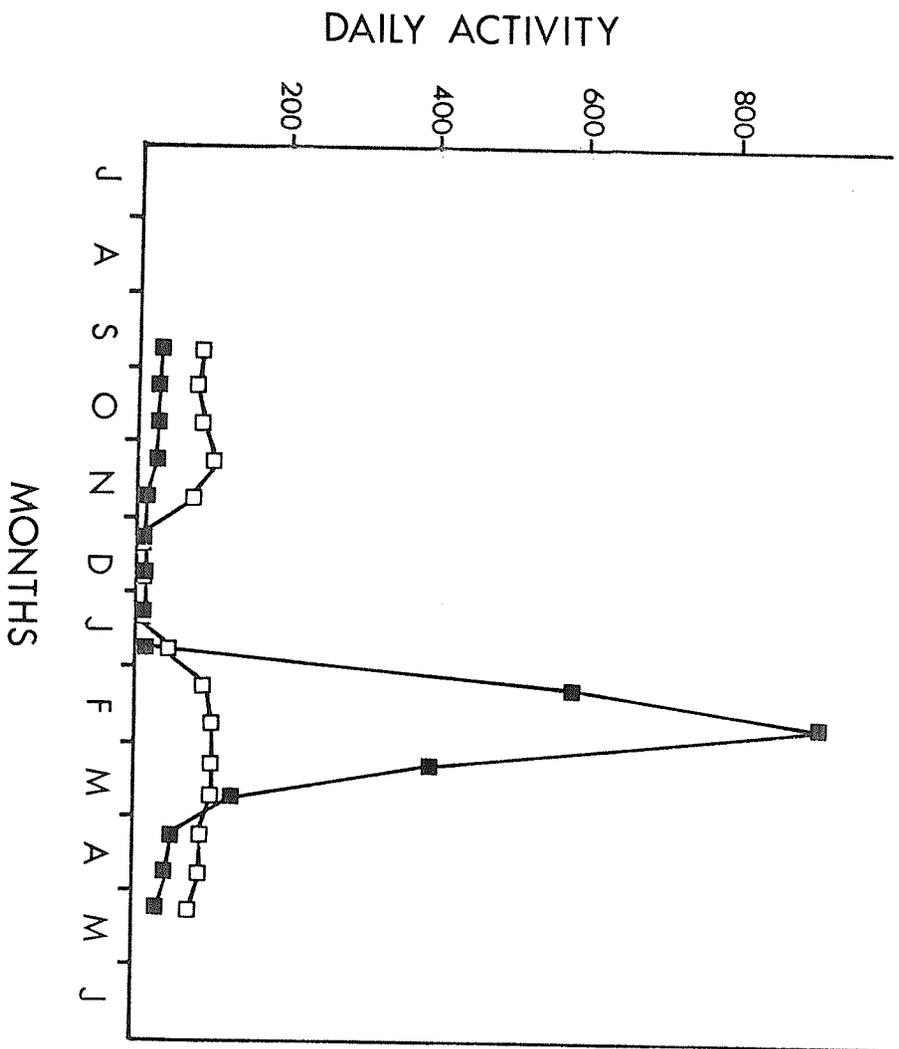
Appendix 3D. (Upper graph) Mean daily activity of an individual female S. richardsoni compared with the mean daily activity of Group II B<sub>2</sub>.

(Lower graph) Mean daily activity of an individual female S. richardsoni compared with the mean daily activity of Group II A<sub>2</sub>.

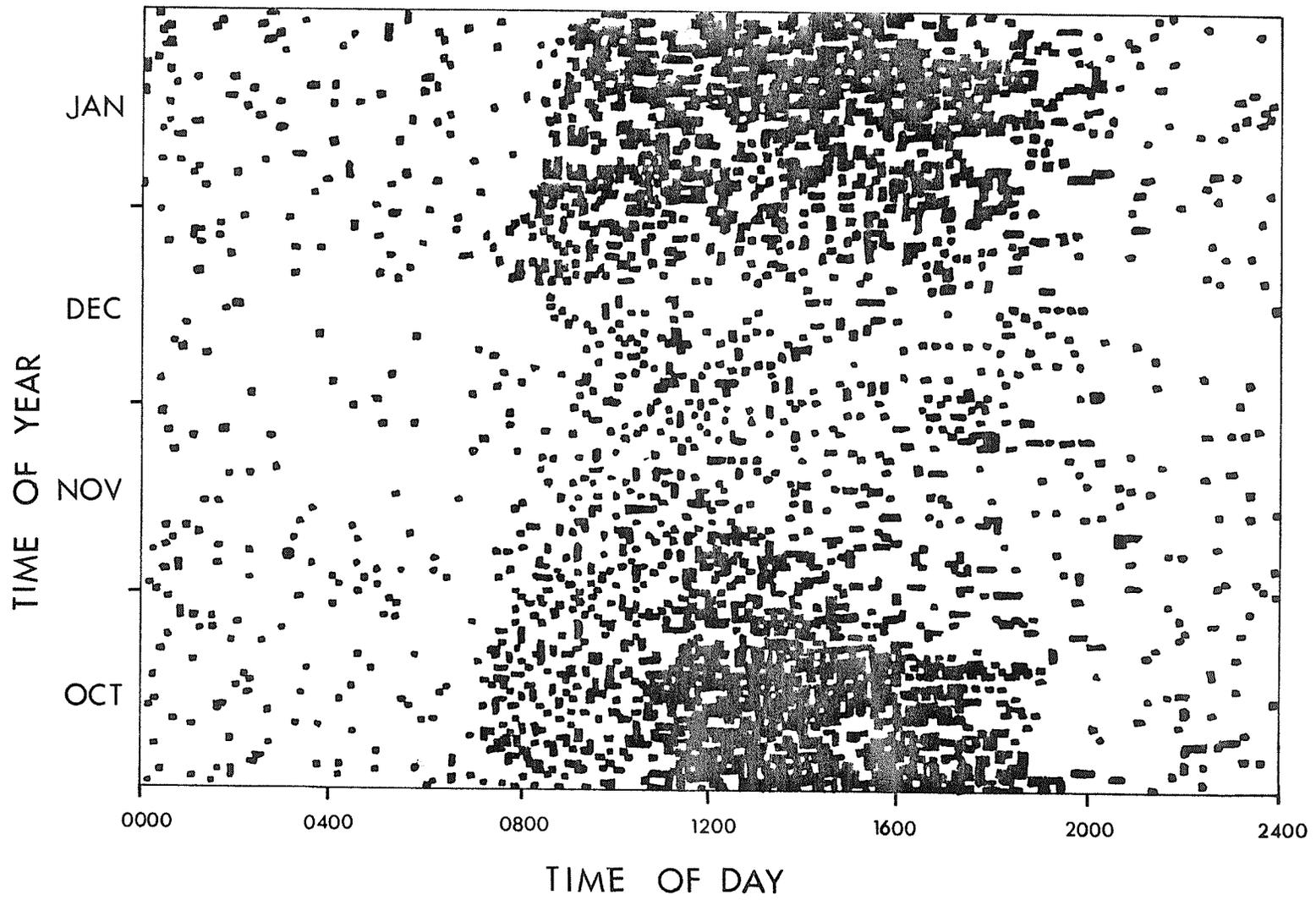
Units of activity are arbitrary (Page 16).

■ Individual animal

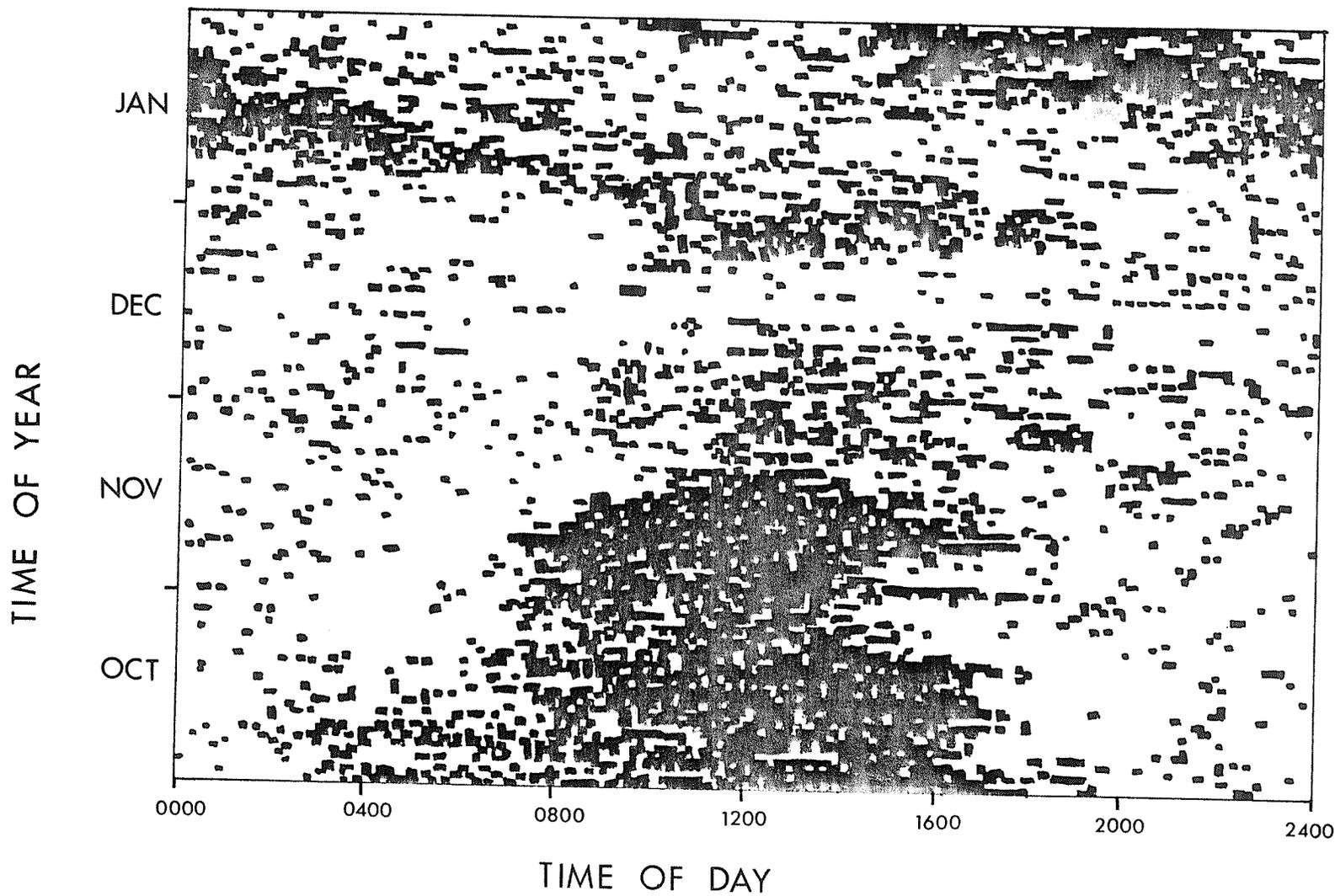
□ Treatment group



Appendix 3E. Daily distribution of activity of one pair of juvenile S. richardsoni from Group I A<sub>1</sub>.



Appendix 3F. Daily distribution of activity of one pair of juvenile S. richardsoni from Group I B<sub>1</sub>.



Appendix 3G. Mean daily activity of individual juvenile S. richardsoni of Group II A<sub>2</sub>.

Date	CAGE NUMBER			
	2A	4A	5A	6A*
Sept. 1-15	35.8	135.8	81.5	136.0
Sept. 16-30	35.9	108.4	92.6	93.4
Oct. 1-15	32.4	103.9	93.1	92.9
Oct. 16-31	30.5	140.6	119.3	78.7
Nov. 1-15	33.4	152.3	149.5	69.8
Nov. 16-31	22.6	118.8	119.0	46.2
Dec. 1-15	6.4	10.6	0	2.5
Dec. 16-31	19.9	5.3	4.0	2.3

\* Data from animals of cage 6A have been expressed on a per animal basis.

Units of activity are arbitrary (Page 16).

Appendix 3H. Mean daily activity of Group I, and Group II individually-housed juvenile S. richardsoni.

Data have been pooled for animals held at different photoperiods.

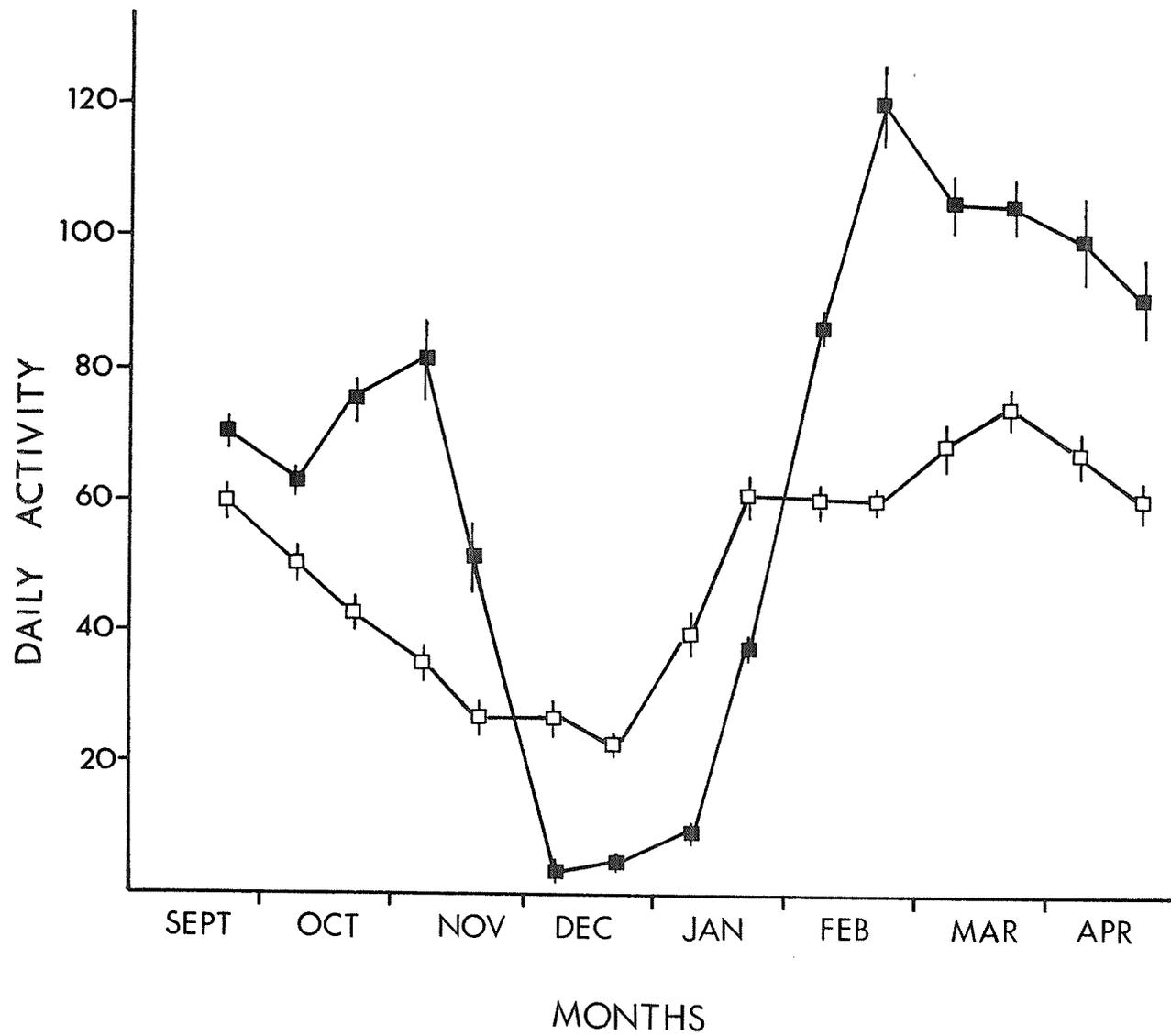
Units of activity are arbitrary (Page 16).

□ Group I

■ Group II

Vertical lines:  $\pm$  SE

Sample size: The majority of means consist of  
60 - 80 24 h measurements.



APPENDIX IV

Food Consumption

Appendix 4A. Mean weekly food consumption of Group I juvenile S. richardsoni held at different photoperiods but otherwise similar experimental conditions.

FOOD CONSUMPTION (g/animal)							
Date	Group I A <sub>1</sub>			Group I B <sub>1</sub>			t-value
	$\bar{X}$	SD	n	$\bar{X}$	SD	n	
Aug. 4-10	247.7	(125.9)	4	263.5	(49.5)	4	-0.23
Sept. 1-7	109.6	(28.6)	4	127.2	(5.3)	4	-1.21
Oct. 2-8	165.7	(20.7)	4	142.8	(30.4)	4	1.25
Dec. 1				<u>LD 00:24</u>			
March 4-10	227.7	(59.3)	4	259.4	(36.7)	4	-0.91
April 1-7	292.2	(24.8)	4	234.3	(63.8)	4	1.69
May 1				<u>LD 12:12</u>			
April 29- May 10	175.4	(18.7)	4	176.7	(23.3)	4	-0.08
June 1-7	118.2	(19.4)	4	122.5	(20.0)	4	-0.31

There were no significant differences in mean weekly food consumption between animals held at different photoperiods.

Appendix 4B. Mean weekly food consumption of Group II *S. richardsoni* held at different photoperiods but otherwise similar experimental conditions.

FOOD CONSUMPTION (g/animal)								
Date	Group II A <sub>2</sub>				Group II B <sub>2</sub>			t-value
	<u>LD 12:12</u>		n	<u>LD 12:12</u>		n	±SD	
	$\bar{X}$	±SD			$\bar{X}$			±SD
July 13-19	295.4	(92.8)	5	217.2	(51.9)	5	1.78	
Aug. 3-9	126.4	(32.0)	5	219.2	(44.8)	5	-3.77**	
Aug. 31- Sept. 6	118.7	(23.0)	5	105.2	(16.0)	5	1.08	
Sept. 28- Oct. 11	122.3	(19.6)	5	129.5	(22.8)	5	-0.54	
Dec. 1				<u>LD 00:24</u>				
Jan. 24-30	144.5	(56.7)	5	138.0	(42.2)	4	0.21	
Feb. 7-13	211.2	(63.2)	5	190.4	(36.5)	5	0.64	
Feb. 28- March 7	252.3	(29.2)	5	203.2	(31.0)	5	2.58*	
March 28- April 3	240.8	(64.4)	5	203.0	(49.6)	5	1.04	
May 1				<u>LD 12:12</u>				
May 2-8	142.2	(31.2)	5	123.0	(28.9)	5	1.01	
May 31- June 6	126.3	(11.4)	5	150.9	(40.7)	5	-1.30	

\* Statistically significant;  $p < 0.05$

\*\* Statistically significant;  $p < 0.01$ .

Appendix 4C. Mean weekly food consumption of individual juvenile S. richardsoni in subgroups II A<sub>2</sub> and II B<sub>2</sub>.

Date	Subgroup II A <sub>2</sub>					Subgroup II B <sub>2</sub>				
	Cage Number									
	1A	2A	4A	5A	6A*	1	2	4	5	6*
July 20-26	379.9	369.3	261.0	253.9	250.1	254.4	204.5	226.8	341.2	258.5
July 27-2	188.3	182.8	171.4	205.1	237.2	310.2	251.3	254.3	311.1	269.9
Aug. 3-9	90.8	125.0	142.4	102.8	171.2	276.2	233.6	224.3	209.7	152.4
Aug. 10-16	92.2	120.9	149.1	96.1	115.1	144.8	159.5	112.9	164.6	92.2
Aug. 17-23	102.5	123.2	98.9	112.9	130.7	114.3	162.7	69.6	130.0	115.5
Feb. 11-20	203.3	282.1	195.1	184.2	228.2	210.6	-	224.8	189.3	199.2
Feb. 21-27	290.7	279.7	245.1	189.0	229.0	182.0	129.3	225.0	290.2	184.9
Feb. 28-6	299.0	262.9	236.1	230.4	233.1	206.4	156.4	215.1	241.4	196.8
March 7-13	265.7	235.1	244.8	214.2	240.4	178.5	152.3	223.5	265.1	152.4

\* Data from animals in cages 6A and 7 have been expressed on a per animal basis.

APPENDIX V

Graphical Representation of Data from  
Appendices 1A, 1B, 3A, 3B, 4A and 4B.

Appendix 5. Body weight, weekly food consumption and daily activity of juvenile S. richardsoni at different photoperiods but otherwise similar conditions.

Open symbols: Photoperiod LD 12:12

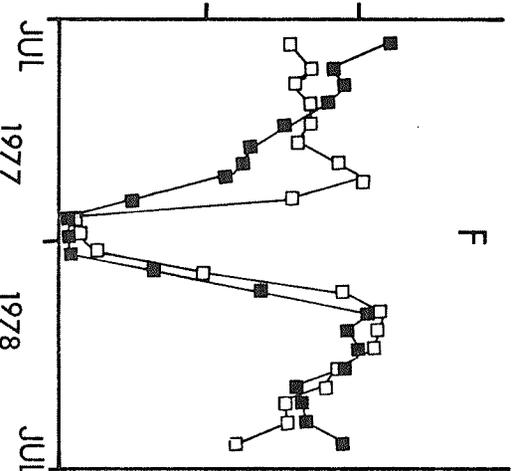
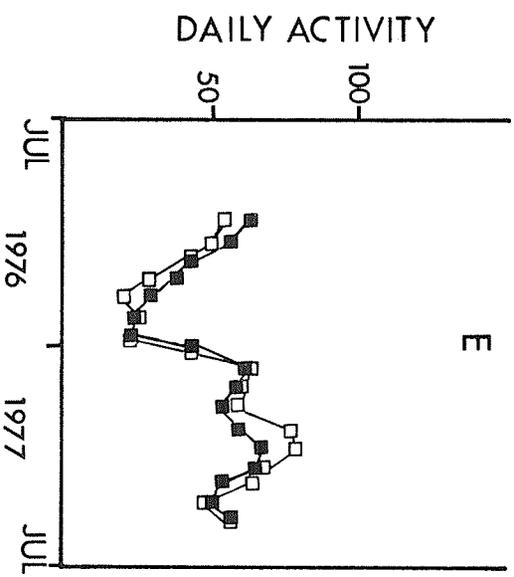
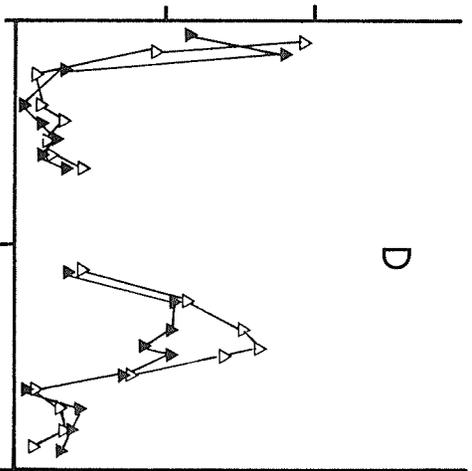
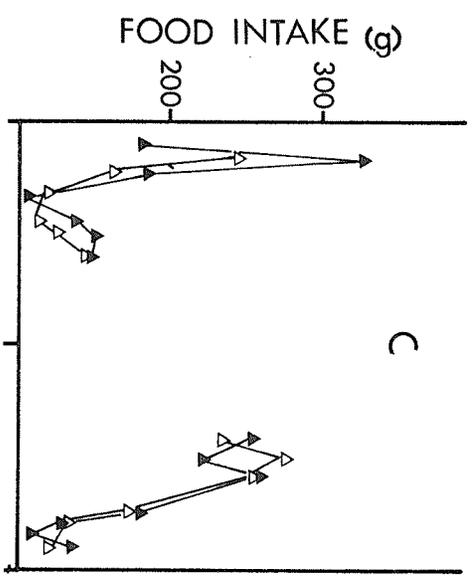
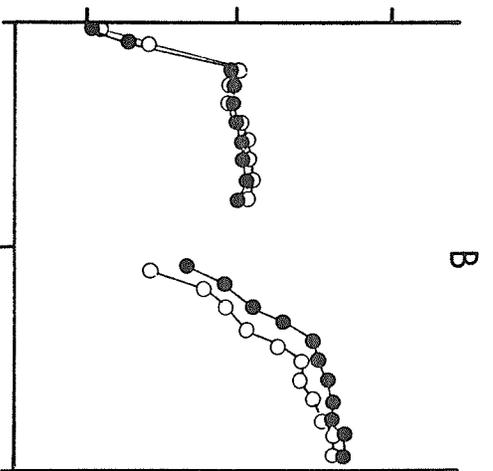
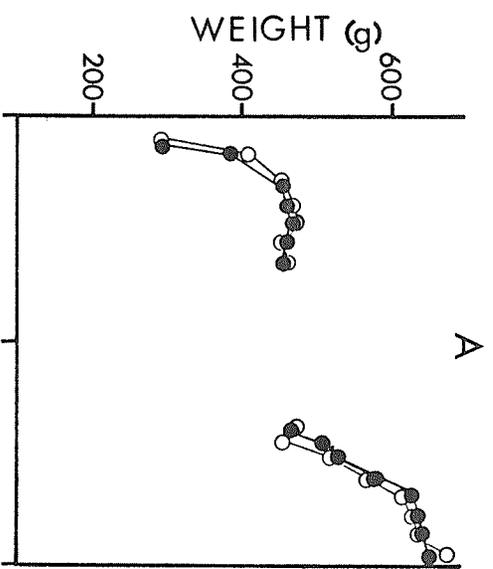
Solid symbols: Photoperiod LD 12:12 July-Dec.

LD 00:24 Dec.-May

LD 12:12 May-July

Group I - Graphs A, C, E

Group II - Graphs B, D, F



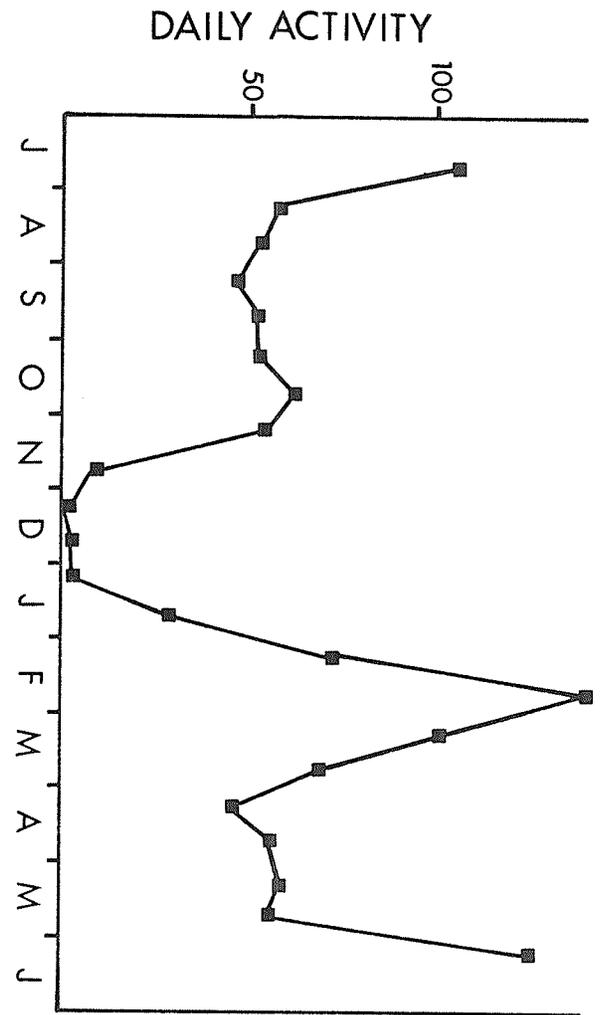
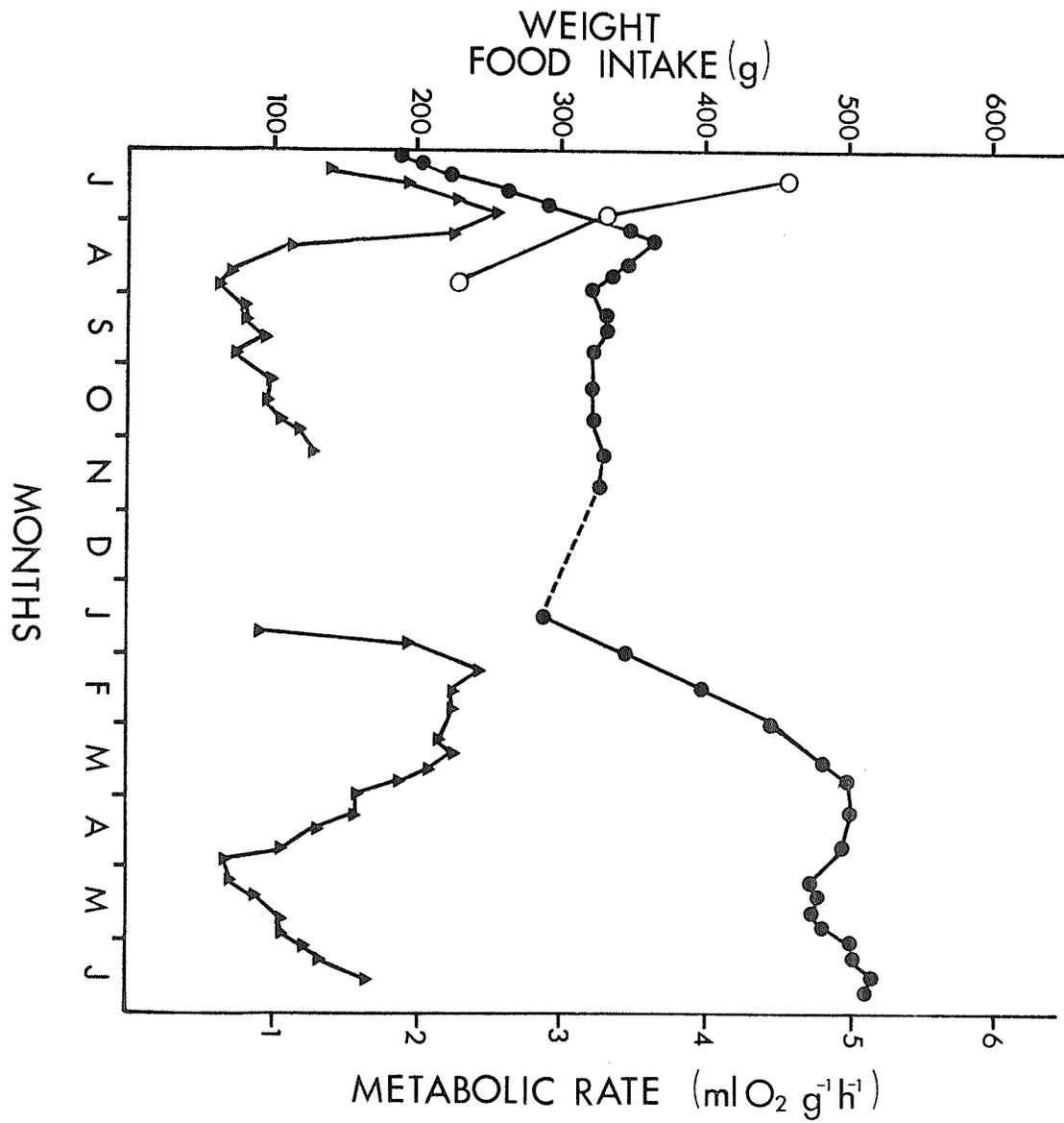
TIME OF YEAR

APPENDIX VI

Interrelationship of Daily Activity, Weekly Food  
Consumption, Metabolic Rate, and Body Weight

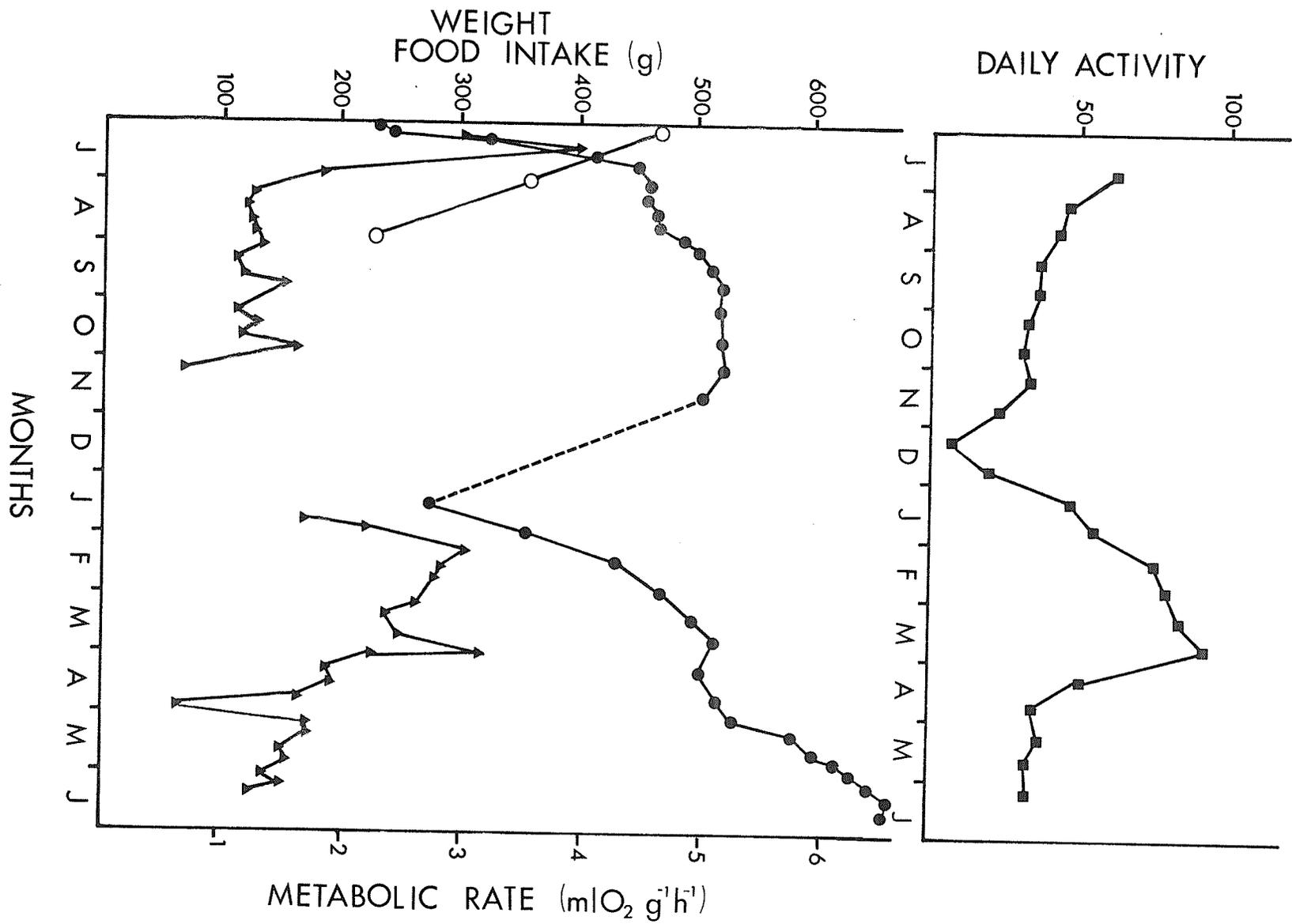
Appendix 6A. Daily activity, weekly food consumption, weight-specific metabolic rate, and body weight of a female S. richardsoni representative of Group II B<sub>2</sub> animals, held at LD 00:24 (Dec. - May).

- Daily activity
- ▲ Food consumption
- Weight-specific metabolic rate
- Body weight
- Period of food deprivation



Appendix 6B. Daily activity, weekly food consumption, weight-specific metabolic rate, and body weight of a female S. richardsoni representative of Group II A<sub>2</sub> animals, held at LD 12:12.

- Daily activity
- ▲ Food consumption
- Weight-specific metabolic rate
- Body weight
- Period of food deprivation



APPENDIX VII

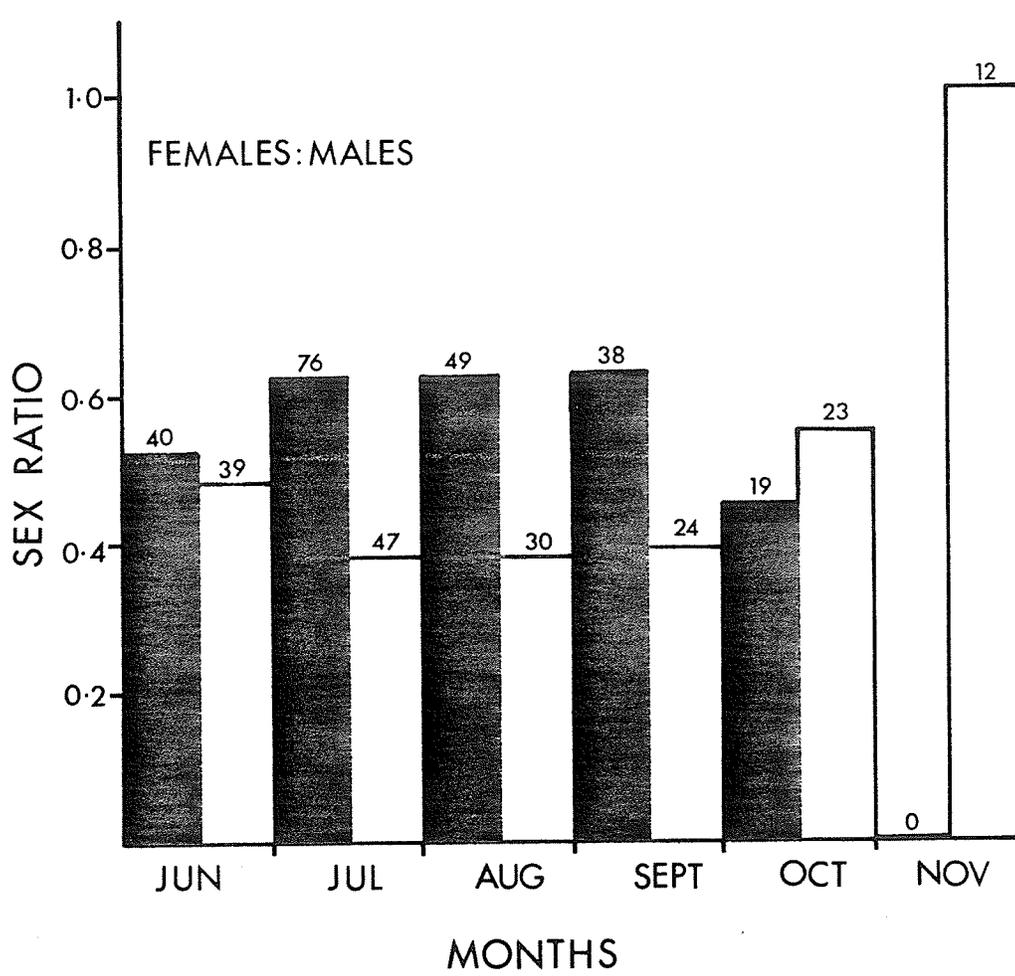
Sex Ratio of Juvenile S. richardsoni

Appendix 7. Sex ratio of juvenile S. richardsoni in their natural habitat.

Numbers = Sample size

■ Females

□ Males



Dep Col  
Thesis  
# 2193

Erratum

I, Deborah Helen Harding, wish to disclose that a consistent error was made in calculating metabolic rate values presented in my M.Sc. thesis entitled "CHANGES IN BODY WEIGHT AND ACTIVITY OF JUVENILE RICHARDSON'S GROUND SQUIRRELS, SPERMOPHILUS RICHARDSONI, UNDER CONTROLLED LABORATORY CONDITIONS. Correct values are shown in the Figures and Tables that follow this page.

Figure 7. Interrelationship between mean body weight (upper graph), and mean standard metabolic rate expressed on an hourly basis per animal (centre graph) and per unit weight (lower graph), in female juvenile S. richardsoni held at LD 12:12 with food ad libitum.

○ Group I

● Group II

Vertical lines:  $\pm$  SE

Numbers = Sample size

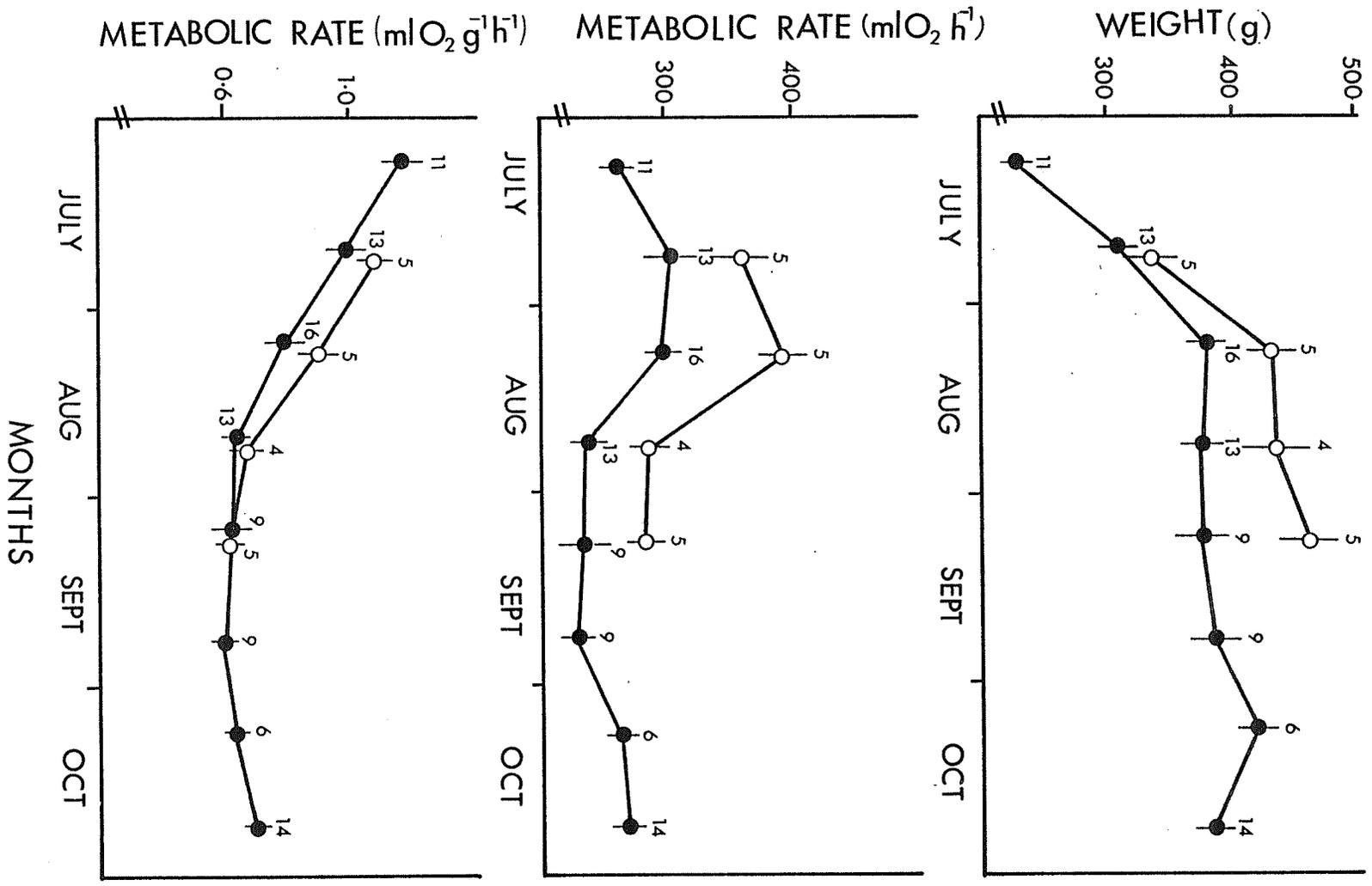


Figure 8. Interrelationship between mean body weight (upper graph) and mean standard metabolic rate, expressed on an hourly basis per animal (centre graph) and per unit weight (lower graph), in male juvenile S. richardsoni held at LD 12:12 with food ad libitum.

Vertical lines: + SE

Numbers = Sample size

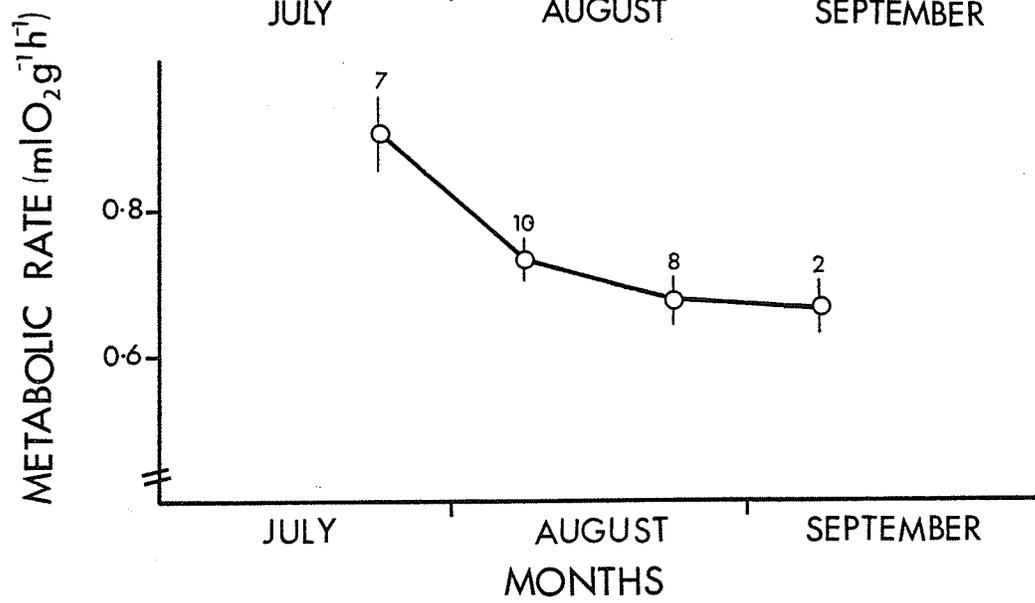
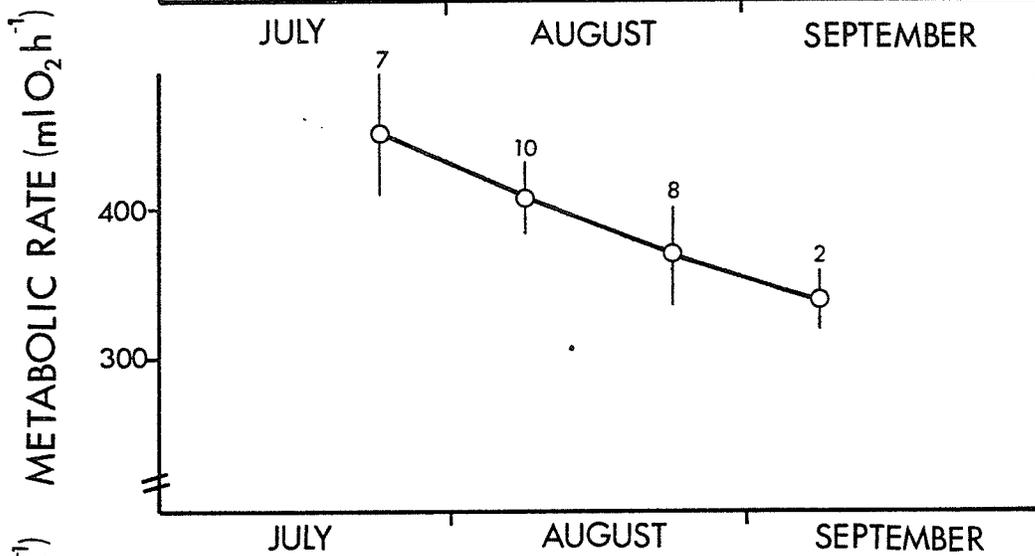
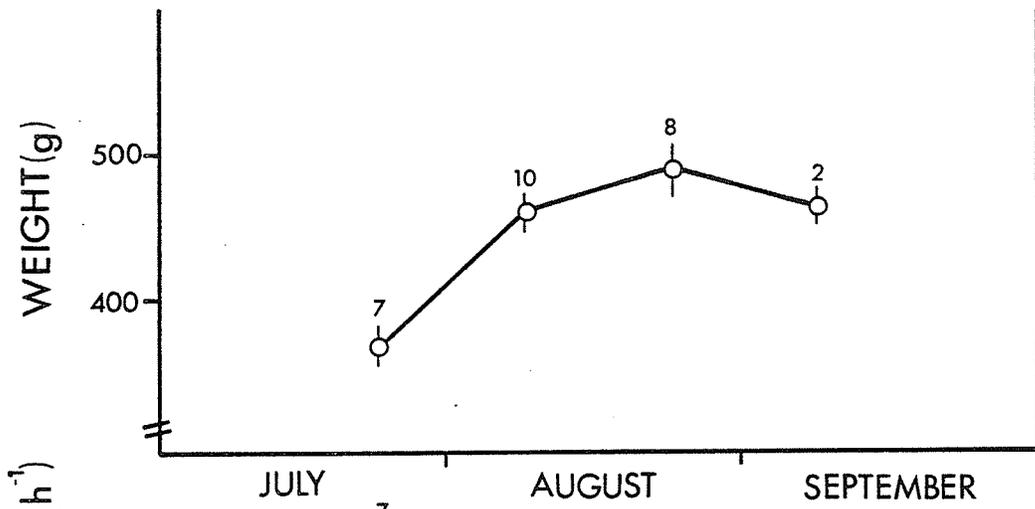


Figure 15. Daily activity, weekly food consumption, weight-specific metabolic rate and body weight of a female S. richardsoni representative of Group II B<sub>2</sub> animals held at LD 00:24 (Dec. - May).

- Daily activity
- ▲ Food consumption
- Metabolic rate
- Body weight
- Period of food deprivation

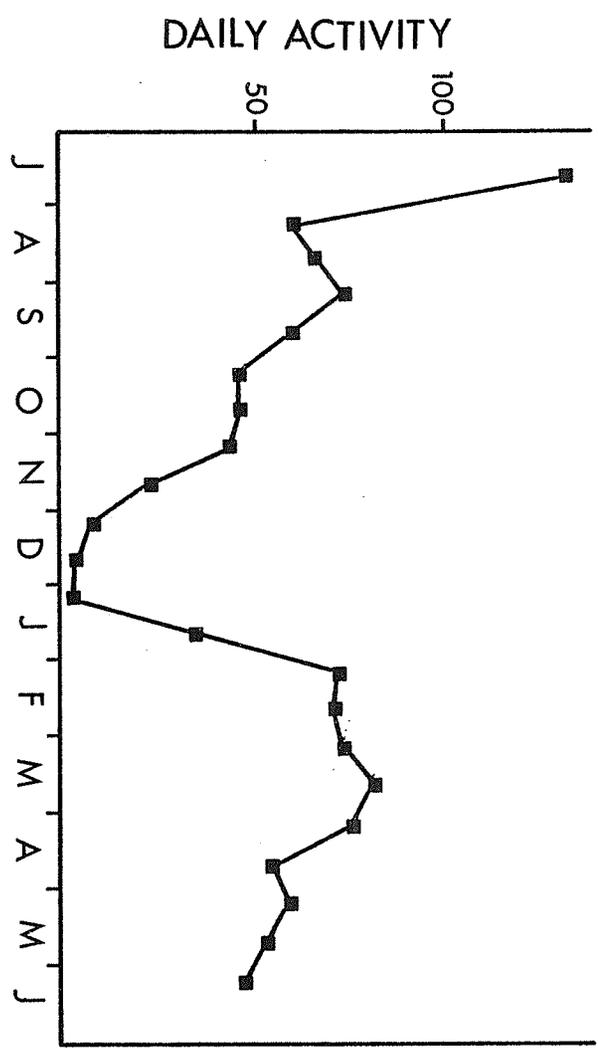
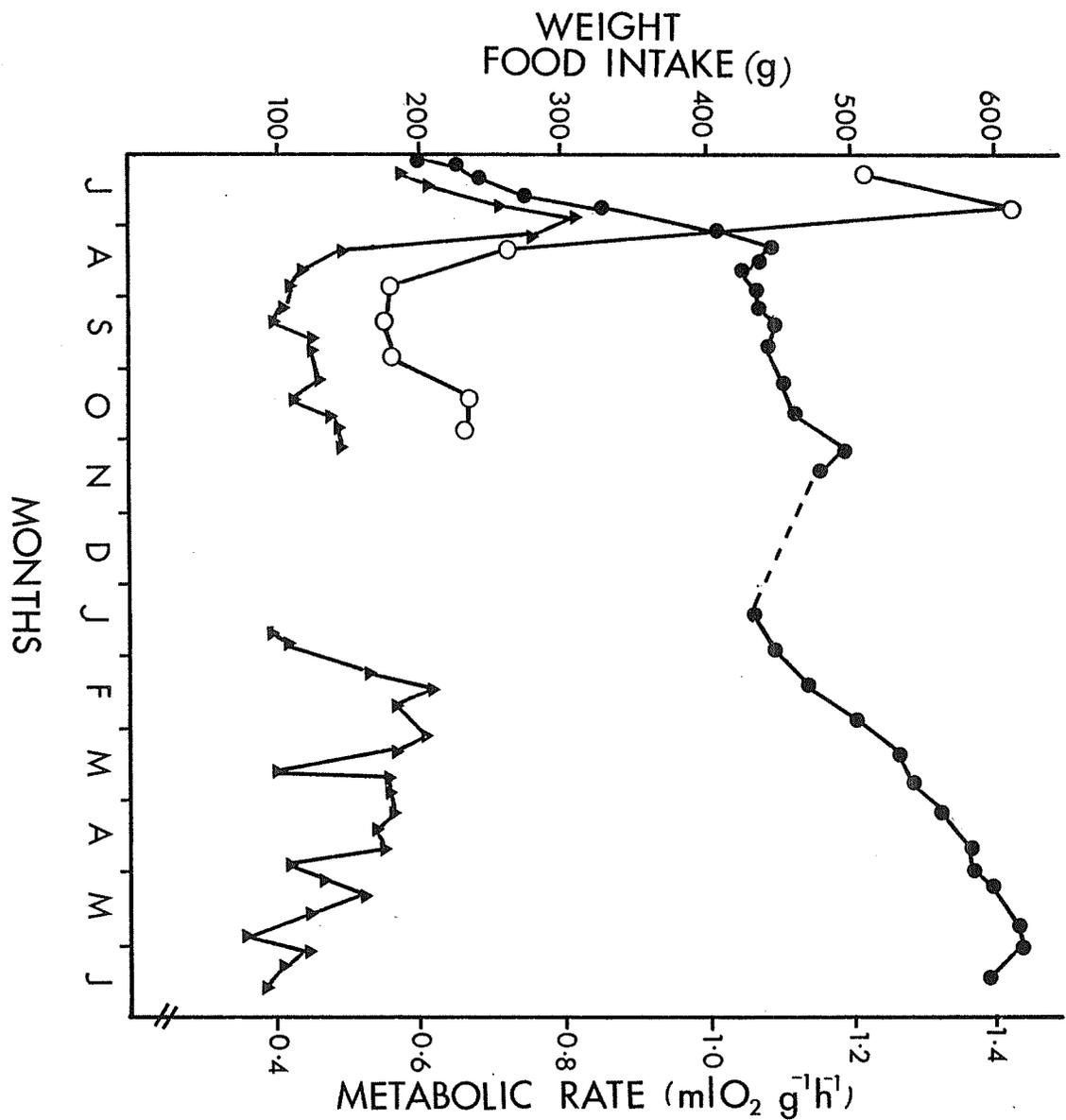
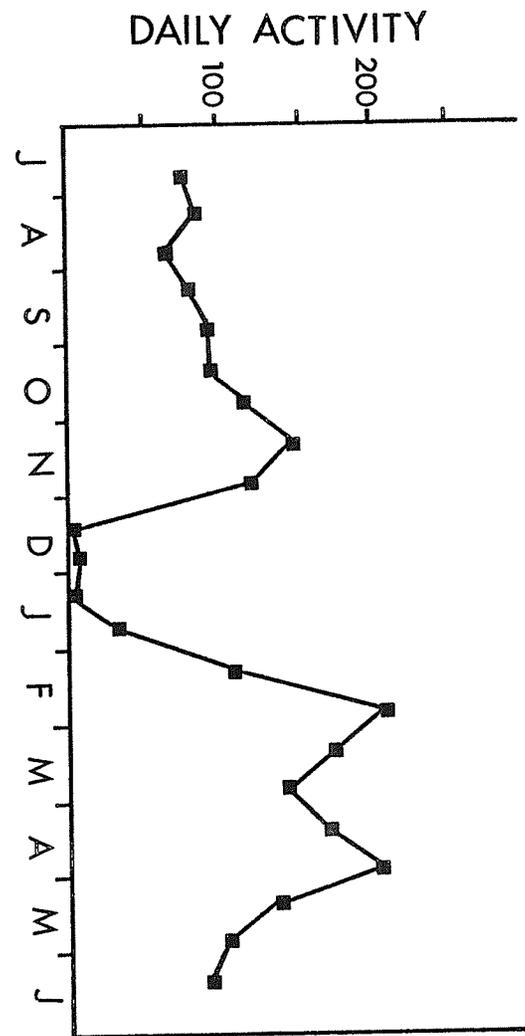
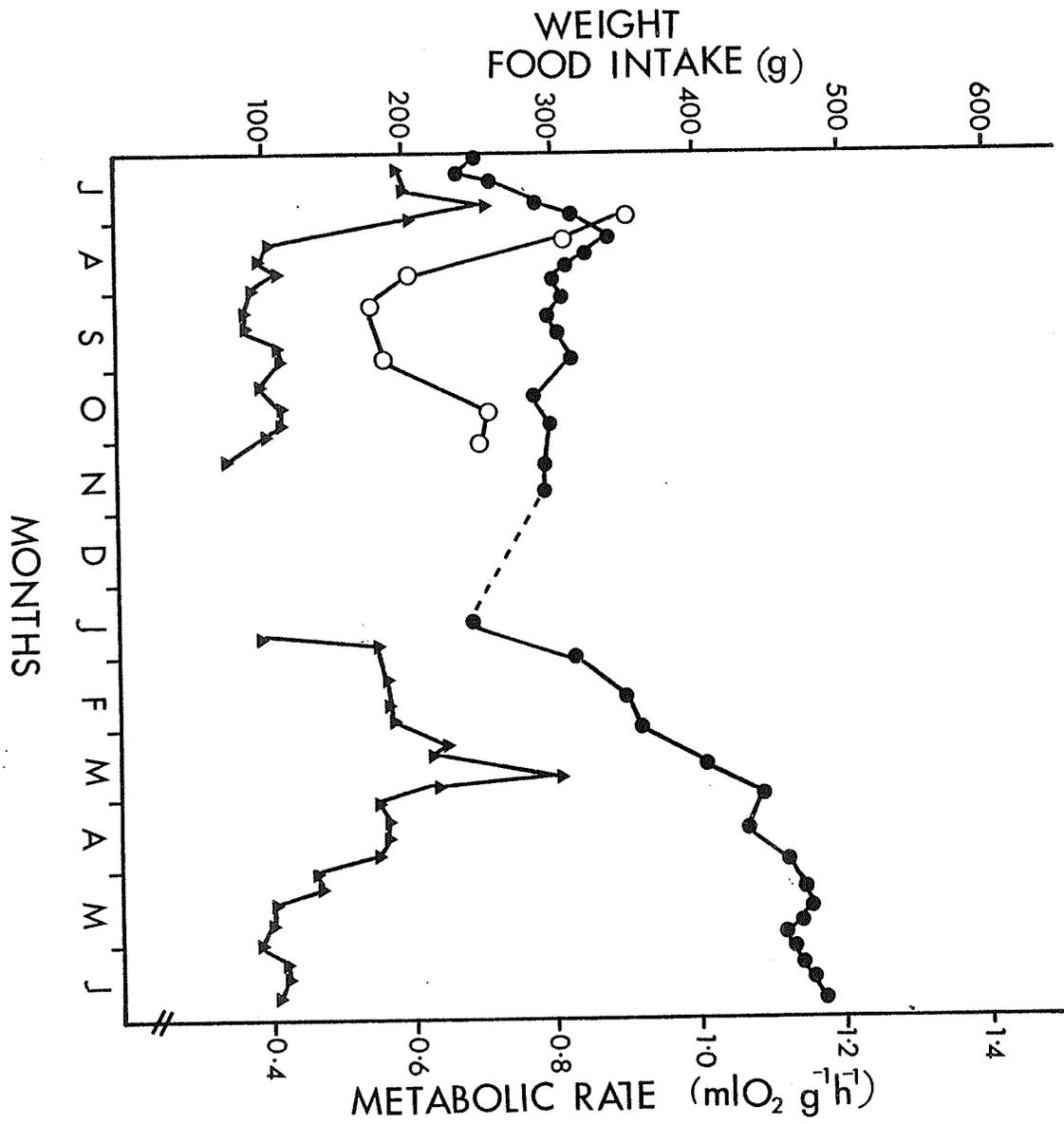


Figure 16. Daily activity, weekly food consumption, weight-specific metabolic rate and body weight of a female S. richardsoni representative of Group II A<sub>2</sub> animals held at LD 12:12.

- Daily activity
- ▲ Food consumption
- Metabolic rate
- Body weight
- Period of food deprivation



Appendix 2B. Mean standard metabolic rate expressed on a hourly basis per animal and per unit weight, and mean body weight of Group I S. richardsoni.

Date	FEMALES						n
	$\dot{V}O_2$ (ml h <sup>-1</sup> )		$\dot{V}O_2$ (ml g <sup>-1</sup> h <sup>-1</sup> )		Weight (g)		
	$\bar{X}$	+SD	$\bar{X}$	+SD	$\bar{X}$	+SD	
July 15-31	363.0	(35.5)	1.08	(0.07)	336	(42.5)	5
Aug. 1-15	391.3	(34.4)	0.91	(0.10)	433	(42.8)	5
Aug. 16-31	289.6	(13.7)	0.67	(0.10)	437	(57.4)	4
Sept. 1-15	281.8	(14.5)	0.61	(0.07)	464	(44.9)	5

Date	MALES						n
	$\dot{V}O_2$ (ml h <sup>-1</sup> )		$\dot{V}O_2$ (ml g <sup>-1</sup> h <sup>-1</sup> )		Weight (g)		
	$\bar{X}$	+SD	$\bar{X}$	+SD	$\bar{X}$	+SD	
July 15-31	458.6	(111.7)	1.23	(0.25)	371	(24.3)	7
Aug. 1-15	418.5	(62.6)	0.86	(0.10)	464	(36.5)	10
Aug. 16-31	378.2	(99.0)	0.77	(0.17)	493	(58.7)	8
Sept. 1-15	343.4	(23.4)	0.73	(0.06)	470	(9.0)	2

Appendix 2C. Weight-specific standard metabolic rate of  
Group I male and female juvenile S. richardsoni.

DATE	$\dot{V}O_2$ (ml g <sup>-1</sup> h <sup>-1</sup> )						
	Males			Females			t-value
	$\bar{X}$	+SD	n	$\bar{X}$	+SD	n	
July 15-31	1.23	(0.25)	7	1.08	(0.07)	5	1.25
Aug. 1-15	0.86	(0.10)	10	0.91	(0.10)	5	-0.84
Aug. 16-31	0.77	(0.17)	8	0.67	(0.10)	4	1.03
Sept. 1-15	0.73	(0.06)	2	0.61	(0.07)	5	1.98

There were no significant differences in standard metabolic rate between males and females.

Appendix 2D. Mean standard metabolic rate expressed on an hourly basis per animal and per unit weight and mean body weight of Group II S. richardsoni.

Date	$\dot{V}O_2$ (ml h <sup>-1</sup> )		$\dot{V}O_2$ (ml g <sup>-1</sup> h <sup>-1</sup> )		Weight (g)		n
	$\bar{X}$	+SD	$\bar{X}$	+SD	$\bar{X}$	+SD	
July 1-15	265.8	(42.7)	1.16	(0.16)	230	(27.9)	11
July 16-31	307.5	(73.9)	0.99	(0.21)	312	(40.6)	13
Aug. 1-15	299.6	(62.8)	0.79	(0.13)	377	(47.5)	16
Aug. 16-31	236.9	(46.0)	0.63	(0.08)	376	(58.2)	13
Sept. 1-15	232.9	(64.6)	0.62	(0.18)	374	(58.1)	9
Sept. 16-31	228.4	(34.8)	0.60	(0.05)	384	(59.9)	9
Oct. 1-15	266.8	(21.6)	0.63	(0.03)	421	(33.2)	6
Oct. 16-31	268.5	(48.3)	0.71	(0.09)	382	(70.5)	14

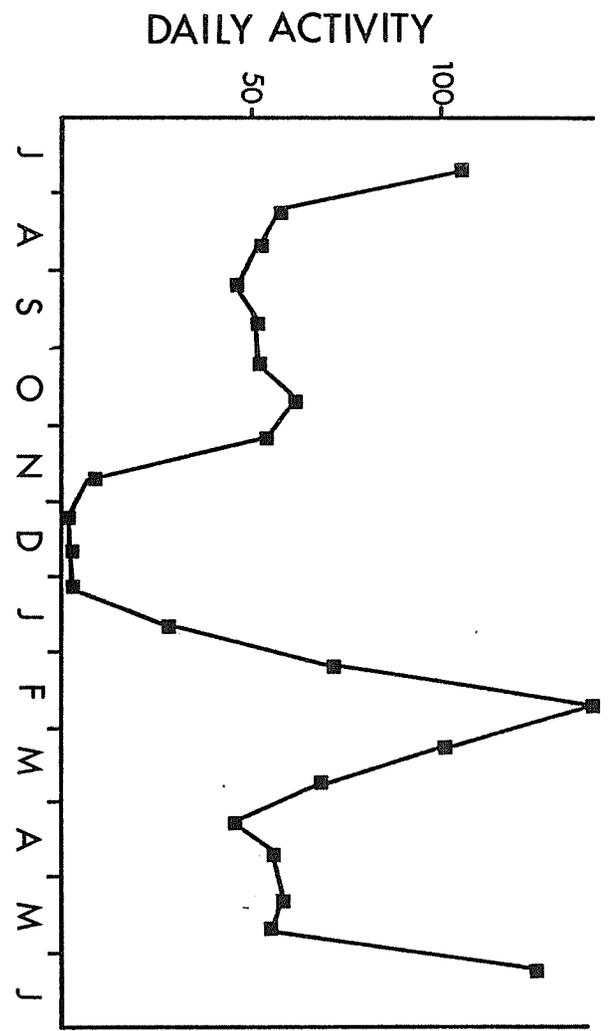
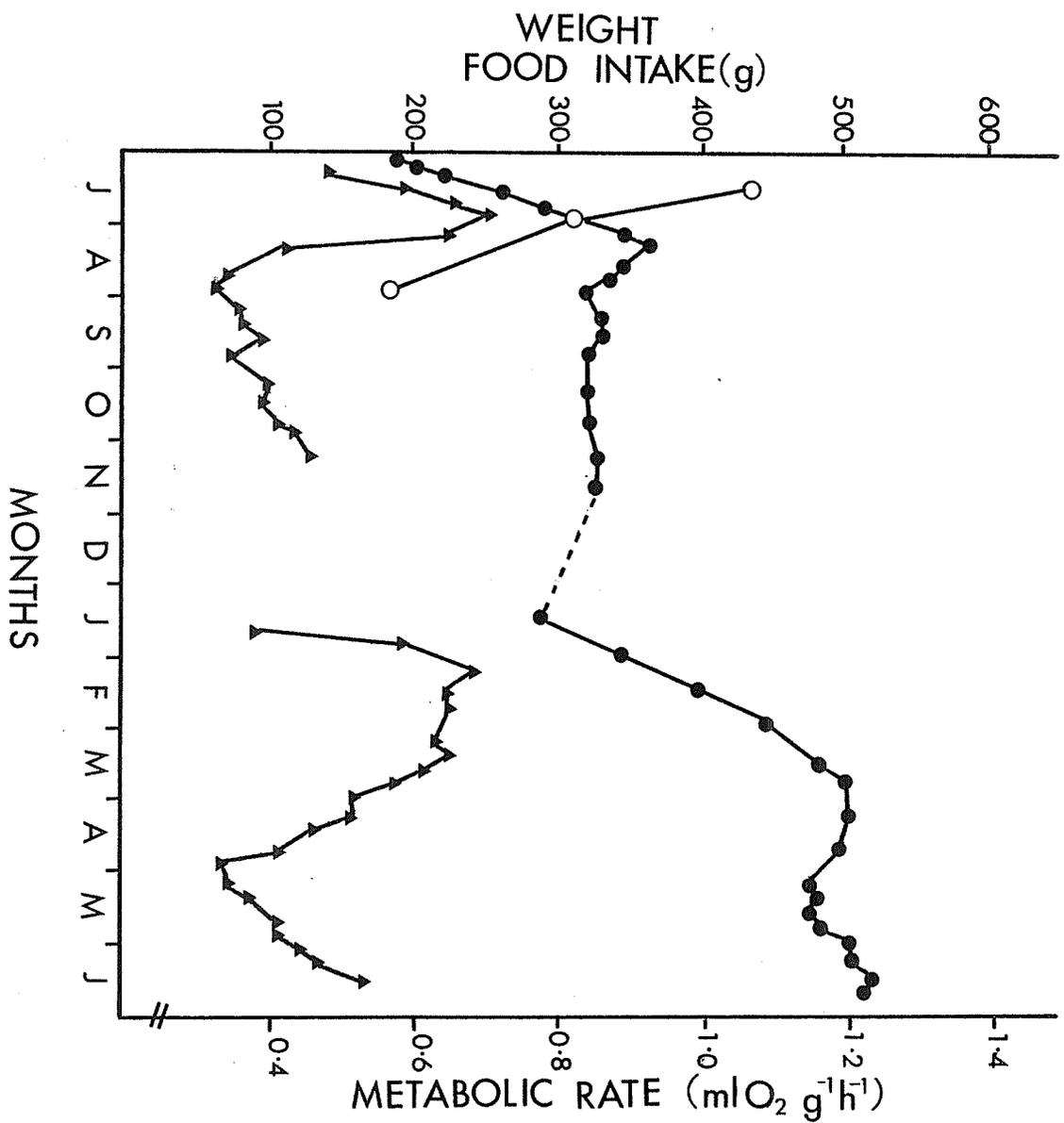
Appendix 2E. Weight-specific standard metabolic rate of Group I and II female juvenile S. richardsoni.

Date	<u>Group I</u>			<u>Group II</u>			t-value
	$\bar{X}$	$\pm$ SD	n	$\bar{X}$	$\pm$ SD	n	
July 15-31	1.08	(0.07)	5	0.99	(0.21)	13	0.96
Aug. 1-15	0.91	(0.10)	5	0.79	(0.13)	16	1.80
Aug. 16-31	0.67	(0.10)	4	0.63	(0.08)	13	0.94
Sept. 1-15	0.61	(0.07)	5	0.62	(0.18)	9	-0.13

There were no significant differences in standard metabolic rate between Group I and II females.

Appendix 6A. Daily activity, weekly food consumption, weight-specific metabolic rate, and body weight of a female S. richardsoni representative of Group II B<sub>2</sub> animals, held at LD 00:24 (Dec. - May).

- Daily activity
- ▲ Food consumption
- Weight-specific metabolic rate
- Body weight
- Period of food deprivation



Appendix 6B. Daily activity, weekly food consumption, weight-specific metabolic rate, and body weight of a female S. richardsoni representative of Group II A<sub>2</sub> animals, held at LD 12:12.

- Daily activity
- ▲ Food consumption
- Weight-specific metabolic rate
- Body weight
- Period of food deprivation

