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THE EFFECTS OF DAYLENGTH AND TEMPERATURE ON THE HIBERNATING RHYTHM OF THE MEADOW JUMPING MOUSE (ZAPUS HUDSONIUS)

presented by

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THE EFFECTS OF DAYLENGTH AND TEMPERATURE ON THE HIBERNATING RHYTHM OF THE MEADOW JUMPING MOUSE (*ZAPUS HUDSONIUS*)

By

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ABSTRACT

THE EFFECTS OF DAYLENGTH AND TEMPERATURE ON THE HIBERNATING RHYTHM OF THE MEADOW JUMPING MOUSE (*ZAPUS HUDSONIUS*)

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Results from four treatment combinations involving different levels of daylength (LD 15.33:8.67, LD 12:12) and temperature (5 and 20°C) demonstrated that significantly more animals prepared for and entered into hibernation when held under short daylengths than under long daylengths ($P < 0.001$). Within a photoperiod level, temperature had no effect upon the number of animals initially preparing for and entering into hibernation ($P > 0.20$). Rhythms in hibernating-nonhibernating activity were demonstrated only under short daylengths but the period lengths were not the same at the two temperatures (332.0 ±24.3 SD days at 5°C vs 157.2 ±60.9 SD days at 20°C, $P < 0.005$). In addition, cycles in body weight under LD 12:12, 20°C were shorter than the cycles in hibernation-nonhibernation activity (57.2 ±60.9 SD days vs 102.8 ±71.2 SD days, $P < 0.05$). In a fifth treatment combination, animals were exposed to three-month clock-shifted, gradually decreasing daylengths (simulated June 21 daylength on September 21). Seven of the eleven animals prepared for and six of these entered hibernation at simulated dates corresponding to the time span animals in nature undergo these changes. Two animals prepared for and entered hibernation two

weeks ahead of the first occurrence seen in nature and two animals underwent these changes very early. These results indicated that meadow jumping mice are using the decreasing daylengths of late summer and fall as a stimulus for preparation and initiation of hibernation. This differs from the stimulus used by Zapus princeps.

Arousal of field animals is correlated with soil temperature. The first males emerged from hibernation when the soil temperature at 100 cm equals approximately 7°C while the first females aroused two weeks after the males when the soil temperature at the same depth approximated 9°C.

The following scenario is then proposed for Zapus hudsonius. The long daylengths of spring and summer stimulate reproduction which continues through mid-August. Beginning in late August, the decreasing daylengths begin to stimulate animals to prepare for and enter into hibernation and this continues through mid to late October. Hibernation then continues until mid-April to early May depending upon the level of the soil temperature around the hibernaculum. When the soil temperature increases to a certain level, the animals emerge from their hibernaculum and become active for the summer. Therefore, it appears that two factors are important in the yearly cycle of Zapus hudsonius. Photoperiod signals the end of the active interval and, possibly, soil temperature signals the end of the hibernation interval.

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Much of the credit for the success of this project must go to my wife, Michele, who helped me through many hours of laboratory and field work.

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INTRODUCTION

Hibernating mammals prepare for and enter into hibernation during a certain time span each year. This preparation for hibernation can take many forms. Some species cache food in their burrows and feed on these stores intermittently during the winter while others undergo drastic weight gains, thereby storing energy in the form of body fat. Successful hibernation can only take place after a sufficient amount of energy has been stored by either or both means.

Increased energy reserves are not the only factor involved in the preparation for hibernation. Recent evidence has indicated that many biochemical changes are associated with the preparation for hibernation (Behrisch, 1978). These changes involve the production of new isozymes capable of maintaining body functions at the low body temperatures achieved during hibernation.

Whatever the changes taking place before hibernation, it would be beneficial for a hibernating mammal to begin to prepare for hibernation well before adverse environmental conditions occur. Hypotheses concerning the timing of preparation and initiation of hibernation have taken several forms. Hock (1955) suggested that the decreasing day-lengths of late summer and autumn served as the stimulus for the onset of hibernation in the arctic ground squirrel, Spermophilus undulatus. He reasoned that an environmental factor must be predictable and dependable if it is to be used as a stimulus for preparation and initiation of hibernation, and daylength seemed to be the most dependable environmental factor.

A test of Hock's hypothesis on the golden-mantled ground squirrel, Spermophilus lateralis, led to a different conclusion. Pengelley and Fisher (1957) reported that when individuals of this species were maintained under constant conditions of photoperiod and temperature for up to four years, hibernating activity alternated with nonhibernating activity in a pattern somewhat similar to that occurring in nature. These results, later to be expanded by experiments utilizing many different photoperiod and temperature conditions (Pengelley, 1965; Pengelley and Asmundson, 1969, 1970; Pengelley and Fisher, 1963; Pengelley et al., 1975; Scott and Fisher, 1970), led to a hypothesis invoking endogenous rhythmicity. Two phenomena were noted in regards to this endogenous cycle. First, the period of the rhythm was not exactly a year in length. In most cases the period was less than one year. This led to the coining of the term "endogenous circannual rhythm" which indicates an intrinsic rhythm with a period of approximately one year. Secondly, the period of the rhythm proved to be temperature independent or nearly so; the length of the period at 12°C was not statistically different from that at 3°C. This aspect of temperature independence was considered important because it was analogous to the temperature independence of circadian rhythms and indicated the possibility of an endogenous cellular basis for the rhythm. However, Brown (1976) has taken this aspect of temperature independence to mean that the rhythm is not endogenous. He bases this on the fact that all known cellular chemical reactions are not temperature independent. I recognize this dichotomy but since I am not attempting to determine the basis of any possible rhythm, I will use Pengelley and Fisher's description of the rhythm for comparative purposes. At the present time, no entraining factor(s) (Zeitgeber) has been determined through experimentation to entrain a circannual rhythm to a period of 365 days.

It had been demonstrated by different researchers (see Mrosovsky, 1978, for a comprehensive review) that endogenous (circannual rhythm) and exogenous (photoperiod and temperature) factors vary in their importance for different species of mammalian hibernators. It was my purpose in conducting these experiments to determine the relative roles that endogenous and exogenous factors play in the preparation for and entrance into hibernation in the meadow jumping mouse, Zapus hudsonius. Much of the early research conducted on hibernating mammals dealt with rodents of the squirrel family, Sciuridae, and this group is where the concept of endogenous circannual rhythmicity was developed. Recent research (Cranford, 1978; Mrosovsky, 1977) has demonstrated that some species in different rodent families do not show endogenous circannual rhythms. This study on the meadow jumping mouse represents the second look at a member of the Family Zapodidae.

Answers to the following questions were sought: (1) Is the hibernation-nonhibernation cycle and/or weight cycle in Zapus hudsonius governed by a circannual rhythm of the type described by Pengelley and Fisher (1957); (2) If a circannual rhythm as previously described is not present, are other types of rhythmicity demonstrated and under what set of controlled conditions might they be expressed; and (3) What role do photoperiod and/or temperature play in controlling the preparation for the entrance into hibernation? In particular, I sought to determine if the occurrence of preparation and initiation of hibernation was more prevalent under certain conditions than others. This would give insight into the role of photoperiod and/or temperature in the preparation and initiation of hibernation. Depending upon which factor (if any) was more important, I sought to determine if that factor could be used as a stimulus capable of providing information concerning time of the year.

To facilitate the understanding of events occurring during hibernation, several terms must be defined. The hibernation interval is that time from the first evidence of hibernation in the fall to the last evidence of the state in the spring. However, the animal does not remain in hibernation continuously over this time span as arousals and re-entries occur at intervals whose length appears to be characteristic for a species at a specified environmental temperature (T_a) (Pengelley and Fisher, 1961; Twente and Twente, 1965). The time period between arousals will be defined as a hibernation bout. Arousals occurring during the hibernation interval will be classified as intermittent arousals whereas the arousal that ends a hibernation interval will be alluded to as the terminal arousal. The time from terminal arousal in the spring to first entrance into hibernation in the fall is termed the active interval. The hibernation interval plus the active interval comprise the hibernation-nonhibernation period.

Field data can also give some insight into the hibernating life history strategy. In particular, live trapping studies can give insight into the dates of emergence from and entrance into hibernation, the hibernation-nonhibernation period length, the timing or reproduction, and the mortality rate over the hibernation interval.

Two indepth natural history monographs have been written on the meadow jumping mouse (Quimby, 1951; Whitaker, 1963) as have many shorter notes (Babcock, 1914; Blair, 1940; Dilger, 1948; Hamilton, 1935; Manville, 1956; Sheldon, 1934; Whitaker and Mumford, 1971), but these have not dealt in depth with the aforementioned topics for individual animals. For example, information is lacking concerning the hibernation-nonhibernation period length of individual animals in the wild. Comparison of data on this point from the field with those obtained in the laboratory is important in any discussion concerning a circannual rhythm. If the period lengths from the laboratory and field animals are both circannual, this would mean that the cycles of the field animals are not being entrained to a period of exactly 365 days. An analysis of the dates of entrance into hibernation is important in determining possible modulation of dates of entrance by T_a.

The number of litters produced per year and their timing is also important for a hibernating species. While nonhibernators may extend their breeding season from early spring to late fall, and in some cases through the winter, hibernators must complete their breeding within the brief time span of late spring to late summer.

Juveniles are reported to be the last animals to enter into hibernation (Quimby, 1951), being preceded sequentially by the male and female adults. Data from live trapping will be able to discern if there is differential mortality between these groups. It is of interest to know what proportion of these various groups survive to constitute the following year's population. In particular, it is of interest to note the life spans of meadow jumping mice and the relation of life span to the presence or absence of an endogenous circannual rhythm.

MATERIALS AND METHODS

Laboratory Experiments

Over a three-year period, 92 meadow jumping mice (*Zapus hudsonius*) which had either been live-trapped near East Lansing, Michigan, or born to captured females or mated pairs from the same area, were assigned to five treatment combinations (T.C.'s) involving manipulations of photoperiod and temperature. Of these five T.C.'s, the first four composed a completely random statistical design with a 2 x 2 factorial arrangement of treatments (Figure 1). The factors used in this arrangement were length of photoperiod and level of temperature, each being set at two levels. The photoperiod levels were LD 15.33:8.67 and LD 12:12, while the temperature levels were 20° and 5°C. The LD 15.33:8.67 photoperiod represents that photoperiod observed at the latitude of East Lansing, Michigan, on the longest day of the year, June 21. By assigning only animals which had been captured before or within a 14-day period after June 21 to the two treatments involving this long photoperiod, it was known that the individuals had not been subjected to any appreciable decrease in daylength during their active phase that particular summer (7 minutes maximum). The shorter photoperiod was chosen because it had been used in most previous circannual rhythm experiments (Pengelley, 1965; Pengelley and Asmundson, 1969, 1970; Pengelley and Fisher, 1963; Pengelley *et al*.,

Figure 1. Experimental design and results. Number in center of each box represents the number of animals surviving to 137 days into each T.C. P equals the number of animals preparing for hibernation, while H equals the number of animals hibernating out of those animals surviving for at least 137 days. S equals LD 12:12, L equals LD 15.33:8.67, C equals 5°C, and W equals 20°C.

PHOTOPERIOD

TEMPERATURE	LD 12:12	LD 15.33:8.67
5C	T.C. SC 18 P=18 H=16	T.C. LC 12 P= 2 H= 1
20C	T.C. SW 13 P=12 H= 9	T.C. LW 12 P= 0 H= 0

1975; Scott and Fisher, 1970). In this way, direct comparisons could be made between Zapus hudsonius and other hibernating species. The two temperature levels were chosen to give a substantial difference in T_a for comparison between treatments. As stated previously, temperature independence is one property of the circannual rhythm described by Pengelley and Fisher (1957). It was known that hibernation was possible in this animal at both 20° and 5°C (Muchlinski, unpublished data). Therefore, the 15°C temperature difference allowed a test of the temperature independence hypothesis.

Twenty individuals were assigned to each of these four T.C.'s. Because of the inability to capture 80 animals in one summer, all four T.C.'s could not be begun at the same time. Therefore, the following procedure was used.

The first 20 animals (14 males, 6 females) captured before or shortly after June 21, 1976, were assigned to T.C. LW (LD 15.33:8.67, 20°C). The dates of capture for these animals ranged from May 1 to July 2, 1976. Mortality was high in this T.C. so four additional animals (3 males, 1 female) were put under this regime on July 5, 1977. The surviving members of the 1976 group were maintained under these constant conditions for 749 days, while the four individuals started in 1977 were run to a maximum of 370 days.

By late August 1976, it was possible to capture a substantial number of additional animals, and these were used to establish T.C.'s SC (LD 12:12, 5°C) and SW (LD 12:12, 20°C). Both of these T.C.'s were begun on August 24, 1976, and were composed of animals captured between July 3 and August 23, 1976. Assignment to these two T.C.'s was made on basis of date of capture, sex, and age of the individual. Every second individual in order of capture or birth was assigned to T.C. SC with some minor adjustments made to ensure that the number of males, females, adults, and juveniles was equal between T.C.'s (T.C. SC: 9 males, 11 females, 5 juveniles included in these numbers; T.C. SW: 10 males, 10 females, 4 juveniles included in these numbers).

Those individuals composing T.C. SW were put under the prescribed conditions on August 24 while those composing T.C. SC were subjected to LD 12:12 starting on August 24 but were exposed to stepwise drops in T_a. The animals were lowered from room temperature (approximately 20°C) to 10°C for one week and then to 5°C. In these two T.C.'s, survivors were maintained under constant conditions for a maximum of 686 days.

Treatment combination LC (LD 15.33:8.67, 5°C) was begun on June 21, 1977. Animals used in this T.C. were either captured between May 20 and July 5 or born to mated lab pairs before June 21. As in T.C. SC, stepwise drops in T_a from room temperature to 5°C were implemented. This T.C. was accidentally terminated 137 days after initiation because of the introduction of a toxic substance into the environmental chamber. The majority of the animals were killed, and those that survived were moved to another room thereby ending the treatment.

In the case of all animals used in the T.C.'s, an attempt was made to subject animals to similar conditions before they were assigned to their respective T.C. As individuals were trapped, they were brought into an animal colony room. There the animals were subjected to room temperatures (20°-25°C) and simulated natural daylengths using an astronomical timer (Paragon Astro Dial). All animals were given food (Wayne Lab Blox) and water <u>ad libitum</u>. In addition, sunflower seeds were given to all animals on the day of capture. Laboratory-born animals came from pairs housed in this same room. All animals were housed individually in plastic cages measuring 27.9 x 17.8 x 12.7 cm or 26.7 x 20.3 x 15.9 cm and were given a nest box measuring 9 x 9 x 8.2 cm lined with cotton for females and wood shaving for males. Wood shavings covered the floor of all cages.

After assignment to its respective T.C., each animal was maintained in a walk-in environmental chamber under the constant conditions of that particular T.C. until expiration of the individual or termination of the experiment. The T_a in each T.C. was maintained within 1.5°C at the set level, while the light intensity measured at the top of each cage was maintained at approximately 85 lux.

All nonhibernating animals were weighed to the nearest 0.5 gram at one week intervals for the first year of the T.C. and every second week thereafter. Reproductive condition was also noted at this time with males being scored as testes scrotal, barely scrotal, or nonscrotal while females were scored as having easily visible nipples or nonvisible nipples. Hibernating animals were weighed only during or shortly after an intermittent arousal. This minimized disturbances which may have altered the length of time spent in hibernation.

Hibernation activity was monitored by the use of tracking plates placed in front of the nest box opening. The plates were covered with a mixture of alcohol and baby powder, and evaporation of the alcohol left a smooth surface of talc which would be disturbed by the animal if it left or entered the nest box. The plates were checked once per day, and the animal was scored as active for the preceding evening if the plate had been disturbed or hibernating if the plate had not been disturbed. The first time a plate was found intact, the animal was checked to confirm the hibernating state. A continuous record of hibernating or nonhibernating activity was maintained over the course of each T.C.

Several power interruptions and environmental room breakdowns did occur over the course of the T.C.'s. A power outage occurred for approximately two hours in T.C.'s SL, SW, and LW on October 3, 1976. Also, a temperature breakdown occurred in T.C.'s SW and LW for five days starting on January 21, 1977, allowing T_a to rise to 26°C. No temperature breakdowns occurred in the 5°C T.C.'s. Therefore, animals in T.C.'s SW and LW were never exposed to T_a's below 20°C and animals in T.C.'s SL and LC were never exposed to T_a's above 5°C.

Treatment combination 5 was established in August 1978 to test the influence of a clock-shifted, naturally decreasing photoperiod on the preparation for and entrance into hibernation. The 12 animals comprising this T.C. were captured between July 13 and August 18, 1978, from the East Lansing, Michigan, area. Eight of the animals, that were captured before July 20, were placed on LD 15.33:8.67, 20°C on this date. Prior to this date and since the date of capture, the animals were housed in a colony room maintained at 20°-27°C and LD 14:10. Four animals were captured on August 18 and were immediately placed under LD 15.33:8.67, 20°C. Each animal was housed individually in a cage measuring 29.8 x 24.1 x 20.3 cm. Wood shavings were placed to a depth of 12 cm which allowed the animal to burrow under the shavings for cover. This set-up was used because it had been determined through observations that larger cages with excess bedding material reduced mortality.

All animals were maintained under these conditions until September 21, 1978, at which time they were three months out of phase with the natural environment. An astronomical timer (Paragon Astro Dial, set for latitude 42°N) was set to simulate the June 21 photoperiod on September 21 and thereafter the simulated photoperiod continued to lag three months behind the natural environment. The temperature was maintained at 20° ±1.5°C at all times, and the light intensity was approximately 85 lux. As in T.C.'s LW, LC, SW, and SC, animals were given food (Wayne Lab Blox) and water *ad libitum*.

Beginning on August 18, animals in T.C. 5 were weighed, and reproductive condition was ascertained, once per week. As an animal was observed to undergo a weight increase indicating preparation for hibernation, tracking plates were set into the cage to check for hibernating activity. These plates were then checked daily to ascertain the first day of hibernation. As in the previous T.C.'s, the animal was checked at the first sign of a nondisturbed tracking plate to visually observe the hibernating state. Since the purpose of this T.C. was only to determine if decreasing photoperiods were capable of stimulating preparation for and entrance into hibernation, no continuous record of hibernating activity was maintained after the initial entrance into hibernation.

On October 17, the overhead neon lights were inadvertently turned on, and this was not discovered until October 21. The simulated dates for this occurrence were July 17 to July 21. One power interruption occurred for 25 minutes at approximately 4:00 a.m. on November 29. The lights were not readjusted.

Statistical comparisons among T.C.'s SC, LC, SW, and LW were based mainly on nonparametric analyses although parametric tests were used in several instances. Nonparametric procedures were favored because of the small sample sizes present in most T.C.'s, the high incidence of nonequality of variance, and the non-normal distribution of data. In those cases where it was determined that variances were equal and normality was present, parametric tests were used. Normality was tested for by the chi-square goodness of fit for continuous distribution test (Steel and Torrie, 1960), and the F-test was used to determine equality of variance (Snedecor and Cochran, 1967).

Field Procedure

In June 1976, a 1.38 hectare live-trapping grid was established at the Institute of Water Research at Michigan State University, Ingham County, Michigan, for the purpose of gathering demographic data related to the hibernating life history strategy of Zapus hudsonius. The main trapping grid was composed of 144 Longworth live traps set in 18 rows (25 feet apart) with eight traps (50 feet apart) per row. In the spring of 1977, two rows (100 feet apart) with eight traps per row were set as auxillary lines to the west of the main grid while three rows (100 feet apart) with eight traps per row were set to the east of the main grid, giving an additional 1.63 hectares of trapping area.

The main grid was operated on two consecutive mornings and the intervening afternoon each week. Trapping was begun in mid-April before emergence of the mice from their hibernacula and continued through the fall until two weeks went by with no captures. The latter circumstance signified that all animals residing on the grid had taken up residence in their hibernacula for hibernation. The auxillary trap lines were run for four weeks in the spring after emergence of the animals and for four weeks in the fall before the majority of the animals had taken up residence in their burrows. This was an attempt to increase the number of animals marked for estimating overwintering survival. All traps were baited with whole oats, cotton was placed in the rear portion of the trap for nesting material, and cover boards were placed on top of the traps.

Individual meadow jumping mice were marked by toe clipping and weighed, and note was taken of their reproductive condition. As in the laboratory, males were categorized as testes scrotal, barely scrotal, or abdominal, and females were categorized as nipples easily visible or nonvisible. In addition, female reproductive condition was noted by the condition of the vaginal orifice (perforate or nonperforate) and pregnant females were discernable by obviously bulging abdomens. Lactating females could be noted by the size of the nipples.

Individuals newly captured before July 1 each year were classified as adults at the time of capture. After July 1, new individuals weighing less than 15 g at the time of first capture were classified as juveniles. Animals caught for the first time after July 1 and weighing more than 15 g could not be placed in either category with 100 percent certainty until the following year when they could be classified as adults.

The trapping grid was operated in the summer and fall of 1976, the spring, summer, and fall of 1977 and 1978, and the spring of 1979. Data on the following parameters were gathered: (1) minimum number alive, (2) reproduction, (3) dates of emergence from and entrance into hibernation, and (4) survivorship over the hibernation interval. A demographic analysis computer package maintained by Dr. Walt Conley, Department of Fishery and Wildlife Sciences, New Mexico State University, was used to analyze portions of the data.

RESULTS

Laboratory Results

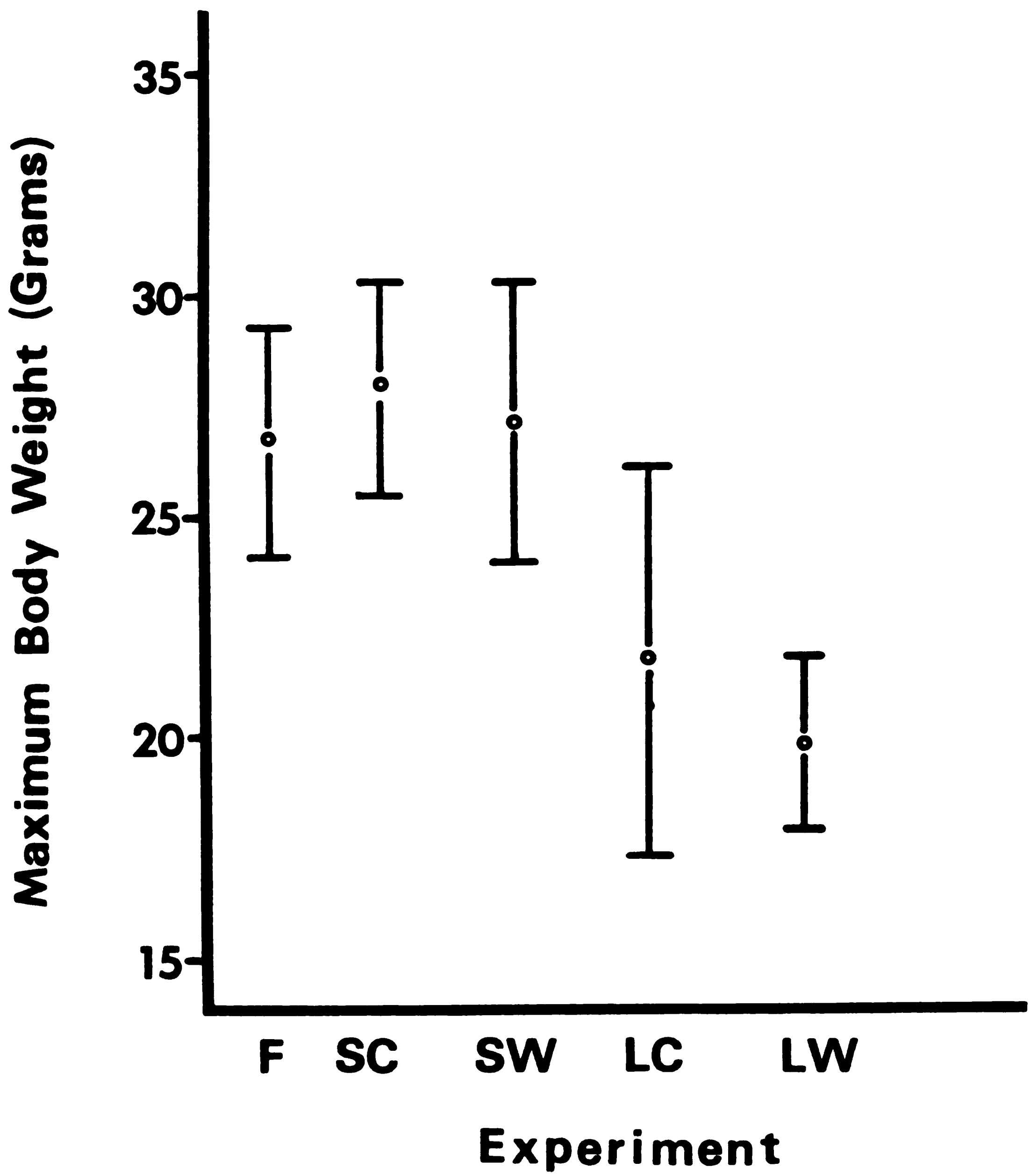
Animals were observed to prepare for (increase in weight to $\geq$ 25 g) and enter into hibernation in all four T.C.'s composing the factorial arrangement of treatments. However, the number of individuals undergoing these changes and their timing varied between T.C.'s. Because of the early termination of T.C. LC, statistical comparisons concerning the effect of photoperiod and/or temperature on the first preparation and initiation of hibernation can only be made up to 137 days into each T.C. However, this alters the outcome of the analysis little, for in T.C.'s SC, SW, and LW combined only a single animal entered hibernation after 137 days (animal 47 in T.C. LW, which was first observed in hibernation on day 171). In T.C. LC which was terminated early, the only animal to enter hibernation did so on day 70, while the same animal and a second reached peak weights on days 57 and 43, respectively. It is unlikely that any additional animals would have either prepared for or entered into hibernation in T.C. LC.

The number of individuals preparing for hibernation and the number that actually entered hibernation in each T.C. within the first 137 days are shown in Figure 1. A 2 x 4 chi-square test demonstrated that the distribution observed of those preparing for hibernation differed from that expected by chance ($X^2 = 44.36$, df = 3, $P < 0.005$). Six 2 x 2 chi-square tests were then computed using all possible combinations of two T.C.'s. Only those combinations within a photoperiod level were not significantly different from one another (SC vs LC, $P < 0.001$; SC vs SW, $P = 0.42$; SC vs LW, $P < 0.001$; LC vs SW, $P < 0.001$; LC vs LW, $P = 0.24$; SW vs LW, $P < 0.001$; Fisher Exact Probability chi-square Test, Steel and Torrie, 1960). This indicates that more animals were preparing for hibernation under short daylengths than under long daylengths. To corroborate this conclusion, a Kruskal-Wallis Main Effects and Interaction Test (Bradley, 1968) was conducted on the mean maximum weight achieved in each T.C. within 137 days (Figure 2). This demonstrated that only the photoperiod main effect was significant, indicating that the maximum weight attained differed between photoperiod levels ($P < 0.001$) but was not different within photoperiod levels ($0.05 < P < 0.10$). Therefore, animals under LD 12:12 reached the same peak weight regardless of the temperature, as did those animals under LD 15.33:8.67. However, the mean maximum weight attained under LD 12:12 was greater than that under LD 15.33: 8.67.

A 2 x 4 chi-square test conducted on the number of animals hibernating in the four T.C.'s was also significant ($X^2 = 33.32$, df = 3, $P < 0.005$). Again, all combinations of two T.C.'s were compared, demonstrating that all between-photoperiod comparisons, were significant (SC vs LC, $P < 0.001$; SC vs SW, $P = 0.48$; SC vs LW, $P < 0.001$; LC vs SW, $P = 0.003$; LC vs LW, $P = 0.40$; SW vs LW, $P < 0.001$).

At LD 12:12, there were no differences between temperatures in the animals' initial response. Those animals initially preparing for hibernation at 20°C did so in 57.0 ±26.3 SD days while those at 5°C did so in 46.5 ±15.8 SD days ($0.12 < P < 0.66$, Wilcoxon Rank Sum Test,

Figure 2. Mean maximum body weight attained within 137 days in the four laboratory T.C.'s and in a sample of 56 field animals. F equals field group; S, L, C, and W are the same as in Figure 1. Sample sizes for the laboratory groups are SC = 18, SW = 13, LC = 12, LW = 12. Vertical bars represent ±1 standard deviation.


Maximum Body Weight (Grams)
35
30
25
20
15
F
SC
SW
LC
LW
Experiment

Snedocor and Cochran, 1967). Those animals first hibernating at 20°C did so in 62.5 ±11.4 SD days while those at 5°C did so in 55.0 ±18.0 SD days ($0.40 < P < 0.50$, $t = 0.78$, $df = 23$). Therefore, with respect to the initial preparation for and entrance into hibernation, the animals responded the same regardless of the T_a. The important factor was photoperiod.

LD 15.33:8.67, 20°C

As previously stated, animal 47 began to hibernate on day 171. Subsequently this animal went through a hibernation interval followed by an active interval (Figure 3). Although two hibernation invervals are shown on the figure, the second was not coincident with a weight increase and the animal was never found to be torpid over the nocturnal period. The only time the animal was found torpid was during daylight. Therefore, this should probably be considered more like daily torpor than hibernation.

All other individuals remained at low summer weights (example, Figure 3) and were judged to be in reproductive condition (testes scrotal or medium nipples). It also appeared that molting proceeded abnormally in that animals were often found with bare patches of skin that were only slowly filled in with hair. A listing of the animals, their dates of capture, and the length of time spent under these particular conditions can be found in Table 1.

LD 15.33:8.67, 5°C

Only two of 12 animals prepared for hibernation, and only one of 12 entered hibernation within 137 days. The two animals preparing for hibernation reached peak weight on August 23 and October 14,

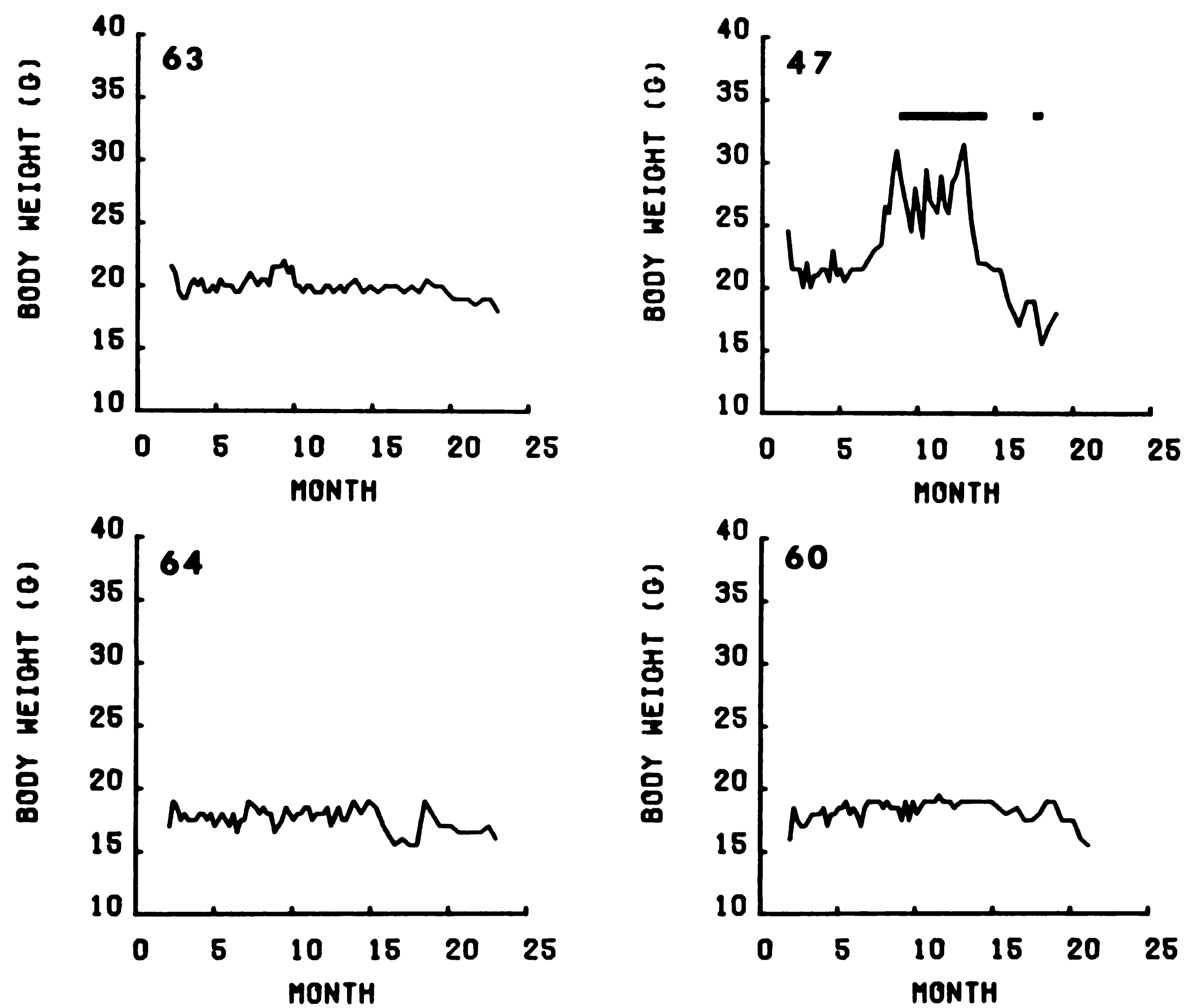


Figure 3. Body weight graphs for four animals from LD 15.33:8.67, 20°C. The black bars represent hibernation intervals. Animal number is given in upper left corner of each graph.

TABLE 1

Animals which survived more than 137 days
under LD 15.33:8.67, 20°C

Animal No.	Sex	Date of Capture	Length of Survival (Days)
41	M	5/2/76	260
5	M	6/28/77	335
10	F	6/28/77	342
16	M	6/28/77	355
7	M	6/28/77	370
62	M	6/24/76	562
47	F	5/23/76	565
56	F	6/21/76	565
60	M	6/24/76	631
54	M	6/20/76	749
63	F	7/2/76	749
64	F	7/2/76	749

respectively, while the individual entering hibernation did so on September 6. This timing indicates that an endogenous rhythm may have been expressed in these individuals because these changes occurred at a time which corresponded to the documented occurrence of these changes in nature (see Field Results section). However, it is also possible that these two animals were stimulated to prepare for and, in one case, enter into hibernation directly by the low temperatures. All other individuals maintained low stable weights and remained reproductively active. The death of the majority of the animals from a toxic substance precludes further analysis.

LD 12:12, 20°C

In this T.C., 12 of 13 animals underwent weight gains to reach a peak weight greater than or equal to 25 grams, and nine of these animals hibernated. A number of animals exhibited more than one hibernation interval (Table 2). Six of the nine animals underwent at least two hibernation intervals, two went through at least three intervals, and one animal died while in its fourth hibernation interval. The mean hibernating-nonhibernating period length for the animals that hibernated at least twice was 157.2 ±60.9 SD days, establishing that rhythmicities do occur under these conditions with a period of approximately five months. Complete records of weight and hibernation activity for 12 of the 13 animals in this T.C. are found in Figures 4, 5, and 6.

For those animals that did undergo two or more hibernation intervals, the second interval was shorter than the first ($P < 0.005$, paired $t = 5.34$, $df = 5$, a posteriori). In animals 100 and 105, the third

TABLE 2

Days spent in the hibernating or active state over the course of the experiment for those animals that hibernated at least once. LD 12:12, 20°C

Animal No.	Sex	Hibernating	Active	Hibernating	Active	Hibernating	Active	Hibernating
72	M	36	406 X	-	-	-	-	-
74	F	48	159	2	420 X	-	-	-
82	F	85	185	19	216 X	-	-	-
88	FJ[1]	48	91	23	455 X	-	-	-
90	F	91	105	41	354 X	-	-	-
100	F	50	64	23	44	1	157 X	35 X
105	MJ[1]	80	78	60	46	30	115 X	-
107	F	185	452 X	-	-	-	-	-
109	M	28	566 X	-	-	-	-	-

X denotes that animal dies in that phase.

[1]These animals were known to be juveniles at start of the T.C.

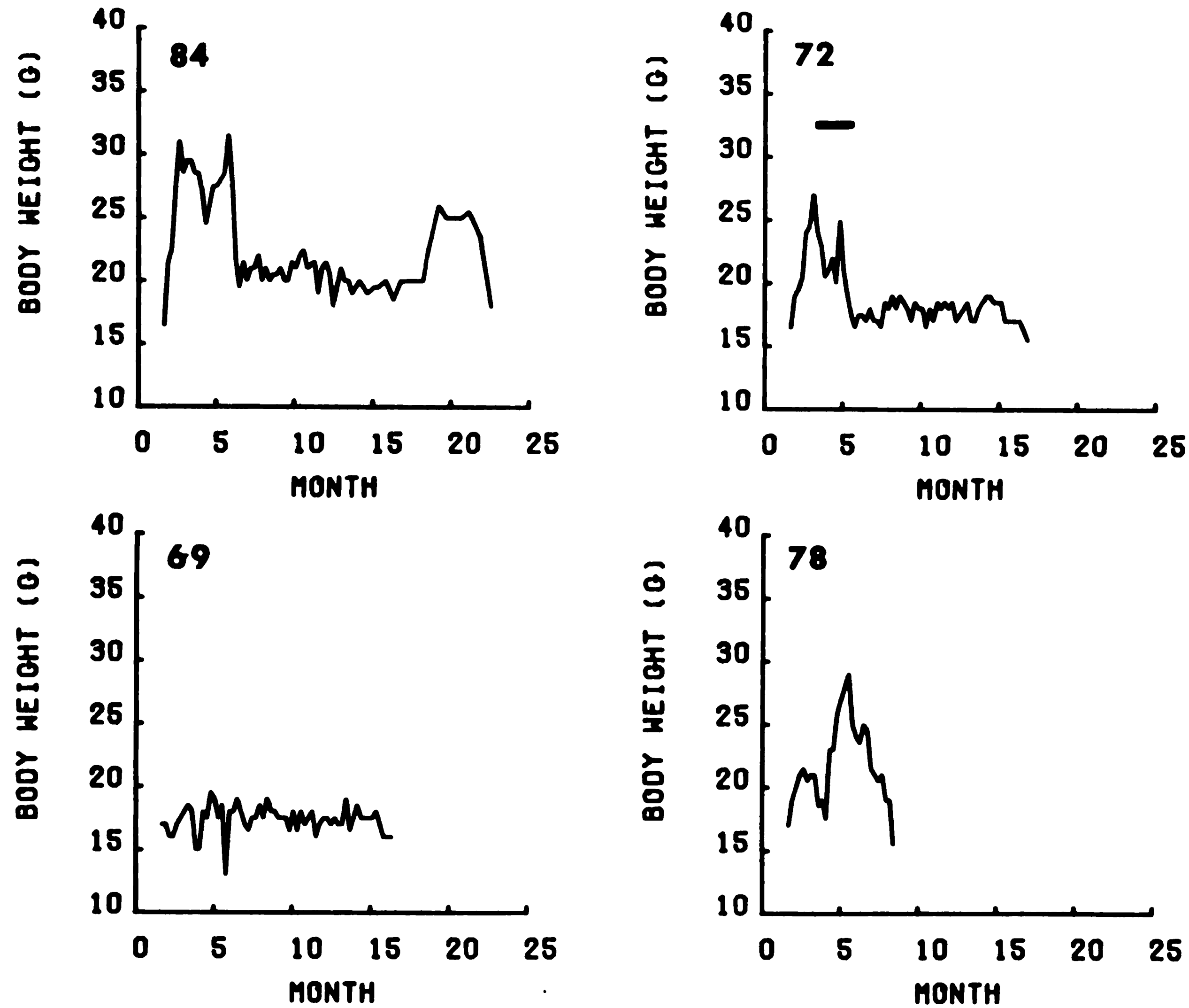


Figure 4. Body weight graphs for four animals from LD 12:12, 20°C. The black bars represent hibernation intervals. Animal number is given in upper left corner of each graph.

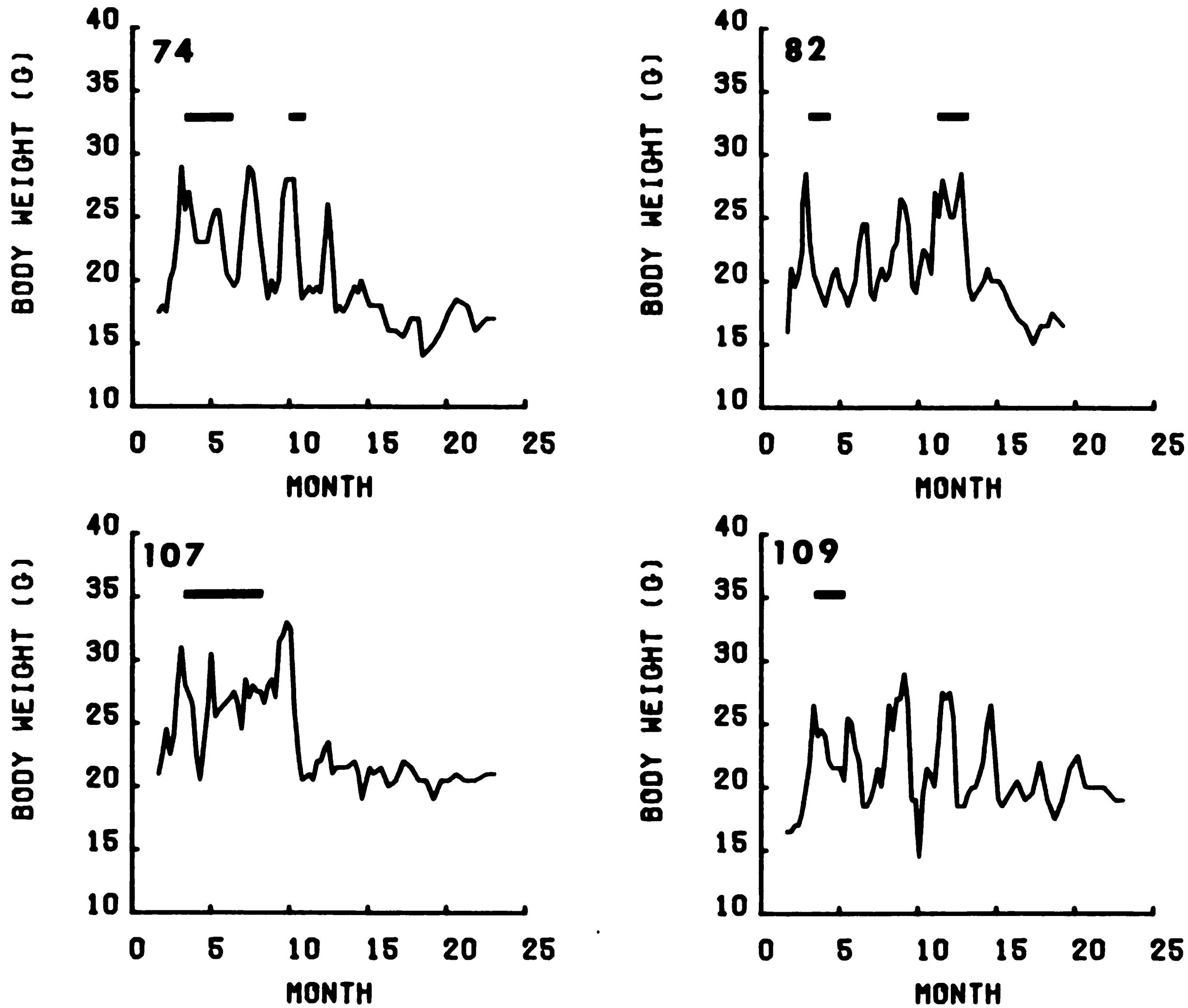


Figure 5. Body weight graphs for four animals from LD 12:12, 20°C. The black bars represent hibernation intervals. Animal number is given in upper left corner of each graph.

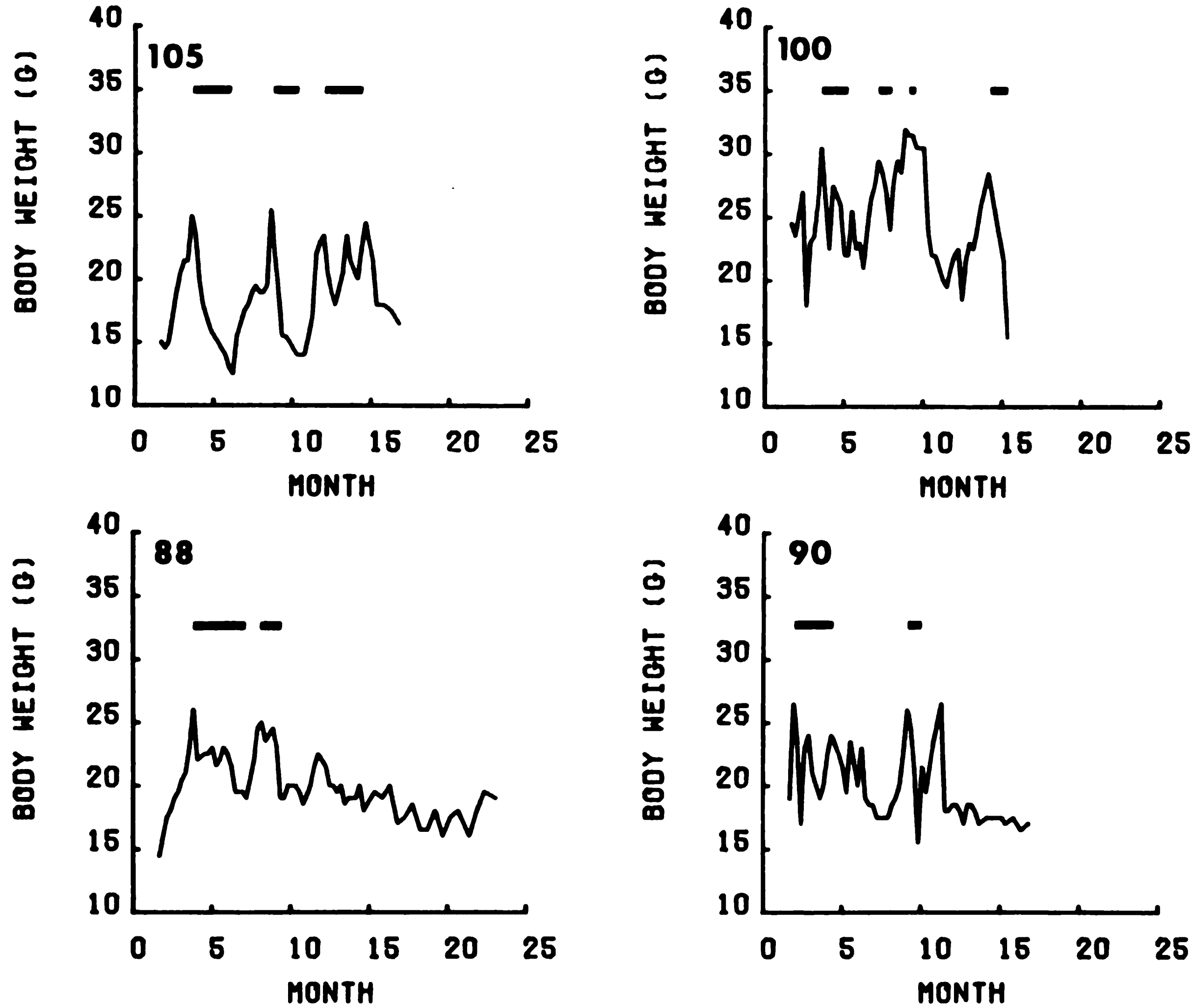


Figure 6. Body weight graphs for four animals from LD 12:12, 20°C. The black bars represent hibernation intervals. Animal number is given in upper left corner of each graph.

hibernation interval was shorter than the second, but small numbers did not allow a statistical test. If the animals are arranged according to the length of time they survived under the experimental conditions after the beginning of the first hibernation interval, survival is correlated with the length of the second active interval ($r = +0.9882$, $P < 0.05$). This indicates that those animals which remained active and did not hibernate for a third time survived the longest. The other nine simple correlations possible with these tabulated data were not significant.

The fact that hibernation did not occur after every weight increase signalling preparation for hibernation signifies that hibernation depends upon more than just a sufficient energy reserve. Because hibernation did not occur every time an animal underwent a weight increase (Figures 4, 5, and 6), the hibernating-nonhibernating period length may not be a true measure of the existing rhythmicity. This is consistent with a hypothesis of multifactor causation for the appearance of hibernation. The period length of weight cycles with amplitudes greater than or equal to 5 grams was 102.8 ±71.2 SD days, which is significantly less than the period length for hibernation-nonhibernation cycles ($P < 0.05$, $df = 34$, $t = 2.05$). The period lengths of weight cycles for individual animals are shown in Table 3. As can be seen, all of the periods are less than six months except for one cycle by animal 109 which was approximately equal to six months and one cycle by animal 84 which was just over one year in length. Since only one cycle out of 27 approached one year in length, it is probable that it was brought about by the skipping of one or two shorter cycles.

TABLE 3

Period lengths for weight cycles and maximum-minimum weights for animals that went through at least two weight gains under LD 12:12, 20°C

Animal No.	Sex	Period Lengths	High (g)	Low (g)	High (g)	Low (g)	High (g)	Low (g)	High (g)	Low (g)	High (g)	Low (g)	High (g)
74	F	126, 77, 84	27.0	19.5	29.0	18.0	28.0	18.5	26.0	-	-	-	-
82	F	112, 70, 91	28.5	18.0	24.5	19.5	26.5	19.0	28.0	-	-	-	-
84	F	105, 375, 42	31.0	24.5	31.5	19.5	25.5	20.0	26.0	-	-	-	-
88	FJ[1]	140	26.0	19.0	25.0	-	-	-	-	-	-	-	-
90	F	28, 42, 147, 70	26.5	17.0	24.0	19.0	24.0	17.5	26.0	15.5	26.5	-	-
100	F	35, 28, 91, 29, 168	27.0	18.0	30.5	22.5	27.5	21.5	29.5	24.0	32.0	18.5	28.5
105	MJ[1]	168, 105, 42	25.0	12.5	25.5	14.0	23.5	18.0	23.5	-	-	-	-
107	F	63, 154	31.0	20.5	30.5	24.5	33.0	-	-	-	-	-	-
109	M	189, 91, 84	26.5	18.5	29.5	14.5	27.5	18.5	26.5	-	-	-	-

[1]These animals were known to be juveniles at start of the T.C.

The fact that the first and last weight cycles for animal 84 were shorter (105 and 42 days) supports this theory.

In males that prepared for hibernation, the testes regressed shortly before or during the weight increase even if the weight increase did not end in hibernation. At the termination of a hibernation interval, males had barely scrotal testes. In females, the nipples went from easily visible (medium) to not visible (small) shortly before or during the weight increase, and the nipples became visible shortly after terminal arousal. Animals were never found with bare patches of skin, which indicated that molt was proceeding in a regular fashion.

LD 12:12, 5°C

In this T.C., all 18 animals prepared for hibernation. Only 17 of the animals reached a peak weight of 25 grams or more, but animal 104 hibernated after achieving a peak weight of 23.5 grams. Since an individual that hibernates should be prepared to hibernate, this animal was classified as preparing for hibernation. Sixteen animals hibernated and of these, 14 survived through the hibernation interval (Table 4). Only five of these animals went into a second hibernation interval. Animal 70 died shortly after the terminal arousal from the first hibernation interval, but the other animals survived long enough to possibly enter into a second hibernation interval. The five animals that did undergo a second interval had relatively short active intervals (69-121 days), while those animals not entering hibernation for a second time survived from a minimum of 160 to a maximum of 457 days after their terminal arousal.

TABLE 4

Days spent in the hibernating or active state over the course of the experiment for those animals that hibernated at least once. LD 12:12, 5°C

Animal No.	Sex	Hibernating	Active	Hibernating	Active
68	F	258	80	218 X	-
70	M	168	14 X	-	-
73	M	180	160 X	-	-
75	F	211	282 X	-	-
79	M	81 X	-	-	-
83	F	247	257 X	-	-
87	F	218	413 X	-	-
89	F	240	88	75	271 X
91	MJ[1]	20	292 X	-	-
95	M	186	221 X	-	-
97	F	56 X	-	-	-
104	FJ[1]	241	102	234 X	-
106	F	289	69	273	7 X
108	MJ[1]	172	121	169	157 X
110	M	214	271 X	-	-
111	MJ[1]	25	453 X	-	-

X denotes that animal dies in that phase.

[1]These animals were known to be juveniles at start of the T.C.

For those animals that hibernated a second time, the two hibernating intervals were almost equal in duration. The only exception was animal 89 which experienced a much shorter second hibernation interval. Three of the five repeat hibernators survived the second hibernation interval. One animal died shortly after emergence from the second interval, but the others remained active for a considerable length of time. In the latter two, the length of the second active interval (157 and 271 days) was longer than the maximum initial active interval for any animal that entered into hibernation twice. Therefore, it appears likely that these two animals would not have returned to hibernation for a third time.

For those animals that demonstrated two hibernation intervals, the mean period of the first cycle was 332.0 ±24.3 SD days. The mean is significantly greater than the period length demonstrated under LD 12:12, 20°C ($P < 0.005$, Wilcoxon Rank Sum Test) and indicates that the rhythm observed under these conditions can be classified as circannual. However, the majority of the animals (8 of 13) did not demonstrate any rhythm of repeated hibernation even though they survived long enough to do so. Complete records of weight and hibernation for 16 of the 18 animals in this T.C. are to be found in Figures 7, 8, 9, and 10.

The difference in the lengths of the rhythms under LD 12:12, 20 and 5°C can be assigned to the difference in the length of the hibernation interval. The length of the interval at 5°C was significantly greater, 187.0 ±79.7 SD days, than the interval at 20°C, 50.0 ±43.6 SD days ($P < 0.05$, Wilcoxon Rank Sum Test). Even if only the first hibernation interval is used to compare the T.C.'s (because the first interval at 20°C was longer than the second), the interval length was still

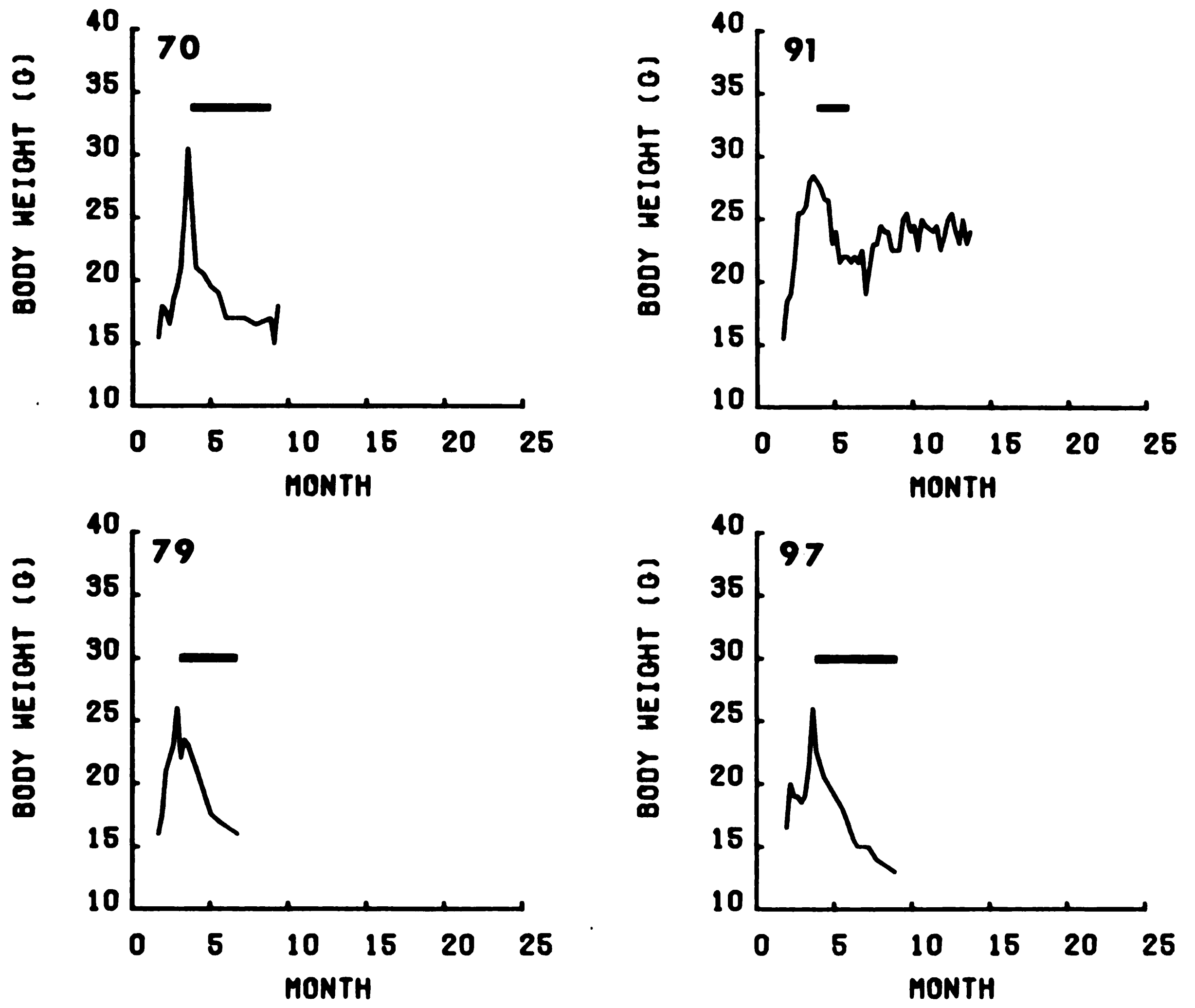


Figure 7. Body weight graphs for four animals from LD 12:12, 5°C. The black bars represent hibernation intervals. Animal number is given in upper left corner of each graph.

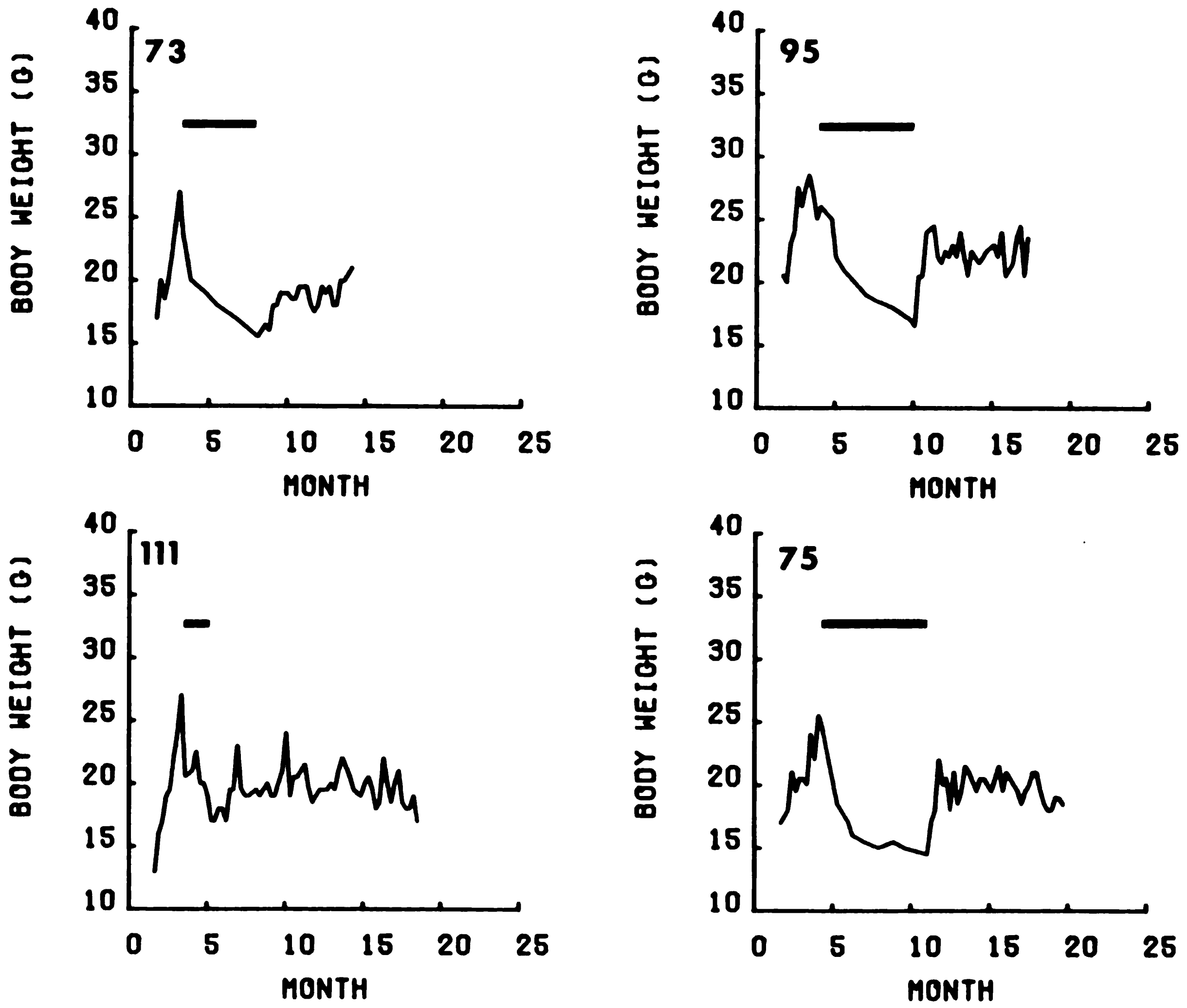


Figure 8. Body weight graphs for four animals from LD 12:12, 5°C. The black bars represent hibernation intervals. Animal number is given in upper left corner of each graph.

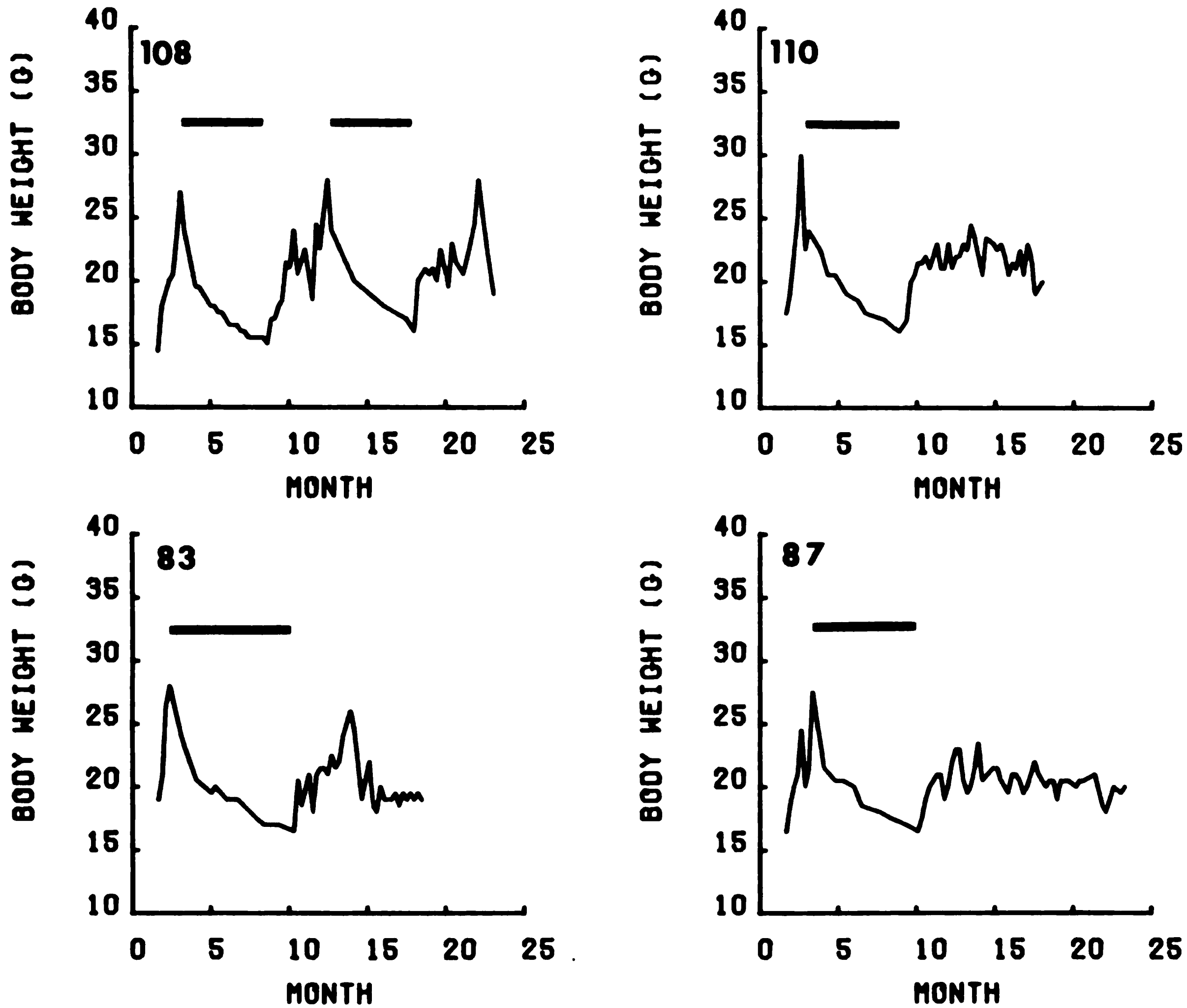


Figure 9. Body weight graphs for four animals from LD 12:12, 5°C. The black bars represent hibernation intervals. Animal number is given in upper left corner of each graph.

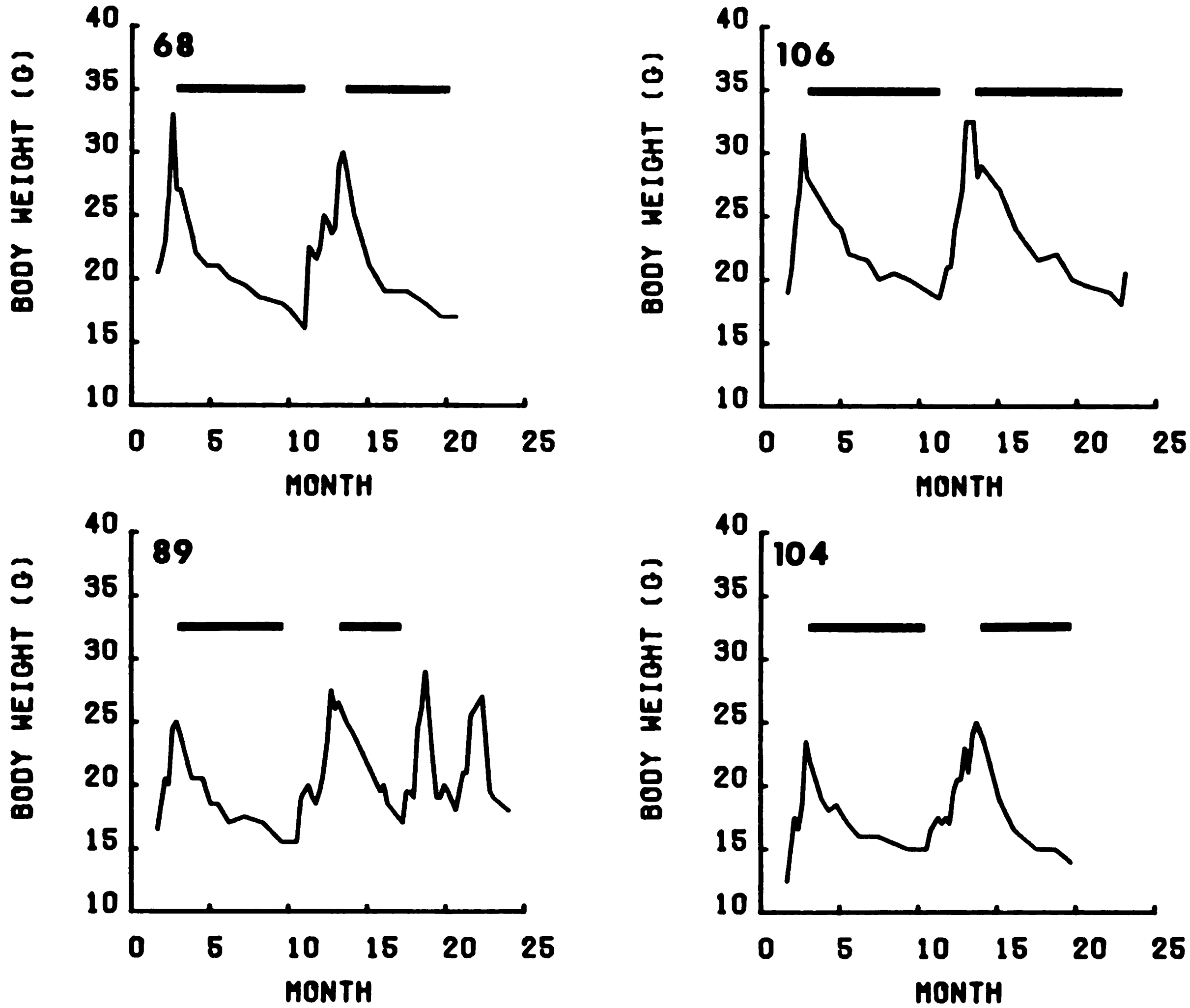


Figure 10. Body weight graphs for four animals from LD 12:12, 5°C. The black bars represent hibernation intervals. Animal number is given in upper left corner of each graph.

greater at 5°C ($P < 0.05$, Wilcoxon Rank Sum Test). The lengths of the active interval were the same at the two temperatures ($P > 0.50$, $t = 0.46$, $df = 12$).

The weight cycles under LD 12:12, 5° (Table 5) and 20°C were also not temperature independent (Figure 11), being longer at 5 than at 20°C (277.6 ±80.4 SD days vs 102.8 ±71.2 SD days, $P < 0.001$, $t = 8.08$, $df = 39$). As in T.C. SW, hibernation did not follow every weight increase. Reproductive condition changes occurred as in T.C. SW. A summary of T.C.'s SC, LC, SW, and LW is in Table 6.

Because reproductive cycles are under hormonal control, it would be of interest to know more about the levels of circulating hormones in the blood stream. In the experiments conducted in this study, all the males that underwent weight gains also underwent gonadal regression. This was true whether hibernation occurred or not. It would be of interest to know whether or not those animals that did hibernate had different levels of circulating hormones than those animals that did not hibernate. It is possible that subtle differences in hormone levels could make the difference between hibernation and activity.

A large amount of variability in the lengths of hibernation and weight cycles was demonstrated in the two short daylength T.C.'s. Although it may be tempting to extrapolate these laboratory results to a discussion of variability in natural populations (i.e., some animals may die in nature because they end hibernation in mid-winter), caution should be exerted because the laboratory animals were maintained under constant conditions which never occur outside of the laboratory. It is possible that some of the variability is present because the animals are affected in an adverse way by the constant conditions. For

TABLE 5

Period lengths for weight cycles and maximum-minimum weights for animals that went through at least two weight gains under LD 12:12, 5°C

Animal No.	Sex	Period Length	High (g)	Low (g)	High (g)	Low (g)	High (g)	Low (g)	High (g)
68	F	343	33.0	16.0	30.0	-	-	-	-
75	F	245	25.5	14.5	22.0	-	-	-	-
83	F	371	28.0	16.5	26.0	-	-	-	-
87	F	343	27.5	16.5	23.5	-	-	-	-
89	F	315, 158, 111	25.0	16.0	27.5	17.0	29.0	18.0	27.0
91	MJ[1]	182	28.5	19.0	25.5	-	-	-	-
95	M	252	28.5	16.5	24.5	-	-	-	-
104	FJ[1]	343	23.5	15.0	25.0	-	-	-	-
106	F	329	31.5	18.0	32.5	-	-	-	-
108	MJ[1]	301, 306	27.0	15.0	28.0	16.0	28.0	-	-
110	M	355	20.0	15.5	24.5	-	-	-	-
111	MJ[1]	210	30.0	15.5	24.5	-	-	-	-

[1]These animals were known to be juveniles at start of the T.C.

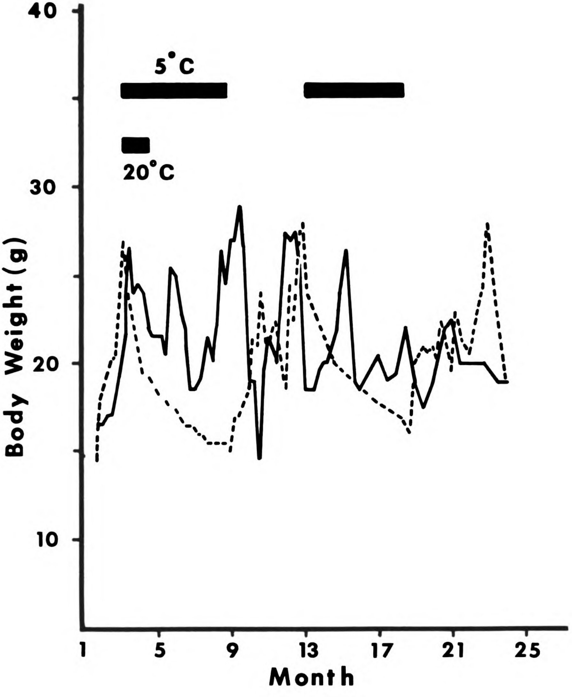


Figure 11. Comparison of weight cycles for one animal at LD 12:12, 20°C (solid line) and one animal at LD 12:12, 5°C (broken line).

TABLE 6

SUMMARY OF T.C.'s SW, LW, SC, LC

Treatment	Mean Hibernation-Nonhibernation Period Length (days)	Mean Hibernation Interval Length (days)	Mean Active Interval Length (days)	Mean Body Weight Period Length (days)	Mean Maximum Body Weight (g)	Mean Minimum Body Weight (g)	Reproductive Cycles	Replacement Hair
SC	332.0 ±24.3 SD	187.0 ±79.7 SD	92.0 ±20.2 SD	277.6 ±80.4 SD	27.24 ±2.8 SD	16.33 ±1.2 SD	yes	normal
SW	157.2 ±60.9 SD	50.0 ±43.6 SD	103.2 ±52.2 SD	102.8 ±71.2 SD	27.40 ±2.5 SD	18.89 ±2.9 SD	yes	normal
LC	--	--	--	--	--	--	no	--
LW	--	--	--	--	--	--	no	abnormal

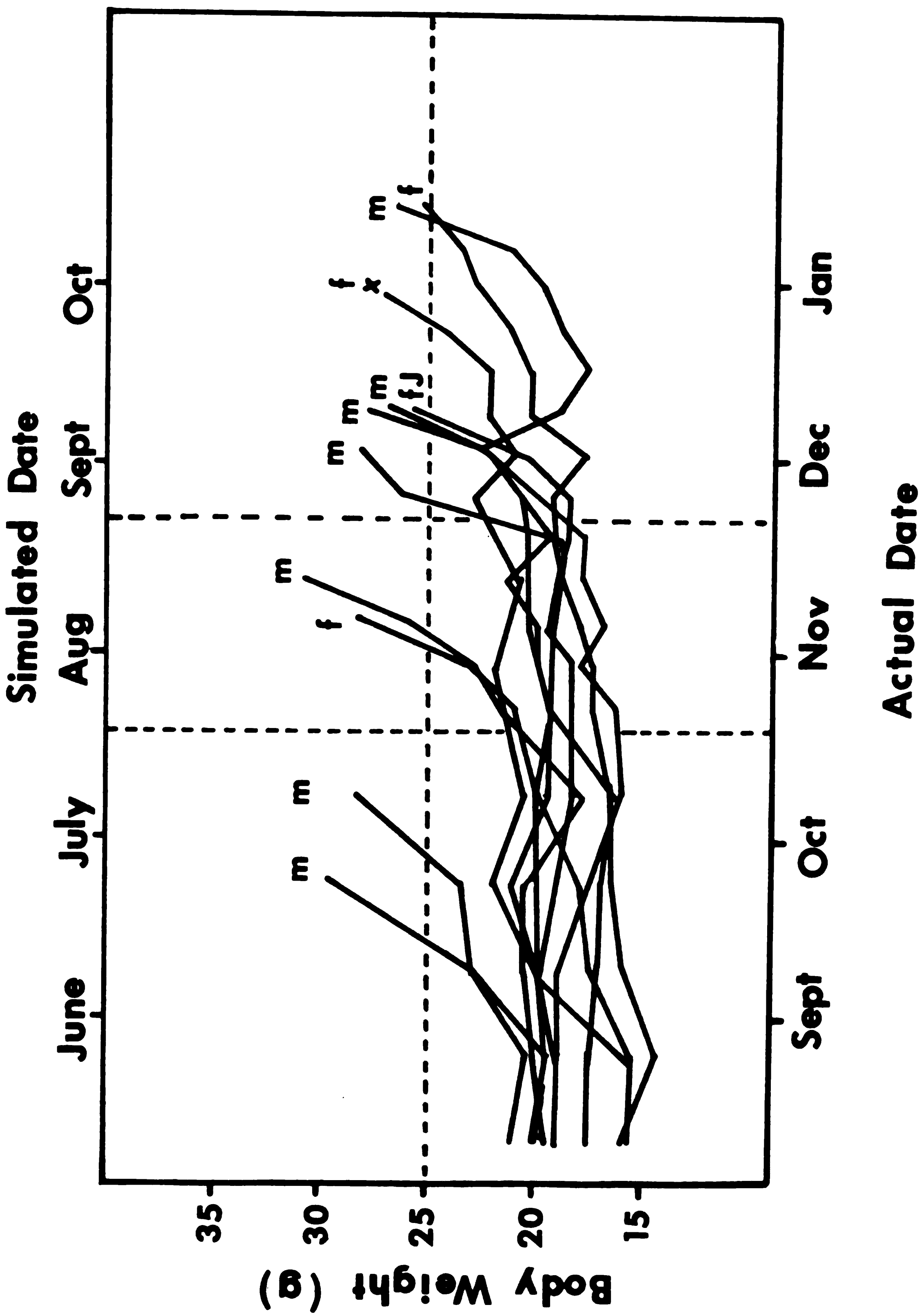
example, an animal in nature would be exposed to increasing daylengths upon arousal in the spring, whereas laboratory animals were exposed to constant daylengths upon terminal arousal. Also, animals in nature would be in total darkness during periodic arousals whereas laboratory animals may be exposed to light during a periodic arousal.

Clock-Shifted Photoperiod Experiment

Of the 12 animals which started this experiment, one died on December 3 while still at a low body weight, 11 survived to prepare for hibernation, and 10 of these hibernated (Figure 12). Two of the animals underwent weight gains at simulated times of late June and early July while two other animals reached peak weight during simulated early to mid-August. The remaining seven animals prepared for hibernation during a simulated time span which corresponded with the time for preparation for hibernation of animals in the field (late August through mid-October).

Concerning the animals that prepared for hibernation outside of the simulated natural time span, it is possible that the two animals which underwent weight gains during August were still being stimulated by the decreasing daylengths. These individuals prepared for hibernation about two or three simulated weeks ahead of the first occurrence observed in nature (August 23). With the possibility of these animals being adults (they were captured after July 1 and weighed more than 15 g, hence they could not be classified as juveniles with 100 percent certainty) and their having access to *ad libitum* food, this early entrance should not be taken as being abnormal. However, difficulty does arise in interpreting the preparation for and entrance into hibernation of

Figure 12. Response of animals to clock-shifted photoperiods. Relationship of weight gain (up to maximum weight attained) to simulated and actual dates. Animals increasing in body weight to $\geq$ 25 g (dashed line) have prepared for hibernation. X indicates that the animal did not hibernate. Dashed line at simulated late August represent first occurrence of hibernation in nature while dashed line at actual mid-October represents approximately the last date an animal would enter into hibernation if an endogenous rhythm was present. Tic marks on X-axis indicate first day of month. M = male, F = female, J = juvenile.


Simulated Date
June
July
Aug
Sept
Oct
Actual Date
Sept
Oct
Nov
Dec
Jan
Body Weight (g)
35
30
25
20
15

the two individuals during actual late September and early October. These events are what one would predict if an endogenous circannual rhythm or some other type of endogenous clock mechanism (e.g., hour-glass timer) were present in Zapus hudsonius.

The results from this experiment were compared to T.C. LW which was used as a control. However, this was not an ideal control group because it was not conducted simultaneously with the shifted daylength T.C. To strengthen the conclusions from the shifted daylength T.C., I would suggest that it be conducted again with a control group held under long daylength and warm temperatures. If enough animals are available, a three-month, clock-shifted daylength experiment in the opposite direction (simulated September 21 daylength on June 21) may also provide some insight.

Field Results: Timing of Events

Animals aroused from hibernation at different times in the spring during the three years of the field study (Table 7). The first males

TABLE 7

The date of first appearance above ground by males and females in the spring

MALES		FEMALES	
Year	Date	Year	Date
1977	April 20	1977	May 5
1978	May 3	1978	May 17
1979	April 26	1979	May 9

aroused approximately two weeks earlier than the first females, and the arousal of both sexes was correlated with soil temperature, with males appearing above ground when the soil temperature at 100 cm below the surface reached approximately 7°C and the females appearing when the soil temperature at the same depth reached approximately 9°C (Figure 13 and Table 8). In 1977, the animals aroused two weeks earlier than in 1978 and one week earlier than in 1979.

When males emerge from hibernation in the spring, the testes are barely scrotal (that is, they are not fully scrotal but are starting to descend). By the time the females emerge, males have scrotal testes. Some families have a perforate vagina at the time of emergence; after two weeks of activity, 100 percent of the females have a perforate vagina (Figure 14). The vast majority of the males born during the summer develop scrotal testes and most juvenile females do develop a perforate vagina, but no females were found to become pregnant in their juvenile year. It is not known if juvenile males can impregnate adult females. Figure 14 shows two peaks in the percent of females pregnant, corresponding to the production of two litters per year. The first litter starts to enter the trappable population in early July while a second burst of juveniles enters the trappable population in early to mid-August.

There were no major differences between years in the timing of entrance into hibernation (Figure 15). Adult males undergo weight gains in late August and are out of the trappable population by early September. Adult females and first-litter juveniles enter hibernation by mid to late September, while second-litter juveniles are the last to enter into hibernation, doing so in early to mid-October. In all

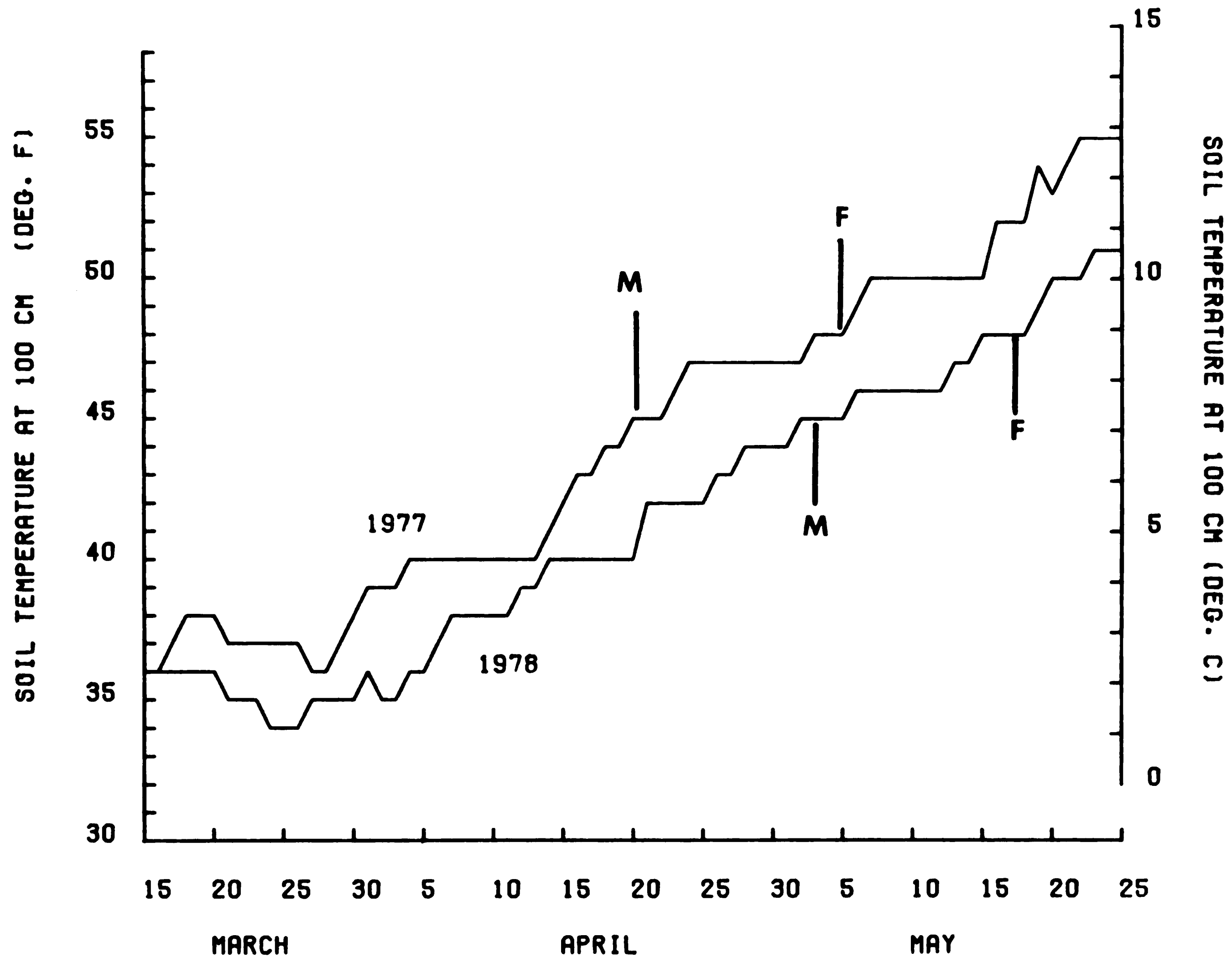


Figure 13. Relationship of soil temperature at 100 cm to arousal of males and females in 1977 and 1978. Arrows represent first appearance above ground by animals. M = males, F = females.

TABLE 8

Distribution of first captures in relation to soil temperature during the spring

Week	Year	Number of Animals	Soil Temperature at 100 cm (°C)
1	1977	5 male, 0 female	7.0
1	1978	3 male, 0 female	7.0
2	1977	5 male, 0 female	8.5
2	1978	8 male, 0 female	8.0
3	1977	1 male, 2 female	9.0
3	1978	3 male, 1 female	9.0
4	1977	1 male, 3 female	10.0
4	1978	2 male, 1 female	10.5
5	1977	0 male, 2 female	11.5
5*	1978	--	
6	1977	0 male, 4 female	13.0
6*	1978	--	

$\bar{x}$ arousal temperature for males 1977 = 8.04 ±1.01°C N=12
$\bar{x}$ arousal temperature for males 1978 = 8.31 ±1.06°C N=16

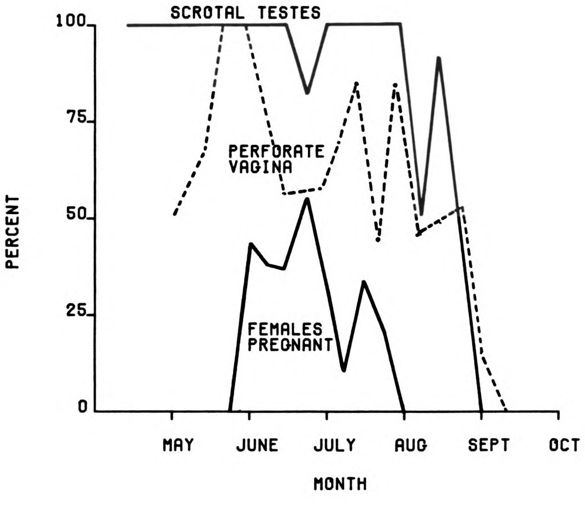
No significant difference between years for males
$P < 0.50$; $t = 0.68$; $df = 26$

$\bar{x}$ arousal temperature for females 1977 = 11.18 ±1.65°C N=11
$\bar{x}$ arousal temperature for females 1978 = 9.75 ±1.06°C N= 2

Significant difference with 1977 between males and females
$P < 0.001$; $t = 5.61$; $df = 21$

*Due to trap predation by raccoons, no animals were captured during weeks 5 and 6 of 1978.

Figure 14. Percentage of reproductive males and females and percent of pregnant females during 1977 trapping season. This graph represents a percentage of the total population (adults plus juveniles) because of the uncertainty in classifying juvenile animals.


SCROTAL TESTES
PERFORATE VAGINA
FEMALES PREGNANT
100
75
50
25
0
PERCENT
MAY
JUNE
JULY
AUG
SEPT
OCT
MONTH

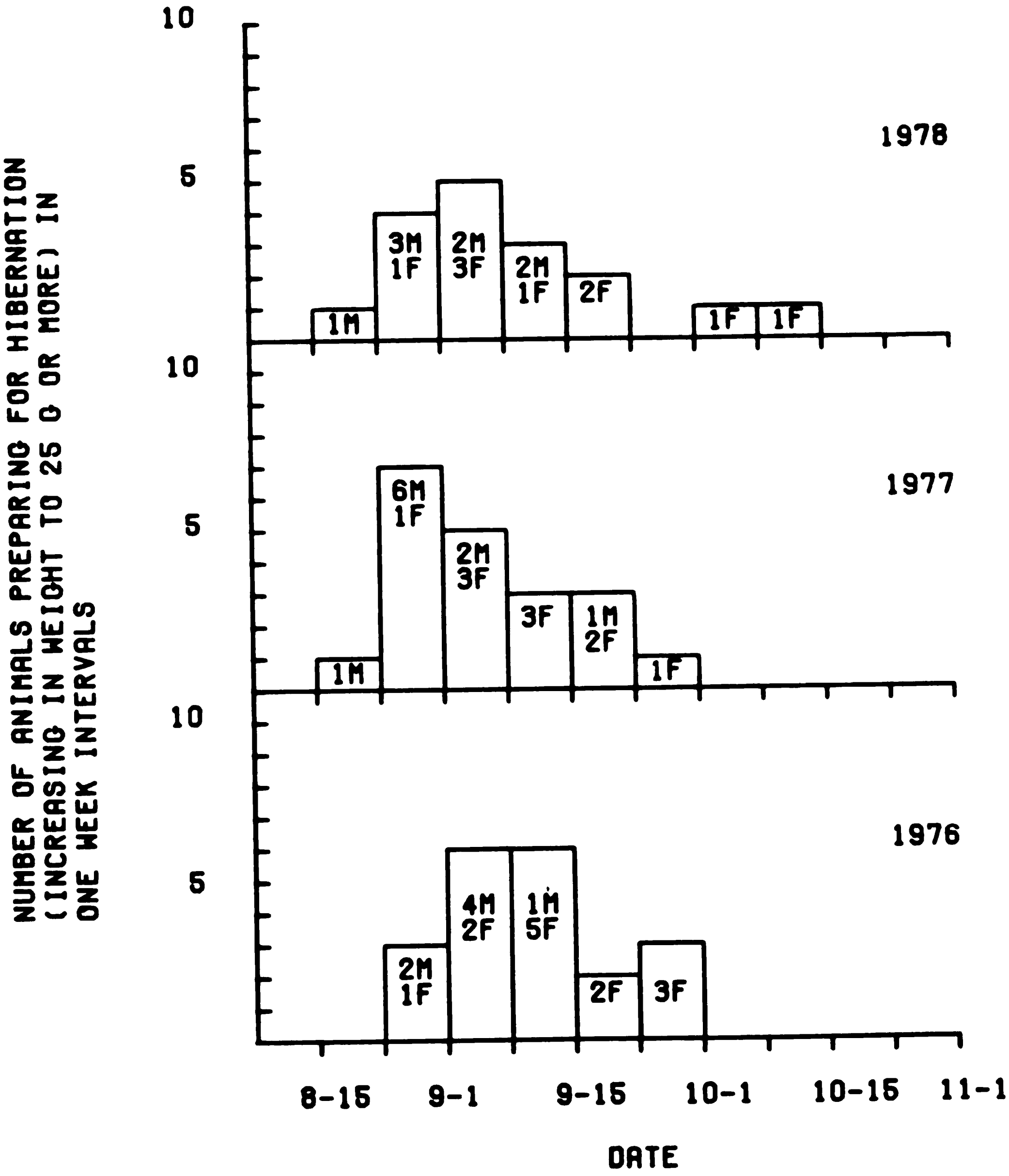


Figure 15. Distribution over time of preparation for hibernation in field animals. M = males, F = females.

three years during which fall trapping was conducted, all animals had entered hibernation by October 20.

The fact that the animals prepared for and entered into hibernation at the same time of year in all three years, but did not arouse at the same time every spring, indicates that the active interval is shorter in some years than in others. Specifically, the 1978 active interval was two weeks shorter than the 1977 active interval. The late arousal of animals in 1978 influenced the timing of the reproductive events occurring during the summer. In 1978, the movement of the second litter into the trappable population was approximately two to three weeks later than in 1977 (Figure 16). This means that the 1978 second-litter animals had two to three weeks less time to prepare for hibernation than the 1977 second-litter animals.

It was possible to obtain data on the hibernating-nonhibernating period length from four animals which were captured after undergoing weight increases in two consecutive years (Table 9). One animal (#20) was known to be a juvenile at its first hibernation. The other animals were not of known age. The important fact about these data is that the period length for all four animals is less than 365 days which indicates that these four animals underwent weight increases earlier their second year than their first. These animals did not demonstrate a rhythm under natural conditions which was exactly a year in length.

<u>Field Results: Survival</u>

If all animals, regardless of weight, first captured after July 1 are classified as juveniles (an overestimate, case 1), 16.6% of the 1977 juveniles and 10.1% of the 1978 juveniles survived to the

Figure 16. Minimum number of animals alive on demographic grid. 76 = 1976, 77 = 1977, 78 = 1978, 1 = entrance of second litter into trappable population in 1977, 2 = entrance of second litter into trappable population in 1978.

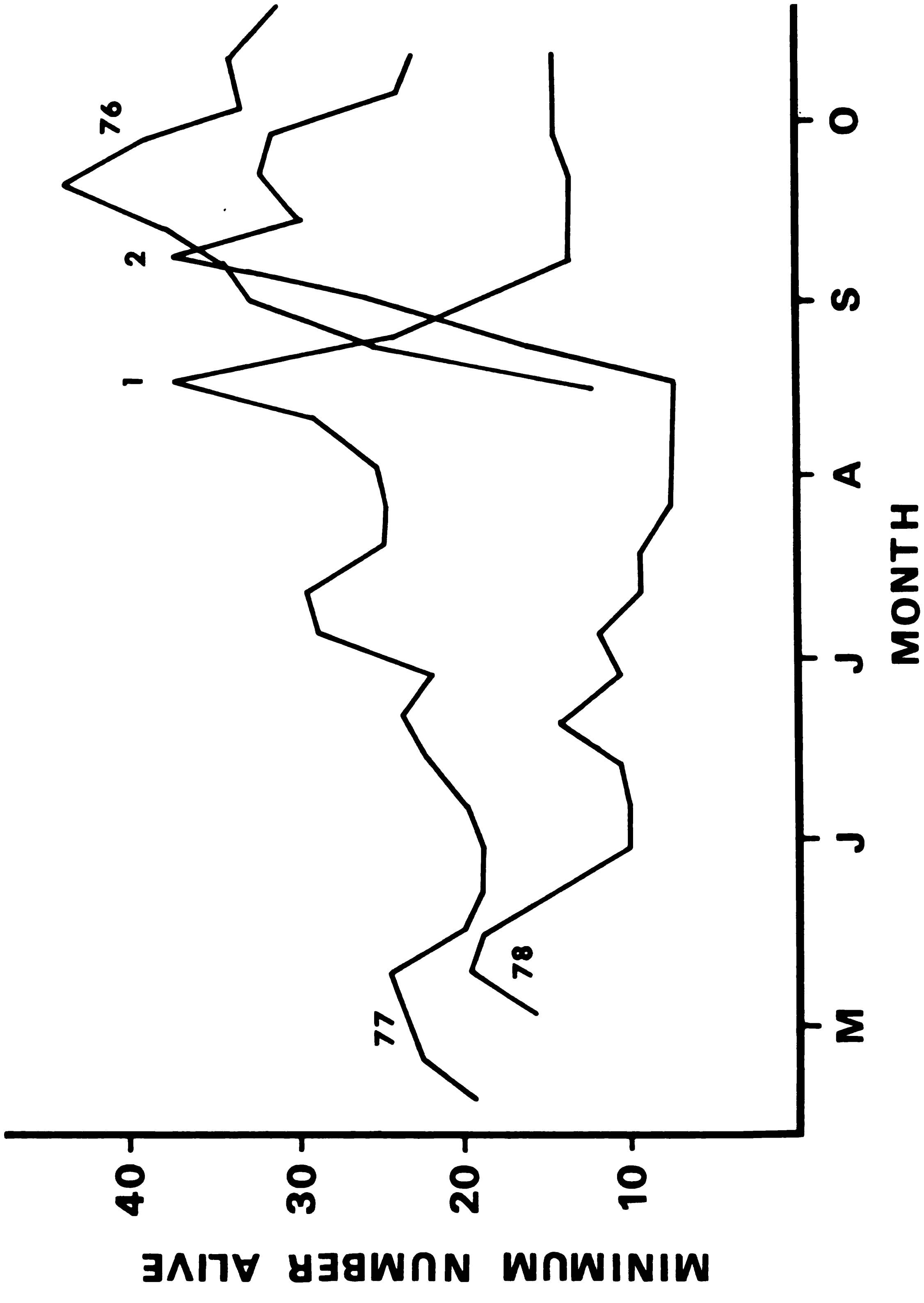

MINIMUM NUMBER ALIVE
40
30
20
10
MONTH
M
J
J
A
S
O
76
77
78
1
2

TABLE 9

Maximum weight to maximum weight period lengths for four animals captured after undergoing weight increases in two consecutive years

Animal No.	Maximum Weight to Maximum Weight	Period Length
# 13	September 9 (25.0 g) to August 24 (28.5 g)	349 days maximum
# 14	September 23 (25.0 g) to September 4 (27.0 g)	347 days maximum
# 20	September 30 (27.0 g) to September 4 (25.5 g)	340 days minimum
#130	September 24 (22.5 g) to September 8 (32.5 g)	349 days maximum

following spring. On the other hand, if only animals first captured at 15 g or less are regarded as juveniles (an underestimate, case 2), 12.5% of the 1977 juveniles and 15.6% of the 1978 juveniles survived to the following spring. The true percentage of juvenile survival most likely falls somewhere between these extremes (12.5 to 16.6% for 1977 and 10.1 to 15.6% for 1978).

Broken down into first-litter and second-litter survival rates (the first litter comprises those animals captured between July 1 and August 1, the second litter comprises those animals first caught between August 2 and the end of trapping), case 1 first-litter survival equals 14.2% for 1977 and 0.0% for 1978 as compared to case 2 survival of 22.2% for 1977 and 0.0% for 1978. The survivorship for 1978 first-litter animals is probably low because of trap predation by raccoons. Second-litter case 1 survival equals 18.7% for 1977 and 10.9% for 1978 as compared to case 2 survival of 0.0% for 1977 and 17.2% for 1978.

The low survival for 1977 second-litter animals (case 2) may be due to a small sample size (8). In this case, the case 1 survival rate may be closer to reality. The case 1 survival rate for second-litter animals indicates that the shorter active interval for 1978 may have had the effect of decreasing juvenile survival over the winter; however, the case 2 estimates show the opposite result. More data need to be collected on this aspect of differential mortality before any definite conclusion can be demonstrated.

If a juvenile born in a given year survives the winter to become a breeding adult, it will have a 28.5% chance of surviving through a second hibernation interval and a 8.5% chance of surviving through a third hibernation interval. These statistics are based on 35 animals known to be adults in the spring of 1977. Ten of these animals survived to 1978 and three survived to 1979.

DISCUSSION

The results indicate that an exogenous factor, photoperiod, is very important in controlling the timing of preparation for and entrance into hibernation in *Zapus hudsonius*. In fact, clock-shifted naturally decreasing daylengths can initiate a body weight gain and hibernation response similar to that seen in nature. Ambient temperature, on the other hand, had no effect on preparation and entrance into hibernation, but soil temperature is correlated with arousal from hibernation in the spring.

The following scenario is then proposed for *Zapus hudsonius*. The long daylengths of spring and summer stimulate reproduction which continues through mid-August. Beginning in late August, the decreasing daylengths begin to stimulate animals to prepare for and enter into hibernation and this continues through mid to late October. Hibernation then continues until mid-April to early May depending upon the level of the soil temperature around the hibernacula. When the soil temperature increases to a certain level, the animals emerge from their hibernacula and become active for the summer. Therefore, it appears that two factors are important in the yearly cycle of *Zapus hudsonius*. Photoperiod signals the end of the active interval and, possibly, soil temperature signals the end of the hibernation interval. I will first take up the issue of photoperiod and then come back to discuss the role of temperature later in the paper.

Photoperiod

It is possible that photoperiod has its effect upon this species in one of two ways. Either daylength acts as a Zeitgeber and provides information concerning time of year that entrains an endogenous self-sustaining oscillator or daylength stimulates preparation for and entrance into hibernation in the absence of any endogenous rhythm. In the following sections, I will explore both of these possibilities by examining hypotheses generated by different researchers (Mrosovsky, 1977, 1978; Pengelley and Fisher, 1957; Sansum and King, 1976).

Presence of an Endogenous Circannual Rhythm

The results indicate that no rhythmicities were present under T.C. LW and most likely that no rhythmicities would have been demonstrated under T.C. LC. In addition, temperature independence was not a property of the rhythms that did appear in the two short light cycle T.C.'s. Although the period of the rhythms under T.C. SC could be termed circannual, that under T.C. SW could not.

These factors reject the hypothesis that an endogenous circannual rhythm of the type described by Pengelley and Fisher (1957) for *Spermophilus lateralis* is present in *Zapus hudsonius*. However, the possibility still exists that *Zapus hudsonius* possesses an endogenous circannual rhythm which is expressed only under certain environmental conditions.

This concept of rhythm nonexpression has a firm basis in circadian rhythm research. For example, electroshock of a rat will totally eliminate the locomotor rhythm for a certain time interval but when the animal regains its locomotor ability, the rhythm reappears in phase as though no perturbation had occurred (Richter, 1965). This indicates that some measuring process was present even though the observable expression of the rhythm was eliminated.

The presence of circannual rhythms under certain conditions but not others occurs in many species. For example, deer demonstrate circannual cycles in antler growth under LD 6:18 or 18:6 but not under LD 12:12 (Goss, 1976), and starlings show circannual cycles in testicular growth under LD 12:12 but not under LD 11:13 or 13:11 (Schwab, 1971). In addition, other experiments demonstrating circannual cycles in birds for body weight, molt, gonad size, and locomotor activity usually have used the photoperiod LD 12:12 (Gwinner, 1971; Lofts, 1971). Pocket mice (Perognathus longimembris) show circannual cycles in above-ground activity under LD 12:12, 16°C but not LD 12:12, 31°C, LD 9:15, 18°C, LD 15:9, 18°C, or LD 9:15, 8°C (French, 1977).

As yet it has not been shown that the results presented by the authors mentioned above are analogous to the rhythm nonexpression concept seen in circadian rhythms. However, rhythm nonexpression does remain a viable hypothesis and one that cannot be refuted by the data that have been presented. In fact, the preparation for and entrance into hibernation of one individual in T.C. LW and the early preparation and entrance of two individuals in the decreasing daylength experiment lend some support to this hypothesis. It is possible that some individuals have narrower limits of envirionmental conditions within which the rhythm can be expressed than others. For example, if a population of animals is considered to represent a normal (bell-shaped) curve with respect to their capacity for exhibiting a rhythm under different photoperiods, one would expect to see fewer and fewer animals demonstrating rhythms the further the photoperiod deviated from some optimal photoperiod level. Some evidence suggests that LD 12:12 may be the optimal photoperiod (French, 1977; Gwinner, 1971; Lofts, 1964; Schwab, 1971). At some level of daylength, all of the animals would exceed their limits of rhythm expression and a particular experiment would record the absence of any rhythmicity. The three animals that prepared for and entered hibernation in the long daylength and decreasing daylength T.C. would have wider limits of rhythm expression than the majority of animals, but LD 15.33:8.67 would not have exceeded their limits of expression.

Other Types of Endogenous Clocks

In Zapus hudsonius, the rhythms in body weight and hibernation exhibited under T.C. SW are not circannual, but the possibility still exists that they are endogenous. In this case, the body weight and hibernation rhythms would not be temperature independent, since they were shorter at 20°C than at 5°C.

Mrosovsky (1977) feels that one mechanism for the production of a temperature dependent rhythm such as that seen in Zapus hudsonius would be an internal oscillator that is very sensitive to body temperature (T_b). If the period of the oscillation has been lengthened by a lowering of T_b, the natural period of the rhythm must be less than or equal to the shortest cycle at the highest T_b achieved during hibernation. An alternate hypothesis put forward by Mrosovsky (1977) is that temperature only affects the expression of the rhythm. When animals are at higher T_b's, cycles of shorter length are expressed and when the animals are at lower T_b's, longer cycles are expressed.

A proposed example of an endogenous, temperature dependent rhythm is discussed by Mrosovsky (1977) for the dormouse (Glis glis). In Mrosovsky's study, dormice held under LD 12:12, 20°C had a mean body weight cycle length of 53 days while animals held under LD 12:12, 5°C had a mean body weight cycle length of 162 days. Mrosovsky (personal communication) also states that dormice show cycles of similar lengths under LD 6:18, LD 18:6, and natural photoperiod.

Although Zapus hudsonius does not respond identically to Glis glis in detail under all experimental conditions, the response of Z. hudsonius and G. glis are similar under LD 12:12, 20 and 5°C. This demonstrates that Z. hudsonius fits the general concept of Mrosovsky (1977) but differs in detail from G. glis. Conceptually, it may be possible that temperature dependent rhythms are present in Z. hudsonius under LD 15.33:8.67, 20 and 5°C, but not expressed. If this is the case, both Mrosovsky's concept and the rhythm nonexpression concept could be involved.

If an exogenous stimulus (such as photoperiod) is capable of setting in motion a series of physiological events inside the animal which run for one year, the animal could prepare for and enter into hibernation in successive years at the correct time provided the stimulus was present. This corresponds to an hour-glass timer (Bünning, 1973), which is capable of providing the animal with a clock, but it is not exactly an endogenous rhythm in that no rhythm could be demonstrated without the exogenous stimulus. This could be the method by which Z. hudsonius measures time over the hibernation and active interval. In the particular case of Z. hudsonius, the decreasing daylengths of late summer and fall could provide the exogenous stimulus that would initiate the hour-glass timer. The hibernation interval and active interval could be coupled to one another and their lengths governed by physiological processes. For example, the active interval length could be determined by the physiological processes of sperm/egg production and breeding while the hibernation interval length could be determined by hormonal influences (see synthesis section).

Mrosovsky (1978) has postulated that the yearly cycle of hibernation in the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) may be controlled by an hour-glass timer which is reset by warm temperatures. Mrosovsky bases his postulate on the fact that a high percentage of the animals maintained in a cold room did not show persistent cycles but became stuck in the reproductive phase after the first hibernation interval. Mrosovsky theorized that warm temperatures may be needed to reset the hour-glass timer so that another hibernation interval could follow. The fact that circannual cycles may tend to be shown by more animals in a warm environment (Mrosovsky, 1978) lends some support to the hour-glass hypothesis.

Several meadow jumping mice responded to LD 12:12, 5°C in a manner similar to *Spermophilus tridecemlineatus* under similar conditions (Figure 8, animals 75 and 95; Figure 9, animals 87 and 110). These four animals became arrested in the reproductive state and did not enter into a second hibernation interval. However, a number of animals did not become arrested in the reproductive state and were able either to enter into a second hibernation interval or go through a second weight gain and loss. Therefore, although some meadow jumping mice behave like *S. tridecemlineatus* under LD 12:12, 5°C, the data are not strong enough to draw a firm conclusion about the possibility of an hour-glass timer being present in Z. hudsonius.

Endogenous Rhythms Not Present

It is possible that the rhythms demonstrated in Z. hudsonius under constant conditions are not endogenous but are in fact forced upon the animals by the particular photoperiod chosen for the experiment (LD 12:12). This particular photoperiod is viewed by Sansum and King (1976) as being short enough to break the photorefractory state in an animal but still long enough to provide photostimulation once the animal becomes photosensitive. The alternate states of photosensitivity and photorefractoriness would then be expressed creating a rhythm.

The major assumption behind this hypothesis is that there is no endogenous oscillator present under conditions when a rhythm is expressed, and underlying nonexpressed rhythms are not present under other experimental conditions. The rhythm produced is totally a result of the experimental conditions perceived by the animal. In Z. hudsonius, the demonstration of rhythms under LD 12:12 and not LD 15.33:8.67 does fit this theory.

One important fact about the cycles present in Z. hudsonius under LD 12:12 that is different from other species is that although the hibernation intervals are not the same length at the two experimental temperatures, the active intervals are. This might be expected if the active interval must run for a certain time once it has been initiated. This would happen if it takes a set amount of time to allow for gonadal growth and sperm/egg production to begin so the animal is capable of breeding. The hibernation interval would still be dependent upon body temperature, leading to cycles of different lengths.

The equality of the active interval lengths under 5 and 20°C for Z. hudsonius is different from a species such as S. lateralis which demonstrates a circannual rhythm as described by Pengelley and Fisher (1957). In this species, the active interval is much longer at the higher temperatures to compensate for the shorter hibernation interval (Pengelley and Asmundson, 1969).

Synthesis

I do not believe that it is possible, with the data that I have presented, to distinguish clearly between the hypothesis of rhythm non-expression, other types of endogenous clocks, or no endogenous rhythm being present. However, I have shown that individual meadow jumping mice do respond to clock-shifted decreasing daylengths by preparing for and entering hibernation. Therefore, daylength must be considered as a sufficient exogenous cue capable of stimulating the preparation and initiation of hibernation in Z. hudsonius at the appropriate time of the year.

The action of daylength on the animal may be mediated through the pineal gland. In the pineal gland, stimuli from the eyes conveyed via the optic nerve and superior cervical ganglion cause a decrease in the production and release of melatonin which lessens the inhibition on certain physiological events (Wurtman and Axelrod, 1965). Since the production of melatonin occurs during the dark phase of the 24-h cycle (light inhibits synthesis and release), shorter days in the late summer and fall would mean a greater amount of melatonin production. It may

be that there is a threshold for melatonin accumulation in the body, and when that threshold is surpassed, certain changes such as gonadal regression occur. Reiter (1969, 1973) has contended that one of the most important functions of the pineal gland may be to control seasonal reproductive rhythms in photosensitive animals. However, less is known about the effect of the pineal upon hibernation. Spafford and Pengelley (1971) reported that the inhibition of synthesis of serotonin (the precursor or melatonin) disrupted hibernation, and Palmer and Riedesel (1976) demonstrated that daily subcutaneous injections of melatonin resulted in an increase in the incidence and duration of hibernation. However, the work by these two sets of authors was conducted on the golden-mantled ground squirrel, *Spermophilus lateralis*, a species which does not exhibit a photoperiodic response. Injections of melatonin into a photoperiodic species such as *Z. hudsonius* when individuals are held under long daylengths would be instructive.

Temperature

Although soil temperature is correlated with spring arousal of the field population, it was noted in the laboratory experiments that animals did arouse without any change in ambient temperature. There are two possible explanations for this. First, there may be a lower threshold for energy reserves below which the animals cannot remain in hibernation. When an individual reaches a certain energy reserve, arousal might take place. Secondly, the pineal gland may play a role in arousal. The gonads of hibernating mammals undergo spontaneous recrudescence after about 25 to 30 weeks in complete darkness (Hoffman *et al.*, 1965; Popovic, 1960; Reiter, 1972). Since gonadal involution is brought about via the pineal gland (Cusick and Cole, 1959; Hoffman and Reiter, 1965; Hoffman et al., 1965), it is possible that the gonads become refractory to pineal influence or that the pineal gland becomes exhausted and is no longer capable of maintaining gonadal involution after 25 to 30 weeks of complete darkness (Reiter, 1972). Since gonadal regression seems to be a prerequisite for hibernation, recrudescence of the gonads late in the hibernation interval may cause endocrine changes that can terminate hibernation. Soil temperature may just have a fine tuning effect on the date of arousal, allowing slight modulation (one to two weeks) according to above-ground environmental conditions.

Evolution

Hibernation has been observed in species of mammals comprising many different orders and families. Attempts to study the evolution of this phenomenon have been hampered because hibernation seems to be a well controlled and complicated physiological phenomenon yet it is distributed among mammals that are often considered to be primitive (Hudson, 1973). Additional problems arise in attempting to obtain a holistic view of the factors affecting hibernation because researchers have studied the problem of timing of preparation and entrance into hibernation under a wide variety of experimental conditions. Some researchers attacked the problem by attempting to determine the presence or absence of an endogenous rhythm while others bypassed the rhythm concept and only sought to find exogenous factors capable of stimulating hibernation.

However, it appears that at least one unifying concept does come through this vast literature on hibernation. Some animals have been found to possess an endogenous rhythm which is very resistant to influence by exogenous factors while other species, whether they have been found to possess an endogenous rhythm or not, are more easily influenced by exogenous stimuli.

Much of the early work done on hibernators concerning factors capable of stimulating hibernation was confined to the rodent Family Sciuridae (the squirrel family). It has been demonstrated that endogenous circannual rhythms which are resistant to influence by exogenous factors are present in Spermophilus lateralis (Pengelley and Fisher, 1957), Tamius striatus (Scott and Fisher, 1972), and Marmota monax (Davis, 1967). It has also been demonstrated that rhythms close to circannual or circannual but differing in detail from S. lateralis (e.g., a lower percentage of animals demonstrate the rhythms) are present in Spermophilus richardsonii and Spermophilus columbianus (Scott and Fisher, 1970), and Spermophilus variegatus, Spermophilus beechevi, Spermophilus mohavensis and Spermophilus tereticaudus (Pengelley and Kelly, 1966). Spermophilus beldingi shows a circannual cycle in reproductive condition at LD 12:12, 16°C, but hibernation does not occur at that temperature (Heller and Paulson, 1970).

Therefore, it appears that endogenous circannual cycles are widely distributed within the hibernators in the Family Sciuridae although there may be some exceptions. For example, it appears that temperature may be an important exogenous factor capable of initiating an hourglass timing mechanism in Spermophilus tridecemlineatus (Mrosovsky, 1978). Also, Spermophilus undulatus may respond to photoperiod

(Drescher, 1967), but more work needs to be done with both of these species before a circannual rhythm can be ruled out.

Endogenous circannual rhythms have also been reported for hibernators not in the squirrel family. The European hamster, Cricetus cricetus (Family Cricetidae), has demonstrated circannual cycles under LD 12:12, 20°C and possibly at LD 12:12, 7°C. Several animals demonstrated circannual cycles under constant light at 7°C (Canguilhem et al., 1973). The hedgehog, Erinaceus europaeus (Order Insectivora, Family Erinicidae), is cited as showing a circannual rhythm in body weight and hibernation (Kristoffersson and Suomalainen, 1964), but the lighting conditions were not constant as light also entered the animal room through a window (Mrosovsky, 1978). This sheds some doubt on the presence of an endogenous rhythm. In addition, the garden dormouse, Eliomys quercinus (Daan, 1973), and the pocket mouse, Perognathus longimembris (French, 1977), are reported to show circannual cycles in torpor. However, the data on the garden dormouse make a firm statement about circannual rhythmicity tenuous because different populations respond differently to similar experimental conditions, and pocket mice show circannual cycles only under a limited range of photoperiod and temperature conditions, which also sheds some doubt on the observed rhythms being endogenous.

It seems, then, that firmly demonstrated endogenous circannual cycles in body weight and hibernation which are resistant to exogenous influence are, with some possible exceptions (such as Cricetus cricetus), probably limited to the Family Sciuridae (Order Rodentia). Outside of this family, it appears that exogenous factors are usually more important than endogenous factors. For example, Cranford (1978) demonstrated that an endogenous cycle is not present in Zapus princeps (Family Zapodidae), and I have shown in this paper that it is possible that an endogenous cycle is not present in Zapus hudsonius (a different hypothesis can account for the appearance of cycles). Also, photoperiod plays a very important role as an exogenous factor in Z. hudsonius. In addition, golden hamsters (Mesocricetus auratus, Family Cricetidae) are photoperiodic and do not demonstrate circannual cycles (Reiter, 1973), and Peromyscus leucopus (Family Cricetidae), a species capable of daily torpor, has been shown to be photoperiodic although the possibility of an endogenous rhythm has not been looked at (Lynch et al., 1978). Therefore, it appears that the majority of the species examined which are not sciurid rodents rely on exogenous cues and have not evolved an endogenous rhythm that is impervious to a wide variety of exogenous factors.

It also appears that the perception of cueing factors has evolved to meet the requirements of particular species. For example, although Zapus hudsonius and Zapus princeps are very closely related, they use different external cues to stimulate the preparation and initiation of hibernation. In this study, Z. hudsonius responded to photoperiod while in the study by Cranford (1978), Z. princeps was found not to rely on photoperiod but rather on seed availability. This difference is probably related to the habitats these species occupy. In Michigan, Z. hudsonius inhabits prairie meadows, and the animals are active above ground for approximately five months of the year. Z. princeps, on the other hand, inhabits mountain meadows with shorter summers and is active above ground for approximately 3.5 to four months (Cranford, 1978). In the habitat of Z. princeps, seeds do not become available in the diet until about 50 days after arousal (Cranford, 1977). In late years of arousal and plant growth, if the animals were cueing on daylength and always entered hibernation at the same time, they might not have enough time to gain the necessary weight to maintain themselves over the winter. Cueing in on seed availability allows the animals to gain weight when the food supply is most favorable. Meadow jumping mice, on the other hand, do not experience such a limited active interval and the availability of the seed resource seems to be spread over more of the active interval. The intense burst of seed availability does not seem to be present for Z. hudsonius, and therefore, daylength is a more reliable character.

The question then arises, why may some animals not exhibit endogenous circannual rhythms when they occupy the same habitat as some species that do use these rhythms? For example, Z. hudsonius relies heavily on exogenous cues while the woodchuck, Marmota monax, which lives in the same area, has a well demonstrated endogenous circannual rhythm and is very insensitive to exogenous stimuli (Davis, 1976; Mrosovsky, 1978). I believe that an important factor in the evolution of an endogenous circannual rhythm is the life span of the animals involved. In this study, I demonstrated that a very low percentage of the meadow jumping mice survived long enough to enter into hibernation in three consecutive years. On the other hand, it has been demonstrated by two groups of researchers (Armitage and Downhower, 1974; Michener and Michener, 1977) that in some species of sciurid rodents (Marmota flaviventris and Spermophilus richardsonii), a greater proportion of the population may survive through three or more hibernation intervals. For example, Armitage and Downhower (1974) calculated l_x values of

0.215 for 2-3 year old, 0.161 for 3-4 year old, and 0.121 for 4-5 year old female yellow-bellied marmots, Marmota flaviventris.

In most of the hibernating species that have been studied (examples: Carl, 1971; Michener and Michener, 1977; Quimby, 1951), the juveniles born in any given year enter into hibernation after the adults. The following year, these same animals then enter into hibernation on an earlier date than the previous year as I have shown for Zapus hudsonius. Only in preparing for and entering into hibernation in the third year would wild animals come very close to showing an interval of 365 days between one hibernation interval and the next. This would then continue for subsequent years. Endogenous circannual rhythms may not be advantageous for a species in which very few individuals survive to enter into three hibernation intervals because very few animals survive to the point where they would be undergoing preparation for and entrance into hibernation at the same time in two consecutive years. On the other hand, some of the sciurid rodents mentioned above would survive long enough to show a pattern closer to a year in length. In this case, possessing an endogenous circannual rhythm may be more advantageous than relying more heavily on certain exogenous cues. However, the particular advantage (if any) is not known. In general, endogenous rhythms are thought to be adaptive if for some reason an event must take place at a time that is not marked by an obvious environmental reference point (Menaker, 1974). This does not follow for circannual cycles such as hibernation because photoperiod is a clear and accessible environmental cue.

A second reason why this dichotomy in endogenous and exogenous rhythms is present may be the polyphyletic origin of hibernation.

(However, it should be noted that hibernation has been considered to be a monophyletic, residual trait in primitive mammals, e.g., Cade, 1964.) If an endogenous rhythm was present in the basal group of a lineage, one might expect to observe this rhythm in the more recently derived species. As an example, the genera Tamius and Eutamius are proposed as the basal group for the Family Sciuridae (Black, 1963). Therefore, endogenous circannual rhythms in the Family Sciuridae seem logical because they are reported to be present in the genus Eutamius (Heller and Paulson, 1970). On the other hand, endogenous circannual rhythms may not have been present in the basal groups of some other families which contain hibernators, and therefore, exogenous factors have a more important role.

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