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THE CIRCANNUAL CYCLE OF RICHARDSON’S GROUND SQUIRRELS IN SOUTHERN ALBERTA

GAIL R. MICHENER

ABSTRACT.—Times of spring emergence and autumn immersgence were determined for Richardson's ground squirrels (Spermophilus richardsonii) in southern Alberta from 1975 to 1978. Spring emergence of females was synchronous and was not affected by their age, reproductive success in the previous year, or time of autumn immersgence. Time of spring emergence correlated with climatic conditions, in particular with warming of the shallow layers of soil. Time of autumn immersgence was asynchronous, even within the same age and sex class, and was affected by the condition of the animal. Factors affecting fattening, and hence immersgence, included age and sex of the squirrel, its reproductive success that year, and the availability of food. Synchrony was reestablished in the following spring, suggesting that emergence is the point in the annual cycle at which entrainment occurs.

Circannual rhythms enable animals to prepare for future environmental events, such as seasonal changes in food availability and weather conditions, that occur in a predictable sequence. Some mammals hibernate and thus avoid surface activity during autumn and winter when the energy requirements of homeothermy are high but food availability and quality are low. Such mammals, when maintained in a constant environment, exhibit a free-running circannual rhythmicity of activity and of fat deposition and utilization, the length of which is typically less than 365 days (Pengelley and Asmundson, 1969; Scott and Fisher, 1970; Blake, 1972; Davis, 1976). The rhythm of field animals must be synchronized periodically with environmental conditions to avoid discrepancies between the endogenous rhythm and existing conditions. Heller and Poulsen (1970) suggested that circannual rhythms can be synchronized only at the onset of the active season when animals attain breeding competence. The timing of this commitment point may vary between years depending on spring conditions, indicating year-to-year flexibility in the phasing of the rhythm.

Several recent studies (Morton, 1975; Bronson, 1976; French, 1977; Knopf and Balph, 1977; Michener, 1977a, 1978; Cranford, 1978; Yahner and Svendsen, 1978) indicate that spring emergence of hibernating mammals correlates with air or soil temperatures, and that timing of autumn immersgence into hibernation is dependent on the extent of fat deposition and food caching, which, in turn, depends on food quality and availability and on age, sex, and parity of the individual. This study provides a 4-year comparison of the timing of events in the circannual rhythm of Richardson's ground squirrels (Spermophilus richardsonii) in southern Alberta, and considers the adaptive significance of flexibility in the rhythm.

METHODS

The study area was located on flat, fescue grassland in Fire Guard Coulee (50°34′N, 114°18′W, elevation 1,235 m), 5.5 km NW Longview, Alberta. In the springs of 1975, 1976, 1977, and 1978, squirrels were live-trapped at 1-to-6-day intervals on a 3-ha area, which consisted of a main area of 1 ha (under intensive behavioral observation in 1975) and an adjacent area of 2 ha. Techniques on trapping and marking were described by Michener (1977a). At each capture squirrels were weighed to the nearest 10 g and their reproductive condition was noted. In 1978 vaginal smears were collected and stained (Shorr, 1941). In 1975, 1976, and 1977 trapping and observation of squirrels on the main area continued at approximately weekly intervals throughout the summer, until all squirrels had hibernated. In 1978 data collection continued until May.

The trapping data provided information on timing of emergence of adults in spring, and the observation data provided information on the date of spring emergence from hibernation, date
of parturition, date of litter emergence, and date of entry into hibernation for each female and her offspring resident on the main area. The initial estimate of the date of spring emergence, taken as the mid-point of the interval between the last trapping date on which the female was not present and the subsequent date on which she was present, was further refined by back-dating from the time of estrus and/or parturition. Females were assumed to have emerged 2 days prior to the date on which the vaginal smear consisted of cornified epithelium and 26 days before parturition (Michener, 1977b). The date of parturition was estimated to within ±1 day by noting the extent of uterine swelling and condition of the nipples.

During the expected time of litter emergence (about 30 days after birth, Michener, 1977b) the area was checked at 1-to-6-day intervals. Litters were assumed to have emerged on the mid-point date of the interval in which the juveniles first appeared.

The date on which an animal left the active population was taken as the mid-point of the interval between its last sighting for the year and the subsequent day of observation. This date is referred to as the date of entry into hibernation and is used in the ecological sense that it marks the end of the active phase and the beginning of the hibernation phase of the annual cycle.

Because some animals were lost to predation or dispersal during the summer I had to make a judgement as to whether an animal had actually gone underground or had disappeared due to other causes. Only for squirrels that were recovered in the subsequent spring was there positive evidence that disappearance was due to hibernation. For animals that were not recovered the following year a guideline was used: if disappearance occurred during the same period that a recovered animal had disappeared the squirrel was assumed to have hibernated on the area, if disappearance occurred earlier than that of any recovered animal, disappearance was attributed to other causes.

Environment Canada provided climatological data for the station at High River (50°29‘N, 114°10‘W, elevation 1,152 m), 30 km E of the study area, and soil temperature data for the University of Calgary station 55 km N of the study area.

RESULTS

The total numbers of adults captured each spring were: 54 females and 14 males in 1975, 57 females and 16 males in 1976, 41 females and 23 males in 1977, and 28 females and 18 males in 1978. In the latter 2 years trapping commenced earlier than in 1975 and 1976, and a number of males caught early in the season were not recaptured subsequently. The effective sex ratios at the time of mating, determined by counting only those squirrels that were recaptured after females began appearing in spring, were 3.9, 3.6, 3.5, and 2.4 females per male in 1975, 1976, 1977, and 1978, respectively.

Each year, males emerged before females and initially accounted for the majority of squirrels active above-ground. Once females began emerging they soon constituted 80% of the population in each year. From the trapping data the following dates were obtained, by extrapolation and interpolation when necessary: date on which females first began emerging, date on which half the females had emerged, and date on which all females had emerged into the above-ground population (Table 1). The emergence pattern in 1975 differed from that of the subsequent 3 years in that emergence of both males and females was delayed until mid-April and all females appeared above ground within a short period. Each year the earliest emerging females were located along a shallow south-facing ridge; females resident on the main area appeared a few days later and with greater synchrony (Table 1).

Late emergence of squirrels in 1975 was associated with a long, cold winter and late spring conditions (Fig. 1). In 1975 the break in daily maximum air temperatures from 0°C to 10°C did not occur until 11 April, whereas in 1976, 1977, and 1978 spring temperatures of 10°C were first attained on 16 March, 3 April, and 25 March, respectively. During the period in which all females emerged, daily maximum air temperatures (±SD) averaged 8.0 ± 3.7°C, 10.3 ± 5.2°C, 8.0 ± 6.7°C, and 8.9 ± 5.6°C in 1975, 1976, 1977, and 1978, respectively.
TABLE 1.—Timing of female emergence from hibernation and of spring warming of the soil.

<table>
<thead>
<tr>
<th>Year</th>
<th>&gt;0%</th>
<th>50%</th>
<th>100%</th>
<th>Total area</th>
<th>Main area</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>14 April</td>
<td>16 April</td>
<td>20 April</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>1976</td>
<td>16 March</td>
<td>28 March</td>
<td>7 April</td>
<td>23</td>
<td>10</td>
</tr>
<tr>
<td>1977</td>
<td>22 March</td>
<td>30 March</td>
<td>6 April</td>
<td>16</td>
<td>10</td>
</tr>
<tr>
<td>1978</td>
<td>22 March</td>
<td>26 March</td>
<td>1 April</td>
<td>11</td>
<td>6</td>
</tr>
</tbody>
</table>

First day soil temperature above 0°C

<table>
<thead>
<tr>
<th>Year</th>
<th>Morning</th>
<th>Afternoon</th>
<th>At 1 m depth</th>
<th>Date of soil temperature turnover*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>19 April</td>
<td>13 April</td>
<td>12 May</td>
<td>22 April</td>
</tr>
<tr>
<td>1976</td>
<td>5 April</td>
<td>21 March</td>
<td>5 April</td>
<td>31 March</td>
</tr>
<tr>
<td>1977</td>
<td>6 April</td>
<td>3 April</td>
<td>4 March²</td>
<td>9 April</td>
</tr>
<tr>
<td>1978</td>
<td>30 March</td>
<td>24 March</td>
<td>8 May</td>
<td>3 April</td>
</tr>
</tbody>
</table>

* Date on which all layers of soil above 1 m were at or above the temperature of the 1 m layer; ‡ Temperature then remained at 1°C until 12 April.

Because squirrels hibernated underground it was probable that they were responding to changes in soil temperature rather than air temperature. In each year average temperatures of shallow soil were above 0°C during the period of female emergence compared with sub-0°C temperatures preceding emergence. The first females appeared at about the time afternoon warming of the shallow soil layers began, and the date by which all females had appeared above ground coincided with the date on which shallow soil temperatures were first above 0°C in the morning (Table 1). Emergence did not correlate closely with the time of soil warming at 1 m depth (Fig. 1).

Accurate data on the timing of the emergence of the first males and on the period over which males emerged were not obtained because most males were already active when trapping commenced in 1975, 1976, and 1977. In 1978 males first appeared between 5 and 19 March. The earlier spring emergence of males with respect to females in all years meant that males commenced activity aboveground when maximum air temperatures averaged between 0 and 5°C and at least 2 weeks before soil temperatures began increasing.

The timings of parturition and of juvenile emergence from the natal burrow were directly related to timing of female emergence from hibernation, occurring about 26 and 56 days, respectively, after female emergence (Michener, 1977b), and so these events occurred later in 1975 than in the other 3 years (Fig. 1). Timing of postreproductive events, however, was influenced by factors additional to the time of spring emergence. In each year females that did not produce litters or that lost their litters during lactation fattened and immersed before the successful reproducers, having an active season of 92 ± 10 days (n = 8). Another factor affecting time of immurgence was age. Female immurgence commenced earlier in 1977 than in 1975, in accordance with the difference in spring emergence dates, but some females remained active into September of 1977 whereas none had in the previous years (Fig. 1); these late immerging females were all at least 3 years old and were unable to gain weight post lactation (Michener, 1978). Inclement weather also delayed entry into hibernation. The average number of days that females and their juveniles were active was 3 weeks longer in 1976 than in 1975 or 1977 (Table 2). Mid-summer was marked by above average rainfalls. The 29-year average rainfall in July and August is 107 mm, but in 1976 there were 201 mm of precipitation in these 2 months, of which 154 mm fell on 13 days in the 2-week period from 28 July to 10 August. Of 23 juveniles that were weighed before (20 July) and after (11 August) the rainy period, 17 lost an average of
Fig. 1.—Average daily maximum air temperature (calculated as a 15-day running average, plotted at weekly intervals; open circles) and average daily soil temperature (averaged and plotted at weekly intervals; solid circles) from January 1975 to May 1978. Solid bars indicate time period of spring emergence of adult females (E), parturition (P), emergence of juveniles from the natal burrow (JE), and immersgence of adult females (I) for squirrels resident on the main area. Guidelines are given through 1 April and 1 August for all years.

23 g (SD = 9). Most regained the lost weight by 28 August. Three juveniles maintained weight and three gained 10 to 20 g each. Two of the mothers weighed before and after the rainy period lost 40 g and 60 g. The late immersgence of females and their juveniles in 1976 was apparently related to weather conditions unfavorable for feeding, and hence for weight gain.

Because the time of spring emergence was not known for individual males I could not estimate the number of days that males on the main area were active in each year. However, estimates of their dates of entry into hibernation were made. Three males present in 1975 disappeared on 26 July, 28 July, and 3 August; three males present
TABLE 2.—Average ($\pm$SD) length of the active season in days from spring emergence (adults) or birth (juveniles) to autumn immersgence for squirrels resident on the main area. Sample size in parentheses.

<table>
<thead>
<tr>
<th>Year</th>
<th>Adult females</th>
<th>Juvenile females</th>
<th>Juvenile males</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>111 ± 15 (9)</td>
<td>126 ± 5 (7)</td>
<td>138 ± 6 (7)</td>
</tr>
<tr>
<td>1976</td>
<td>132 ± 18 (10)</td>
<td>143 ± 8 (11)</td>
<td>161 ± 8 (9)</td>
</tr>
<tr>
<td>1977</td>
<td>107 ± 28 (11)</td>
<td>146 (1)</td>
<td>141 ± 7 (5)</td>
</tr>
</tbody>
</table>

in 1976 disappeared on 17 May, 26 May, and 11 July; and two males present in 1977 both disappeared on 5 July. The delayed time of immersgence in 1975 correlated with the delayed emergence in the spring of that year. The dates of disappearance of two of the males in 1976 were unexpectedly early. These males were recovered in 1977. Assuming that they were not overlooked during observation and trapping, they either did have a very short active season or they left the area, hibernated elsewhere at a later date, and then returned to the area in the following spring. In general, males entered hibernation before females; any overlap in timing of immersgence was usually with females that had not successfully reproduced. Because the males present in 1976 immersed before the period of heavy rain, their active season was not prolonged as were the active seasons of parous females and juveniles.

The number of days spent underground in the hibernation phase was estimated for adult females that were recovered each spring. On average, females spent 234 days ($n = 8$, SD = 14) hibernating in 1975–1976, 243 days ($n = 5$, SD = 20) in 1976–1977, and 258 days ($n = 5$, SD = 16) in 1977–1978. The high variation of these averages resulted mainly from the range in dates of fall immersgence. The 1975–1976 hibernation phase was the shortest because females immersed late in 1975, following their late emergence that year, but then emerged early in 1976. Although emergence occurred at a similar time in 1976, 1977, and 1978, the 1976–1977 hibernation season was shorter than the 1977–1978 season because of the late immersgence of females in 1976 associated with their delayed weight gain during the wet summer.

Only a rough estimate of the number of days males spent hibernating could be made because of inadequate information on their time of spring emergence. Assuming that males were active by mid-March in 1976, 1977, and 1978 then male hibernation lasted approximately 225 days in 1975–1976 and 250 days in 1977–1978. If males did immerge as early as May in 1976 then, for some males, hibernation lasted as long as 295 days in 1976–1977.

Juveniles spent less time hibernating than did adults because they were the last squirrels to immerge in fall. Five juvenile females hibernated for an average of 195 days (SD = 6) in 1975–1976 and six for an average of 202 days (SD = 5) in 1976–1977. No yearling females were recovered in 1978 so no estimate could be made for 1977–1978. Because of their late birth in 1975 the yearlings in 1976 were younger (320 ± 2 days) at spring emergence than were the yearlings in 1977 (350 ± 3 days). However, all yearlings produced litters at the same time as older females, indicating reproductive competence at 46 weeks of age. Because male juveniles entered hibernation later than females in fall and then emerged the following spring as yearling adults at about the same time as older males, they had the shortest period of hibernation, which lasted about 160 to 180 days.

Estimates of the lengths of the annual cycles were made for adult female squirrels present on the main area in two consecutive years. The length of the annual cycle from autumn immersgence to autumn immersgence was 381 ± 15 days ($n = 6$) in 1975–1976 and 367 ± 28 days ($n = 4$) in 1976–1977. Because time of entry into hibernation was affected by a female’s age, parity, and rate of weight gain it varied between
females in any year and also between years for the same female. Entry into hibernation was not cued by some factor consistent across all females and so the length of the annual cycle from immersion to emergence varied by as much as 5 to 8 weeks between females.

The annual cycle, estimated by the alternative method of calculating it from spring emergence to spring emergence, was shortest for 1975–1976 (343 ± 3 days, n = 8) because squirrels emerged late in 1975. The annual cycles for 1976–1977 (371 ± 3 days, n = 6) and for 1977–1978 (357 ± 3 days, n = 5) approximated a calendar year, slight variations from 365 days resulting from slight differences in the time of female emergence in 1976, 1977, and 1978. In any year the range in lengths of the annual cycle for individual females was never greater than 9 days, indicating synchrony in the timing of spring emergence for all females. Thus time of emergence was not dependent on age or reproductive history but on some factor acting more or less simultaneously on all females.

**DISCUSSION**

Synchrony in emergence of females suggests that timing of resumption of above-ground activity has been selected to ensure survival and reproductive success. Not only should reproduction be cued to environmental conditions ensuring plentiful food for females in late lactation and for their weaned offspring, but reproduction must occur early enough to allow time for the offspring to gain sufficient weight to survive their first hibernation period. Unpredictable conditions such as inclement weather during the summer (as occurred in 1976) or a delayed spring, which prolongs the period of dependency on fat stores (as occurred in 1975), must be allowed for. Because reproduction should occur as early as possible to maximize the growing season for offspring, but not be so early as to force pregnant females to rely on remaining fat stores as their source of energy, emergence should occur at about the time soil temperatures increase above 0°C and vegetative growth commences. Females gained weight rapidly following emergence and during pregnancy (Michener, 1978) indicating that their use of body fat was negligible.

If it is advantageous for female Richardson’s ground squirrels to come aboveground at the time vegetative growth commences, then female emergence should be cued to environmental factors associated with plant growth. This study has not revealed the proximate cue involved. Although emergence correlates with the rapid increase of daily maximum air temperatures to 10°C (this study, and Michener, 1973), air temperature is not a suitable cue because it fluctuates widely over short periods depending on atmospheric conditions, and it is not detectable underground. The more stable pattern of soil temperature increase in spring would appear to be a more appropriate cue for mammals that hibernate underground. French (1977) noted that spring emergence of *Perognathus longimembris* coincided with the time of vertical isothermality of soil temperatures, and Cranford (1978) found that spring emergence of *Zapus princeps* occurred when the hibernaculum temperature was between 8.0°C and 9.5°C. My female Richardson’s ground squirrels emerged during the period of warming of soil near the surface to above 0°C and before temperatures at the depth of the hibernaculum increased. Either females went to or near to the surface to assess conditions or they used cues other than surface soil temperature to time their emergence.

Although the time of emergence of most female squirrels coincided with the commencement of soil warming, the emergence of males occurred several weeks earlier, before soil temperatures increased and when maximum air temperatures averaged less than 5°C. Females outnumber males, they are mated within several days of their spring emergence (Michener, 1977b), and they breed only once a year. Emergence of males before that of females ensures that a male has the greatest opportunity to
inseminate several females, but means that spring emergence of males is cued by different factors than female emergence or is cued by the same factors acting at different thresholds.

No direct information is available on the relationship between terminal arousal from torpor and emergence aboveground. The rapid appearance of all females in 1975 once spring conditions arrived suggests that many females were aroused and ready to emerge when weather conditions ameliorated. The more protracted period of emergence in the other 3 years suggests that as each female aroused she emerged aboveground, giving a staggered pattern of female emergence. Knopf and Balph (1977) noted a similar variation in the range of emergence dates of Uinta ground squirrels (S. armatus) between late and early springs. Arousals from torpor are more frequent and last longer as spring approaches (Wang, 1973, 1979) thus providing squirrels with more opportunities to assess current environmental conditions. The behavior of squirrels during arousal in the field, and thus the method of assessment of environmental conditions, is unknown. Knopf and Balph (1977) considered that timing of terminal arousal was determined endogenously because they thought it unlikely that environmental cues could influence conditions in the hibernacula. In 1976, 1977, and 1978 my first female squirrels emerged in late March, whereas in 1975 they did not first appear until mid-April. Thus an early arousing female may face a 3-week wait until conditions improve, which would be metabolically expensive if she remained homeothermic. Probably such females return into torpor, with the torpid periods becoming shorter and less frequent. Pengelley and Fisher (1963) have shown that captive golden-mantled ground squirrels (S. lateralis) that are deprived of food continue to hibernate and finally die, presumably of starvation, about 100 days after the terminal arousal of squirrels provided with food. Thus, there may be no set terminal arousal as suggested by Knopf and Balph (1977), but rather there may be more frequent arousals from torpor, any one of which can become the terminal arousal if suitable conditions prevail.

Timing of fall immersgence of the various age and sex classes of squirrels varied by as much as 12 weeks in any year and even within a cohort there was a several-week range in time of disappearance underground, with delayed immersgence corresponding with delayed fattening. Wang (1979) has demonstrated that disappearance underground and onset of torpor are correlated, so the earliest disappearing squirrels can be assumed to spend the most time in torpor. The condition of the animal, rather than exogenous or environmental factors alone, appeared to be an important determinant of the time of autumn immersgence. The lightest squirrels did eventually go underground, suggesting that with approaching winter there is a time beyond which the costs of remaining active outweigh the benefits. Ultimate immersgence of animals in poor condition has been noted for marmots (Armitage et al., 1976) and other sciurids (Mrosovsky, 1971). Some of the factors affecting the ability to acquire sufficient fat stores to enter hibernation were the age and sex of the animal, its reproductive success that summer, and the availability of food.

Pengelley and Asmundson (1975) noted that, for captive golden-mantled ground squirrels held under constant conditions, females that failed to produce litters commenced hibernation earlier and terminally aroused earlier than parous females. Because the nonparous group aroused too early for the presumptive spring, Pengelley and Asmundson (1975) suggested that production of a litter aids in programming a female's entry into and emergence from hibernation at the most advantageous times. This study indicates that successful reproduction does delay entry into hibernation (see also Michener, 1978), but it does not indicate that the earlier immersgence made by nonparous squirrels is disadvantageous. Nonparous females emerged the following spring at the same time as successful reproducers; despite the longer time spent
underground their survival over winter (7 of 9) did not differ from that of successful reproducers (14 of 22), and their subsequent reproductive success (6 of 6) did not differ from that of the successful reproducers (10 of 12). Apparently, for Richardson's ground squirrels under natural conditions, early entry into hibernation as the result of failure to rear a litter is compensated for by a longer period of hibernation such that synchrony is reestablished with the successful reproducers and with spring conditions. Thus, precise timing of autumn emergence is not important for survival and subsequent reproduction, indicating that lactation and gestation are not necessary to synchronize the circannual cycle with environmental conditions.

Under controlled conditions the circannual cycles of hibernating species of sciurids are generally less than 365 days (Pengelley and Asmundson, 1969; Scott and Fisher, 1970); Blake (1972) has argued that it is easier to lengthen a short cycle than to shorten a long cycle. The small amount of information available on the length of the circannual cycle of Richardson's ground squirrels under controlled, laboratory conditions suggests that the cycle is less than 300 days, and may be as short as 220 days (Scott and Fisher, 1970). My data indicate that in the field the annual cycle (from emergence to emergence) more closely approximated a year, but was flexible in length between years. Because parturition and first emergence of the litter aboveground occur approximately 26 and 56 days after emergence (Michener, 1977b), the annual cycle measured from these reproductive events in one year to the next is of the same length as the emergence to emergence cycle and the same length for all reproducing females. Circannual cycles must be entrained by some environmental factor(s) so that animals are active and inactive at appropriate times of year. Heller and Poulson (1970) suggested that such environmental factors act in the spring to synchronize individuals with each other and with their environment, and they consider that terminal arousal and breeding are commitment points from which a new cycle begins. This study indicates that early spring is the only time of the year at which the cycle of Richardson's ground squirrels is synchronized among all individuals and with environmental conditions. Females that do not successfully reproduce and males lose synchrony with reproducitively successful females by fattening and immersing earlier. During the postreproductive season, timings of fattening and entry into hibernation become less synchronous among the successful reproducers. Juveniles immerge after the adults. Thus, in any year squirrels enter hibernation from mid-summer to autumn. Synchrony is reestablished at the time of emergence in the following spring.

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