Canadian Journal of Zoology
Revue canadienne de zoologie

Activity of eastern chipmunks *Tamias striatus* during the summer and fall

Journal:	Canadian Journal of Zoology
Manuscript ID	cjz-2016-0064.R1
Manuscript Type:	Article
Date Submitted by the Author:	14-Jun-2016
Complete List of Authors:	LaZerte, Stefanie; McGill University, Department of Biology, 1205 Penfield; University of Northern British Columbia, Natural Resources and Environmental Studies Kramer, Donald; McGill University, Department of Biology; (retired home address),
Keyword:	ACTIVITY LEVEL < Discipline, Sciuridae, telemetry, torpor, eastern chipmunk, mast, summer lull

SCHOLARONE™
Manuscripts

Activity of eastern chipmunks *Tamias striatus* during the summer and fall

S.E. LaZerte¹ and D.L. Kramer²

S.E. LaZerte and D.L. Kramer, Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal QC H3A 1B1

1. Current address: University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9 stefanie.lazerte@unbc.ca

2. Current address: 512- 831 Dunsmuir Rd., Victoria BC V9A 5B9 donald.kramer@mcgill.ca

Corresponding author:

S.E. LaZerte

3333 University Way, Prince George, BC V2N 4Z9

Phone: 250-960-6050

Fax: 250-960-5539

stefanie.lazerte@unbc.ca

Activity of eastern chipmunks *Tamias striatus* during the summer and fall

S.E. LaZerte and D.L. Kramer

Abstract: Measuring activity of small mammals in the field is challenging because they are often out of view. We used a novel method, based on temperatures of collar radio transmitters, to quantify the proportion of time eastern chipmunks (*Tamias striatus* (L., 1758)) spent active, curled up resting, and torpid during the summer and fall of two years in southern Quebec. Time active over the 24-h day was lower in a non-mast (8%) than a mast year (26%). In the mast year, activity varied strongly from a low of 7% during the summer lull to a high of 35% in the fall. Chipmunks that exploited a feeder had higher activity (33%) than chipmunks that did not (19%). Activity was higher during the day, but some activity occurred at night. Daily activity patterns varied strongly among seasonal periods. There was no evidence of torpor during the summer lull. Torpor started much earlier in the non-mast than in the mast year and occurred more at night than during the day. Overall, our study suggests that activity in this food-storing hibernator is positively influenced by food availability and indicates that thermosensitive radio telemetry is a promising method for recording continuous activity.

Key words: activity level, activity pattern, diurnality, eastern chipmunk, mast, rest, Sciuridae, sleep, summer lull, supplemental feeding, *Tamias striatus*, telemetry, torpor

Introduction

Daily and annual activity patterns are adaptations to temporal variation in the costs and benefits of movement, foraging, mating, and caring for young (reviewed by Halle 2000). The role of specific environmental variables in determining these costs and benefits can be inferred from changes in activity associated with natural or experimental variation in temperature, food availability, predation risk, competition, and mating opportunities (e.g., Schwagmeyer 1988; Abramsky et al. 1996; Cotton and Parker 2000; Nunes et al. 2000; Bacigalupe et al. 2003; Wasserberg et al. 2006; Williams et al. 2014). However, such inferences must take into account changes in physiological state, ecological context, and alternative energy demands. For example, activity may either increase or decrease with food availability, depending on whether an animal is a time minimizer or net energy maximizer, which can change seasonally (e.g., Kohli et al. 2014). Any increases in activity associated with increases in food availability may depend strongly upon environmental temperature (Bacigalupe et al. 2003).

Despite the value of studying activity, accurate measurement of activity in the field is technically challenging, leading to a wide variety of approaches, each with its own advantages and disadvantages. Direct observation (e.g., Kuhn and Vander Wall 2008) allows detailed information to be obtained but may influence the behaviour of the subjects and is not possible when animals are in darkness, dense vegetation, or shelter. Furthermore, often only one individual can be recorded at a time, increasing manpower demands or limiting sample sizes. Live trapping (e.g., Yahner 1977; Hoogenboom et al. 1984) increases sample size but curtails the activity of sampled individuals and may be biased by hunger or other variables that affect trapping success. Passive recording using camera traps, infrared beams, or track pads (e.g., Di Bitetti et al. 2006; Leighton et al. 2010) is less likely to affect behaviour, but restricts measures to a limited number of locations and often cannot distinguish individuals. Global positioning system (GPS) devices provide spatial as well as temporal activity data but may be too

heavy for most small mammals, do not function in dense vegetation or dens, and only count activity associated with substantial physical displacements (Ganskopp and Johnson 2007; Matisson et al. 2008). Measures of den occupancy using temperature probes, light loggers, or other devices (e.g., Osgood and Weigl 1972; Cotton and Parker 2000) allow large samples of relatively undisturbed individual animals but cannot account for rest outside the den or activity within it.

The problems of measuring activity are particularly acute in semi-fossorial mammals. Their small sizes and the tight confines of burrow tunnels limit the sizes and shapes of devices that they can carry. Direct observation, trapping, GPS and den occupancy recording will not detect underground activity, such as burrow construction, feeding, cache maintenance, parental care, and grooming. Indeed, we are not aware of any field studies of activity levels and patterns in semi-fossorial mammals that have measured activity throughout the day and night, including time within the burrow as well as out. Even for common, diurnal, well-studied species such as the eastern chipmunk (*Tamias striatus* (L., 1758)) information is remarkably limited. The only detailed, hourly-scale reports of daily activity patterns are records of number of individuals out of their burrow on three days (DeCoursey and Krulas 1998, DeCoursey et al. 2000). The only measures of activity within the burrow are records of the number of times per night over several nights that 7 individuals fitted with radio transmitters apparently moved away from the sleeping chamber as indicated by a reduction in signal strength (DeCoursey et al. 2000).

As an extension of Osgood and Weigl's (1972) technique, we developed a method using thermosensitive radio telemetry to measure activity in small mammals that rest in a curled posture (LaZerte and Kramer 2011). In brief, the method uses temperature information sent at frequent intervals from transmitters attached to collars, distinguishing high, constant temperatures sent when animals are in a curled posture (rest) from lower, variable temperatures when animals are not curled up (active) and from very low, gradually decreasing temperatures when animals become torpid. The goal

of the present study was to quantify the activity levels and patterns of eastern chipmunks during the day and night both in and out of the burrow by applying this method to previously collected data from chipmunks collared for a study of winter torpor (Landry-Cuerrier et al. 2008). Previous research had indicated that time spent above ground increased (Elliott 1978; Munro et al. 2008) and that torpor expression decreased (Humphries et al. 2003a; Landry-Cuerrier et al. 2008) with increasing food availability. Our specific objectives were to compare average activity levels and hourly-scale activity patterns 1) between two years differing greatly in the amount of food available for hoarding in the fall, 2) between time periods differing in the amount of hoardable food within a year, 3) between day and night, and 4) between individuals with and without access to a supplemental food source. In addition, we examined 5) whether and when torpor occurred during late summer and fall. Because activity during the active season was not a goal of the original data collection, there are some gaps in the record and no data for the early part of the active season.

Materials and methods

Species

Eastern chipmunks (hereafter, chipmunks) are common, solitary, semi-fossorial sciurid rodents native to eastern North America whose ecology and behaviour have been relatively well studied (Snyder 1982). They are widely considered as diurnal, remaining in the burrow throughout the night (Snyder 1982; DeCoursey and Krulas 1998; DeCoursey et al. 2000). In our area, chipmunks are seen outside of their burrows mainly between mid-May and late October. They eat a variety of seeds, fruits, bulbs and occasional animal prey (Elliot 1978; Snyder 1982). Chipmunks store little or no fat prior to hibernation, using a variable amount of torpor to reduce energy demands and depending on seeds of

deciduous trees hoarded in their burrow during the fall as their energy source (Elliot 1978; Snyder 1982; Humphries et al. 2002; Humphries et al. 2003a; Landry-Cuerrier et al. 2008). Seed-producing trees, including maples, beech, and oaks, typically show mastings, alternating years of low and high seed production (Jensen et al. 2012). In many populations, few animals are seen during a period of several weeks in late summer known as the summer lull, but how and why the animals disappear are not well understood (Dunford 1972; Yahner 1977; Elliot 1978). In mast years, the lull is followed by a period of active food hoarding in the fall (Elliot 1978), but in years of mast failure individuals may not appear above ground until the following spring (Munro et al. 2008). In mast years, chipmunks mate in June, leading to juvenile emergence in early September, coincident with the onset of mast availability (Bergeron et al. 2011). The proportion of the winter spent in torpor varies individually and inter-annually, decreasing as food supply increases (Landry-Cuerrier et al. 2008).

Study site

We gathered data on chipmunk activity in 2007 and 2008 in a 500 x 500 m plot of mature, deciduous forest within the Ruiter Valley Land Trust near Mansonville, Quebec, Canada (45° 05' N, 72° 26' W). The site was part of a large, continuous forest with relatively little human influence. Common foods for chipmunks were seeds of the sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.), with some black cherry (*Prunus serotina* Ehrh.) and red maple (*A. rubrum* L.). Maple and beech mast failed in 2007, but there was strong seed production and summer reproduction in 2008 (Bergeron et al. 2011).

As part of a larger study of chipmunk energetics, reproduction, and personality (e.g., Munro et al. 2008; Landry-Cuerrier et al. 2008; Bergeron et al. 2011; Montiglio et al. 2012; Careau et al. 2013),

chipmunks were systematically trapped throughout the active season using Longworth traps (Longworth Scientific Instruments, Abingdon, United Kingdom) baited with peanut butter. Newly captured individuals were marked with metal ear tags and implanted with passive integrated transponder tags (PIT tags, Trovan Ltd.). Recaptured chipmunks were identified and weighed. Experimental provisioning took place between 11 June and 29 September 2008. Trays of black-oil sunflower seeds were available at a single location for 4 hours approximately twice a week, with starting times ranging from 09:30 to 14:30 (36 days total). Trays were continuously monitored during the period of availability to document which individuals visited. Three of the six subjects in 2008 (referred to below as 'provisioned') hoarded sunflower seeds from the trays to their burrows on an average of 25 provisioning days each (range 18-30). Each made an average of 32 trips (range 1-155) per provisioning day, resulting in a total of over 650 collecting trips each (range 656 – 966). In contrast, the other three ('unprovisioned') chipmunks did not use the feeders at all.

Thermosensitive radio telemetry

We fitted unanaesthetized chipmunks with thermosensitive, very high frequency (VHF) radio transmitters (model PD-2CT, Holohil Systems). The transmitters were held under the chin using collars made of wire or tie-wraps covered in plastic heat-shrink tubing. Total mass of the collar, including the transmitter was 4.2g or 4.7% of mean body mass (92g, range = 72 – 105g). Collar temperatures were continuously and remotely monitored by a stationary array of Yagi antennas and data-logging radio-receivers (model SRX-400 W-21, Lotek Wireless, Newmarket, Ontario, Canada), powered by two 6-volt, deep-cycle batteries, with temperatures for each individual typically recorded at intervals of 2 – 30 min (subsampling down to a minimum interval of 12 min), depending on the number of individuals being recorded at any time. Of 25 chipmunks fitted with transmitters during the study, some

disappeared and others were too far from the antennas for consistent recording. Fourteen individuals (Table S1) provided usable data between 24 July - 3 October 2007 (3 males, 7 females, none lactating during study) and 26 June - 3 October 2008 (3 males, 3 females, including one male and one female also recorded in 2007). In 2008, two of the three females produced litters between 30 June and 30 July. The animal care protocol was approved by the McGill University Animal Care Committee (Protocol 4942) and followed the guidelines of the Canadian Council on Animal Care.

Determining activity, rest, and torpor

The proportion of time spent in activity, rest and torpor was estimated from the radio telemetry temperature data using the approach described in detail by LaZerte and Kramer (2011). Because chipmunks sleep in a curled posture that reduces contact between the transmitter and the ambient environment, we categorized periods of high and stable temperature as rest, periods of lower and more variable temperature as activity, and periods of gradually declining temperature lasting at least 6 h and followed by a sharp increase as torpor. Individual records were first divided into continuous bouts of activity, rest, torpor, and undetermined state. Next, these continuous bouts were used to assess the animal's state at each hour and 15, 30, and 45 min past the hour. Note that this procedure provides a conservative measure of rest by only including periods in which the animal was curled up and that it likely misses short bouts of activity or rest. We assessed the accuracy of these categorizations by comparing them to behavioural observations made at the provisioning station and those made as part of another study in which individuals were tracked on a rotating schedule for 10 minutes at a time and their behaviour recorded at 30-s intervals. We expected that all time outside the burrow should be categorized as active and that all resting should occur inside the burrow, because eastern chipmunks have never been reported to curl up to sleep outside their burrows. We had 143 observations that

coincided with temperature records. In 88 cases in which animals were observed outside the burrow, 95% were correctly classified as active. In 55 cases in which animals were classified as resting, 96% were in their burrows, as expected (LaZerte and Kramer 2011).

Records were grouped into seasonal periods of variable duration during which all equipment was fully operational (5 periods lasting 6 – 20 d in the longer study season of 2008, 3 corresponding periods lasting 12 – 26 d in 2007; dates in Table 1). Gaps between periods due to equipment problems generally lasted less than 8 d, except for one longer gap between periods 3 and 4 in mid-August 2008. Not all individuals were sampled in all periods. On average, there were 7 individuals per period (range = 3 – 10; Table 1). We used sunrise and sunset to divide the record into daytime and nighttime, excluding any day or night sequence in which > 25% of an individual's 15-min time samples were undetermined. We also excluded data from any day on which a chipmunk was trapped as well as the following night. Our final data set included a mean of 12 days per individual per period (range = 3 – 25). These sampled days comprised a mean of 73% of the possible recording days in each period (range = 36 – 100%). Because torpor in 2008 began after the study period, we also checked the records from October through December to assess exactly when torpor began in that year.

For each individual in each period, we determined both daily activity patterns and activity levels. Individual daily activity patterns show the variation in activity throughout the day as measured by the proportion of sampled days on which an individual was active at each time interval (hour, 15, 30 and 45 min past the hour), excluding undetermined (i.e., the number of days in a specific period in which the chipmunk was active at a specific time divided by the number of days in the same period in which the animal was active or resting or torpid at that time). Population daily activity patterns were determined by averaging the proportion of time active at each time interval in a given period over all individuals. Activity levels were calculated for each individual in each period over three different time

frames: daytime, nighttime and 24-h day. We first calculated the proportion of 15-min intervals that were scored as active (i.e., number of intervals active/number of intervals active, resting or torpid) for each day, night and 24-h period. We then calculated mean individual activity levels by averaging over all sampled days in each period for each individual; these mean individual activity levels formed the primary data for the statistical analyses (below). Finally, population activity levels were calculated as the mean of all individuals in each period (period means), or in each year (annual means). A similar approach was used to calculate torpor levels across the time frames of daytime, nighttime and 24-h day.

The distribution of activity between day and night was calculated as a diurnality index derived from Hoogenboom et al. (1984; Halle and Weinert 2000): $[2P_d/(P_d + P_n)] - 1$, where P_d is the proportion of the day spent active and P_n is the proportion of the night spent active. This index provides a measure of relative activity in day and night independent of the day length and ranges from -1 (totally nocturnal) to 1 (totally diurnal). Similarly, we calculated the diurnality of torpor, substituting proportion of the day and night torpid for proportion of the day and night active.

Statistical analyses

We used linear mixed models to assess how 24-h activity levels and diurnality varied between years, among seasonal periods within years and with the use of supplemental food. Individual mean activity levels were arcsine square root transformed to achieve normality. Because 2007 had fewer seasonal periods than 2008, we used only data from periods 3 – 5 for between-year comparisons. To compare activity between years and among periods we used custom independent contrasts looking at: (1) differences between years, (2) differences between period 3 and the mean of periods 4 and 5 within

2007, (3) differences between period 3 and the mean of periods 4 and 5 within 2008, (4) differences between periods 4 and 5 within 2007, and (5) differences between periods 4 and 5 within 2008 (Contrast details in Table S2).

To more closely examine differences in activity levels among all periods (1-5) in 2008, we conducted another linear mixed model analysis with period and use of supplemental food as the only explanatory variables. This was followed by a post-hoc analysis using the Benjamini and Hochberg correction (Benjamini and Hochberg 1995) to examine all pair-wise differences in activity levels among periods in 2008. We used a Mann-Whitney *U* test to examine differences in torpor levels between years and a paired Wilcoxon Signed-Rank test to examine differences between periods. We analyzed diurnality of torpor with linear mixed models and only included periods in which torpor occurred.

In all mixed models, chipmunk identity was included as a random factor to account for multiple measures per individual. All analyses were performed in R v3.1.1 (R Core Team 2014). Models were run with nlme v3.1.117 (Pinheiro et al. 2014). Figures were produced with ggplot v0.9.3.1 (Wickham 2009).

Results

Activity levels

Overall, chipmunks spent relatively little time active, with period medians of 24-h activity ranging from 6 – 35% and annual medians of 24-h activity of only 8% in 2007 and 26% in 2008 (unprovisioned 19%, provisioned 33%) (Table 1, Fig. 1). Even considering only daytime activity, period medians ranged from 7 – 65%, with an annual median of 10% in 2007 and 48% in 2008 (unprovisioned 34%,

provisioned 52%). The more than three-fold difference in 24-h activity between years was highly significant when provisioning was controlled statistically (Table 2). In 2007, differences among periods were relatively small, ranging from a low of 6% in period 5 (Autumn) to a high of 11% in period 3 (Late summer) (Fig. 1a). However, in 2008 when overall activity was higher, there was a five-fold difference ranging from a low of 7% in period 2 (Midsummer) to a high of 35% in period 4 (Early autumn) (Fig. 1bc). In 2007, activity significantly decreased after period 3 (Late summer), whereas in 2008 activity significantly increased after period 3 (Late summer) (Table 2). The analysis restricted to 2008 showed that 24-h activity varied significantly among periods ($F_{(4,16)} = 9.679$; $P < 0.001$). The post-hoc pair-wise analysis of period supported a pattern of moderate activity in period 1 (Early summer), followed by a significant reduction in period 2 (Midsummer), an increase in period 3 (Late summer) and high activity in periods 4 (Early autumn) and 5 (Autumn) (Table 3; Fig. 1bc). However, which period showed the least activity differed among individuals (Fig. S2). For example, the two reproductive females showed very low levels in period 2 (Midsummer) but higher levels in period 3 (Late summer), whereas two males showed very low levels of activity in period 3 (Late summer). Analyses using only daytime activity gave results similar to those for 24-h activity, but analyses of nighttime activity showed no effects of year, provisioning or period (S. LaZerte, unpublished analyses).

In 2008, the three chipmunks that used the feeder had a higher median level of 24-h activity (33%) than the three chipmunks that did not have access to supplementary food (19%, Table 1; Fig. 1c). The effect of provisioning was highly significant in the analysis that included periods 3 – 5 of both years (Table 2), but did not quite reach statistical significance in the analysis restricted to 2008 ($F_{(1,4)} = 7.503$; $P = 0.052$).

Diurnality

Chipmunks were sometimes active during the night (2007 4%, 2008 3%) but at lower levels than during the day (2007 10%, 2008 48%; Table 1). The diurnality index was significantly diurnal, as indicated by the intercept in the linear mixed model, which reflects the overall average diurnality index (>0 indicates diurnality, <0 indicates nocturnality; Table 4). There was significantly weaker diurnality in 2007 (0.46) than 2008 (0.80) and an overall mean diurnality index of 0.67 (Tables 1, 4). The annual diurnality values are equivalent to 73% (2007) and 90% (2008) of all active time occurring between sunrise and sunset in a 12L:12D photoperiod. There were no effects of period or provisioning on diurnality and few strong differences between periods within years, although there was slightly less diurnality in period 5 (Autumn) than in period 4 (Early autumn) in 2008 (Table 4).

Daily activity patterns

The mean daily activity pattern of chipmunks varied strikingly among periods (Fig. 2). In 2007, when activity was low in all periods, average activity fluctuated over the day without a strong cyclical pattern. During period 2 (Midsummer) in 2008, when activity was also low, the pattern was similar. However, in the other four periods in 2008, activity was higher and distinct patterns were evident with up to 75% of individuals active, on average, at peak times. In period 1 (Early summer), activity rose gradually over the course of the day to a peak just before sunset followed by a rapid decrease in activity. In period 3 (Late summer), the pattern was similar, but the peak was in the middle of the day followed by gradual decrease until activity dropped suddenly at sunset. In contrast, activity in period 4 (Early autumn) increased sharply after sunrise, reaching a morning peak, dropping gradually over the course of the day followed by a precipitous drop at sunset. In period 5 (Autumn), activity also increased rapidly after sunrise, but the morning peak was followed by a strong decrease and a rise to a second peak just before sunset. In the four periods with higher levels of activity during the day, the

onset of increased activity closely followed sunrise. The offset of activity was associated with sunset but differed between periods. In periods 1 (Early summer) and 3 (Late summer), activity dropped quickly at sunset, reaching the nocturnal mean within minutes (mean = 37.5 min; range = 30 - 45 min), but in periods 4 (Early autumn) and 5 (Autumn), activity continued longer after sunset (mean = 90 min; range = 75 - 105 min). Activity occurred sporadically during the night but did not show an evident cyclical pattern.

We also examined the mean activity patterns for each individual in each period (Fig. S1, S2) to assess how closely they matched the population-scale patterns. For the most part, individual patterns were similar to the population patterns. However, in period 3 (Late summer) 2007 and period 2 (Midsummer) 2008 when mean activity was low and the population did not show a distinct cycle of activity, most individuals did have distinct, short periods of peak activity. Because these peaks occurred at different times of day, the population average did not present a distinct cycle. We did not detect any clear tendency for individuals to show consistent patterns between periods.

Torpor

Torpor expression differed between years (Table 5; Fig. 1). In 2007, the first torpor bout occurred on 21 August. By 25 August, 50% of chipmunks had expressed torpor, and by 9 September all chipmunks had done so. In 2008, no chipmunks expressed torpor during the main study period. Records collected later in the season showed that the first individual expressed torpor on 24 October, 50% had done so by 3 November, and all individuals by 18 December. Time spent torpid in 2007 increased from period 3 (Late summer; 0%) to period 4 (Early autumn; 22%; Paired Wilcoxon Signed-Rank test $W = 0$, $P = 0.006$), and from period 4 (Early autumn) to period 5 (Autumn; 45% $W = 3$, $P = 0.039$, Table 5; Fig. 1a). Because individuals in 2008 did not express torpor until late in the year, the difference between

years in the amount of torpor expressed by individuals during periods 3 - 5 was highly significant (Mann-Whitney $U = 57$, $P = 0.003$; Fig. 1). In 2007, torpor during periods 4 (Early autumn) and 5 (Autumn) in 2007 occupied about twice as much time during the night as during the day (average Diurnality Index Intercept = -0.306 ; $t_8 = -6.329$; $P < 0.001$), equivalent to 65% of torpor occurring at night in a 12L:12D photoperiod. However, the diurnality of torpor did not differ between periods 4 (Early autumn) and 5 (Autumn) ($t_7 = 0.291$; $P = 0.779$).

Discussion

Mean activity levels

Considering that our study covered a substantial portion of the active season, including the fall when food is actively hoarded to support hibernation, chipmunk activity was surprisingly low, with only 8% of the time active in 2007 and only 26% in 2008. It is unlikely that the low activity estimate was a result of overestimating rest or torpor. If substantial activity had been categorized as rest, we would have expected more than 2 of 42 bouts during which we knew that the animal was outside the burrow to have been misclassified as rest (LaZerte and Kramer 2011). Furthermore, torpor had a distinctive signal that was unlikely to have been generated during activity (LaZerte and Kramer 2011). Indeed, activity may have been overestimated because periods in which the animal was not moving but not curled up most likely would have been categorized as activity. Nevertheless, we recognize that short bouts of activity and distant movements out of receiver range may have been missed. Future applications of this method would be improved by linking temperature records to direct behavioural observations.

Although we are not aware of any previous field studies that have estimated activity over the entire 24-h day in chipmunks or any other semi-fossorial mammal, there is some evidence related to activity in such species. Comparable to our levels of activity for 2008, Estep et al. (1978a; 1978b) observed activity levels of about 25% in eastern chipmunks measured by direct observations in small laboratory cages. A similar study of 14 muroid rodent species found only slightly higher levels (mean = 34%, range = 25 – 42%, Baumgardner et al. 1980). In a comparative examination of sleep times, values for semi-fossorial mammals ranged from 12 - 17 h, implying that animals were not sleeping (although they could have been resting) for 7 - 12 h (30 - 50%). Other studies have documented the time spent outside the burrow as an estimate of active time for semifossorial mammals, assuming that animals are continuously active when out of their burrows and ignoring activity within the burrow. Cascade golden-mantled ground squirrels (*Callospermophilus saturatus* (Rhoads, 1895)) averaged about 7.4 h/day (31%) outside the burrow during the active season (Kenagy et al. 1989). However, in two field studies of golden hamsters (*Mesocricetus auratus* (Waterhouse, 1839)), time outside the burrow was even less than our recorded time active (4 – 6%, Gattermann et al. 2008, Larimer et al. 2011). Thus, several studies in both laboratory and field have found activity levels comparable to those in eastern chipmunks in the year with higher activity, but only the hamsters hint at levels as low as our observations in the year with lower activity.

Interannual differences in activity

Chipmunk activity differed strongly between years, with a highly statistically significant difference despite the limited sample size. From late August through early October (periods 4 and 5) when chipmunks gather mast to support hibernation, total daily activity was about 5 times higher in 2008 than in 2007. Considering only unprovisioned chipmunks, activity was still 4 times higher in 2008 than

in 2007. Because we studied only one mast and one non-mast year, we cannot be sure that the difference between years was due to the difference in food availability, but this seems the most likely explanation; to take advantage of increased food availability, chipmunks could increase activity in order to hoard food into their burrow. Previous studies have shown that late summer and autumn live-trap capture rates of chipmunks were greatly reduced during years without fall mast, presumably reflecting differences in above ground-activity, at this and other locations (Munro et al. 2008; Bergeron et al. 2011). Munro et al. (2008) provided evidence that some chipmunks never emerged from their burrows between late summer and the following spring, apparently relying on previously stored food items as their energy source. Our study complements this work by showing that overall activity is reduced during the extended stay in the burrow. Given the large difference in activity, it is somewhat surprising that Careau et al. (2013) failed to find lower daily energy expenditure in non-mast years in the same population of chipmunks. However, the doubly-labelled water technique used by Careau et al. (2013) can be applied only to chipmunks that leave their burrows at least occasionally allowing them to be captured. Thus, individuals with very low activity are less likely to be sampled. Comparisons of activity between years differing in food availability have been carried out only in few other mammalian species. Least weasels (*Mustela nivalis* L. 1766) did not notably change activity level (measured as time outside the den) in response to large changes in their rodent prey population (Jedrzejewski et al. 2000). However, four hibernating species, yellow pine chipmunks (*Tamias amoenus* J. A. Allen, 1890), edible dormice (*Glis glis* (L. 1766)), American black bears (*Ursus americanus* Pallas, 1780), and Asiatic black bears (*Ursus thibetanus* G. Cuvier, 1823), extended their active seasons longer in years of higher food availability (Larivière et al. 1994, Kuhn and Vander Wall 2008, Kozakai et al. 2013, Hoelzl et al. 2015). Unlike eastern chipmunks, however, the proportion of time active before the onset of hibernation was higher for Asiatic black bears in the low food year (Kozakai et al. 2013). Similarly,

when outside the burrow, yellow pine chipmunks were also more active in a low food year (Kuhn and Vander Wall 2008).

Seasonal variation in activity

Seasonal changes in activity documented in this study generally match previous descriptions of this part of the annual cycle in eastern chipmunks, based on visual observation and trapping. These describe high activity in early summer, followed by a late summer lull and then a peak in activity when mast becomes available in the fall (Dunford 1972; Elliot 1978). The late summer decrease in observations and trapping success termed the summer lull was noted by early naturalists [summarized by Allen (1938)] and has attracted the attention of researchers who have suggested that decreased time above ground may be a response to heat, drought, botfly parasitism, low food availability, or the need to prepare the burrow for fall food storage (Allen 1938; Dunford 1972; Yahner 1977; Elliot 1978; Wrazen 1980; Lacki et al. 1984; DeCoursey et al. 2000). However, many reports of changes in above ground-activity have not been able to rule out alternative explanations for the apparent decline, including seasonal variation in population size, vocalization rate, or changes in use of cover and attraction to supplemental food. Empirical observations have not been fully consistent with any of the hypotheses proposed (Dunford 1972; Yahner 1977; Lacki et al. 1984). Our study provides evidence that the lull does represent a major reduction in overall activity rather than an increase in relative activity within the burrow or changes in detectability or trappability. Unfortunately, equipment problems in 2008 resulted in a data gap during much of August, the period in which the greatest reduction in activity was expected. In period 2 (Midsummer), the two reproductive females showed lower activity levels than the other recorded individuals, suggesting that some of the activity reduction may be related to pregnancy or parturition. However, low activity by two males in period 3 (Late summer) indicates that maternal

care cannot be the sole explanation of the lull. Furthermore, we found no indication that eastern chipmunks used torpor during this period, as reported in edible dormice (Hoelzl et al. 2015).

As with yearly variation, seasonal changes in activity may be at least partially explained by changes in food availability. Elliot (1978), who studied chipmunks in the Adirondack Mountains of northern New York in a habitat similar to our site, suggested that the lull occurs after early summer food has been depleted and before beech and sugar maple mast become available. Our observation that the lull in activity in 2007 (the non-mast year) transitioned directly into the start of torpor, with no increase in activity levels, supports this hypothesis. Kuhn and Vander Wall (2008) argued that seasonal changes in foraging activity were related to food availability in yellow pine chipmunks, and similar arguments have been made for American and Asiatic black bears (Larivière et al. 1994; Kozakai et al. 2013). In a species that depends on stored food supplies, such as eastern chipmunks, food availability may explain patterns of activity within as well as between years.

Supplemental feeding

There was evidence that individuals that accessed the supplemental feeders increased their activity level. In the combined analysis, provisioning had a highly significant positive effect on activity, but in the analysis including only 2008 the effect of provisioning showed only a trend. Given the small sample sizes and potentially confounding effects of reproductive status of two females in periods 1 to 3, these results need to be considered as only suggestive. Nevertheless, even during periods 4 (Early autumn) and 5 (Autumn) when mast was available, the difference in mean activity levels of chipmunks that did (45%) and did not (26%) access the feeders was substantial. Although individual records indicated that the three chipmunks which used the feeder were usually actively hoarding sunflower seeds for most of the time that supplemental food was available, the increased activity of provisioned

chipmunks cannot be explained simply as continuous foraging in response to the provisioned food. The feeders were accessible for only two 4-h time blocks per week (5% of total time), suggesting that the chipmunks were using their additional stored energy to engage in other activities. Possibly, access to a steady supply of storable food triggered an increase in food searching and hoarding behaviour in these individuals. However, without direct observation and a longer term experiment, this remains speculation. Two previous studies suggested that supplemental food increased activity during the lull in chipmunks (Ryan and Larson 1976; Lacki et al. 1984). However, design problems in both studies render the conclusions uncertain.

In contrast to the trend in our study, decreases in activity have been found in other field studies providing supplemental food to other mammalian species including wood mice (*Apodemus sylvaticus* (L. 1758)), macaques (*Macaca sylvanus* (L. 1758) and *M. mulatta* (Zimmermann, 1780)) and black bears (Akbar and Gorman 1996; Beckmann and Berger 2003; El Alami et al. 2012; Jaman and Huffman 2013). This difference may be a result of the ability of chipmunks to hoard large amounts of food. For such species, intense activity during potentially brief periods of food availability allow individuals to maximize the size of their hoard and improve chances of surviving periods of food shortage. Species not capable of hoarding would be expected to reduce foraging activity once their daily needs have been met.

Diurnality

Our study shows that chipmunks are strongly diurnal. Like most sciurids (Roll et al. 2006), chipmunks have been widely recognized as diurnal (Snyder 1982), based on consistent failure to find chipmunks above ground after dark in many field studies, including some using radio tracking (DeCoursey and Krulas 1998; DeCoursey et al. 2000). Even in small laboratory cages lacking sleeping

chambers, chipmunks are primarily diurnal (Estep et al. 1978a; 1978b). Our study extends previous field observations by showing that diurnality is strong, even when potential activity within the burrow is taken into account. Nevertheless, our results provide evidence for some activity at night, with about 3 - 4% of the time defined as not resting.

It is interesting that chipmunks do not show more nocturnal activity because it would be possible for animals to engage in activities such as feeding, food store maintenance, grooming, and burrow maintenance at night. During the day or night, these activities are likely to be carried out in complete or nearly complete darkness. The potential for nocturnal activity in the burrow is raised by observations of weak or absent circadian patterns in some fossorial species that rarely emerge above ground (Lovegrove 1988; Loevy et al. 2013), by movements away from the nest chamber during the inactive period in other semifossorial species e.g., diurnal movements in nocturnal kangaroo rats (*Dipodomys microps* (Merriam, 1904)) (Kenagy 1973), and by substantial nocturnal activity of other diurnal semifossorial species under laboratory conditions (Hagenauer and Lee 2008; Barak and Kronfeld-Schor 2013).

The diurnality index was stronger in the mast year (16 times more activity during the day) than in the non-mast year (2.5 times). Previous studies have found that diurnality can change in response to risk of predation or human persecution (e.g., Fenn and Macdonald 1995; Kitchen et al. 2000), competition (e.g., Gutman and Dayan 2005), and season (e.g., Hoogenboom et al. 1984; Fortin et al. 2013). However, in the present case, the quantitative inter-annual difference in diurnality appears to be the mathematical consequence of a large difference in diurnal activity with little change in nocturnal activity.

Daily activity patterns

During periods with high average activity, chipmunks showed strong population-level activity patterns over the course of the day with distinct peaks indicating that the proportion of time spent active changes over the day and that there is substantial synchrony among individuals within the population. However, the shape and timing of the peaks differed among periods. Although the number of individuals observed was limited, the number of days per individual in the 4 periods with high activity ranged from 5 - 19 (mean = 10), so mean patterns could not be explained by individual events such as changes in weather or presence of a predator. The feeder was unlikely to be a direct determinant of the timing of activity because the feeder was present only two days per week, availability starting times ranged from 09:30 to 14:30, and those chipmunks that used the feeder appeared to be active at similar times whether the feeder was open or not.

Previous studies of chipmunks failed to identify distinct daily peaks in activity measured by trapping success or time above ground (Dunford 1972; Yahner 1977), and the lack of a clear daily pattern was also mentioned by Humphries et al. (2002). However, Getty (1981) noted that above-ground activity in chipmunks tended to be synchronized, despite strong spatial avoidance among neighbours. Radio-tracking larger numbers of chipmunks (20 - 40 individuals) over 3 single days to assess time above ground in a more southern population (Virginia) showed distinct midday or late morning peaks with a gradual drop through the afternoon in mid-summer and early September, similar to our observations in 2008 period 4 (Early autumn). Furthermore, during the acorn-collecting season in early October, there was more continuous activity, but with distinct midday and late afternoon peaks separated by a small reduction in the early afternoon, somewhat like our observations in 2008 period 5 (Autumn) (DeCoursey and Krulas 1998; DeCoursey et al. 2000).

Some other small mammals show seasonal changes in the timing and number of peaks of activity. For example, semifossorial degus (*Octodon degus* (Molina, 1782)) and tree squirrels tend to show

bimodal activity patterns in the summer and unimodal peaks in the winter (Wauters 2000, Kenagy et al. 2002, Bacigalupe et al. 2003). We are not aware of any other studies that have found major changes in the timing of peak activity such as the switches we observed between early morning and late afternoon. Whether these changes are consistent responses to changes in the seasonal environment or whether they involve idiosyncratic interactions within populations remains to be determined.

Torpor

Torpor occurred more than 2 months earlier in the non-mast year than in the mast year. Torpor onset did not appear to be a response to changes in the weather. In 2007, between August 21 when the first individual showed torpor and August 25 when half the monitored population had done so, temperatures in our study site remained summerlike with daily maxima of 20-26 C and minima of 9-19 C (overall mean 18 C). Our observations suggest that the late summer and autumn disappearance of chipmunks in non-mast years documented by Munro et al. (2008) is likely to have involved the use of torpor. To the best of our knowledge, August 21 is the earliest date at which torpor has been documented in eastern chipmunks in the field. However, DeCoursey et al. (2000, p. 172) briefly mentioned “considerable torpor” during an August drought with mast failure in Virginia. Landry-Cuerrier et al. (2008) found that the amount of time spent in torpor was greater after a non-mast year than after a mast year, but they did not investigate the time of torpor onset. Our results coupled with these other studies suggest that early torpor onset may be a direct result of low food availability resulting from a non-mast year or a mast failure. However, while experimental studies have also supported a direct negative of the amount of hoarded food on time spent in torpor by individual chipmunks in the field, they did not find an effect on the time of torpor onset (Humphries et al. 2003b; Munro et al. 2005). In a related species, yellow pine chipmunks entered their burrows about 2 weeks earlier in a poor food year than in a good food year,

but whether they also initiated torpor earlier was not investigated (Kuhn and Vander Wall 2008).

During the periods when chipmunks were torpid in 2007, they spent about twice as much time torpid at night as they did during the day. A few studies have found evidence for circadian patterns in the timing of torpor during early hibernation (Strumwasser 1959; Kortner and Geiser 2000). As in our study, torpor seems to occur more in the phase in which the animal is normally less active in some cases (Strumwasser 1959) but not all (Canguilhem et al. 1994).

Conclusions

This study has provided evidence for large changes in activity of chipmunks on the time scales of hours, day versus night, seasons, and years. There is evidence that increases in the availability of storable food (from both natural and anthropogenic sources) may increase the activity at the scale of individuals, years and seasons, but the number of years studied limits this conclusion. We found further evidence that inter-annual differences in food availability may influence the onset of torpor. Our method using thermosensitive telemetry provides a way to quantify activity in multiple individuals at the same time and at an hourly time scale with minimal disturbance.

Acknowledgements

The Ruiter Valley Land Trust graciously permitted us to perform this study within their protected areas. Many field technicians and graduate students worked on the field site and provided valuable help and support. In particular, we thank D. Munro, V. Careau, M. Landry-Cuerrier, P. Bourgault, and P. Bergeron for their help in collecting telemetry data. K. Turgeon and P. Leighton offered valuable statistical advice. B. Vickery, Q. Fletcher, M. Landry-Cuerrier, M. Humphries, and P. Leighton provided feedback on an earlier version of the manuscript. Funding was provided by a team grant from

Le Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) held by D. Kramer, D. Garant, M. Humphries, D. Réale, and D. Thomas, and a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) to D. Kramer. An NSERC Canada Graduate Scholarship and McGill University provided personal support for S. LaZerte.

Draft

References

- Abramsky, Z., Strauss, E., Subach, A., Kotler, B.P., and Riechman, A. 1996. The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. *Oecologia*, **105**(3): 313–319. doi:10.1007/BF00328733.
- Akbar, Z., and Gorman, M.L. 1996. The effect of supplementary food upon the activity patterns of wood mice, *Apodemus sylvaticus*, living on a system of maritime sand-dunes. *J. Zool. (Lond.)*, **238**: 759–768.
- Allen, E.G. 1938. The habits and life history of the eastern chipmunk, *Tamias striatus lysteri*. New York State Museum Bulletin, **314**: 1–122.
- Bacigalupe, L.D., Rezende, E.L., Kenagy, G.J., and Bozinovic, F. 2003. Activity and space use by degus: A trade-off between thermal conditions and food availability? *J. Mammal.* **84**(1): 311–318. doi:10.1644/1545-1542(2003)084<0311:AASUBD>2.0.CO;2.
- Barak, O., and Kronfeld-Schor, N. 2013. Activity rhythms and masking response in the diurnal fat sand rat under laboratory conditions. *Chronobiol. Int.* **30**(9): 1123–1134. doi:10.3109/07420528.2013.805337.
- Baumgardner, D.J., Ward, S.E., and Dewsbury, D.A. 1980. Diurnal patterning of 8 activities in 14 species of muroid rodents. *Anim. Learn. Behav.* **8**(2): 322–330. doi:10.3758/BF03199612.
- Beckmann, J.P., and Berger, J. 2003. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *J. Zool. (Lond.)*, **261**: 207–212. doi:10.1017/S0952836903004126.
- Benjamini, Y., and Hochberg, Y. 1995. Controlling the false discovery rate - a practical and powerful approach to multiple testing. *J. R. Stat Soc. B*, **57**(1): 289–300.

- Bergeron, P., Reale, D., Humphries, M.M., and Garant, D. 2011. Anticipation and tracking of pulsed resources drive population dynamics in eastern chipmunks. *Ecology*, **92**(11): 2027–2034.
- Canguilhem, B., Malan, A., Massonpevet, M., Nobelis, P., Kirsch, R., Pevet, P., and Leminor, J. 1994. Search for rhythmicity during hibernation in the European hamster. *J. Comp. Physiol. B*, **163**(8): 690–698. doi:10.1007/BF00369521.
- Careau, V., and Garland, T. 2012. Performance, personality, and energetics: Correlation, causation, and mechanism. *Physiol. Biochem. Zool.* **85**(6): 543–571. doi:10.1086/666970.
- Careau, V., Reale, D., Garant, D., Pelletier, F., Speakman, J.R., and Humphries, M.M. 2013. Context-dependent correlation between resting metabolic rate and daily energy expenditure in wild chipmunks. *J. Exp. Biol.* **216**(3): 418–426. doi:10.1242/jeb.076794.
- Cotton, C.L., and Parker, K.L. 2000. Winter activity patterns of northern flying squirrels in sub-boreal forests. *Can. J. Zool.* **78**(11): 1896–1901. doi:10.1139/cjz-78-11-1896.
- DeCoursey, P.J., and Krulas, J.R. 1998. Behavior of SCN-lesioned chipmunks in natural habitat: A pilot study. *J. Biol. Rhythms*, **13**(3): 229–244. doi:10.1177/074873098129000075.
- DeCoursey, P.J., Walker, J.K., and Smith, S.A. 2000. A circadian pacemaker in free-living chipmunks: essential for survival? *J. Comp. Physiol. A*, **186**(2): 169–180. doi:10.1007/s003590050017.
- Di Bitetti, M.S., De Angelo, C.D., Di Blanco, Y.E., and Paviolo, A. 2010. Niche partitioning and species coexistence in a Neotropical felid assemblage. *Acta Oecol.* **36**(4): 403–412. doi:10.1016/j.actao.2010.04.001.
- Dunford, C. 1972. Summer activity of eastern chipmunks. *J. Mammal.* **53**(1): 176–180. doi:10.2307/1378838.
- El Alami, A., Van Lavieren, E., Rachida, A., and Chait, A. 2012. Differences in activity budgets and diet between semiprovisioned and wild-feeding groups of the endangered Barbary macaque

- (*Macaca sylvanus*) in the central High Atlas Mountains, Morocco: Activity budget and diet of Barbary macaque. *Am. J. Primatol.* **74**(3): 210–216. doi:10.1002/ajp.21989.
- Elliot, L. 1978. Social behavior and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack Mountains. *Smithson. Contrib. Zool.* No. **265**: 1–107.
- Estep, D.Q., Canney, E.L., Cochran, C.G., and Hunter, J.L. 1978a. Components of activity and sleep in 2 species of chipmunks - *Tamias striatus* and *Eutamias dorsalis*. *Bull. Psychon. Soc.* **12**(5): 341–343.
- Estep, D.Q., Fischer, R.B., and Gore, W.T. 1978b. Effects of enclosure size and complexity on the activity and sleep of the eastern chipmunk *Tamias striatus*. *Behav. Biol.* **23**(2): 249–253. doi:10.1016/S0091-6773(78)91910-7.
- Fenn, M.G.P., and Macdonald, D.W. 1995. Use of middens by red foxes - risk reverses rhythms of rats. *J. Mammal.* **76**(1): 130–136. doi:10.2307/1382321.
- Fortin, J.K., Ware, J.V., Jansen, H.T., Schwartz, C.C., and Robbins, C.T. 2013. Temporal niche switching by grizzly bears but not American black bears in Yellowstone National Park. *J. Mammal.* **94**(4): 833–844. doi:10.1644/12-MAMM-A-238.1.
- Ganskopp, D.C., and Johnson, D.D. 2007. GPS error in studies addressing animal movements and activities. *Rangeland Ecol. Manage.* **60**(4): 350–358.
- Gattermann, R., Johnston, R.E., Yigit, N., Fritzsche, P., Larimer, S., Oezkurt, S., Neumann, K., Song, Z., Colak, E., Johnston, J., and McPhee, M.E. 2008. Golden hamsters are nocturnal in captivity but diurnal in nature. *Biol. Lett.* **4**(3): 253–255. doi:10.1098/rsbl.2008.0066.
- Getty, T. 1981. Territorial behavior of eastern chipmunks (*Tamias striatus*): Encounter avoidance and spatial time-sharing. *Ecology*, **62**(4): 915–921. doi:10.2307/1936989.

- Gutman, R., and Dayan, T. 2005. Temporal partitioning: An experiment with two species of spiny mice. *Ecology*, **86**(1): 164–173. doi:10.1890/03-0369.
- Hagenauer, M.H., and Lee, T.M. 2008. Circadian organization of the diurnal caviomorph rodent, *Octodon degus*. *Biol. Rhythm Res.* **39**(3): 269–289. doi:10.1080/09291010701683425.
- Halle, S. 2000. Ecological relevance of daily activity patterns. *In Activity Patterns in Small Mammals. Edited by S. Halle and N.C. Stenseth.* Springer Berlin Heidelberg. pp. 67–90.
- Halle, S., and Weinert, D. 2000. Measuring and analysing activity of small mammals in the laboratory and in the field. *In Activity Patterns in Small Mammals. Edited by S. Halle and N.C. Stenseth.* Springer Berlin Heidelberg. pp. 285–312.
- Hoelzl, F., Bieber, C., Cornils, J.S., Gerritsmann, H., Stalder, G.L., Walzer, C., and Ruf, T. 2015. How to spend the summer? Free-living dormice (*Glis glis*) can hibernate for 11 months in non-reproductive years. *J. Comp. Physiol. B*, **185**(8): 931–939. doi:10.1007/s00360-015-0929-1.
- Hoogenboom, I., Daan, S., Dallinga, J.H., and Schoenmakers, M. 1984. Seasonal change in the daily timing of behavior of the common vole, *Microtus arvalis*. *Oecologia*, **61**(1): 18–31. doi:10.1007/BF00379084.
- Humphries, M.M., Thomas, D.W., Hall, C.L., Speakman, J.R., and Kramer, D.L. 2002. The energetics of autumn mast hoarding in eastern chipmunks. *Oecologia*, **133**(1): 30–37. doi:10.1007/s00442-002-1014-5.
- Humphries, M.M., Kramer, D.L., and Thomas, D.W. 2003a. The role of energy availability in mammalian hibernation: An experimental test in free-ranging eastern chipmunks. *Physiol. Biochem. Zool.* **76**(2): 180–186.

- Humphries, M.M., Thomas, D.W., and Kramer, D.L. 2003b. The role of energy availability in mammalian hibernation: A cost-benefit approach. *Physiol. Biochem. Zool.* **76**(2): 165–179. doi:10.1086/367950.
- Jaman, M.F., and Huffman, M.A. 2013. The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh. *Primates*, **54**(1): 49–59. doi:10.1007/s10329-012-0330-6.
- Jedrzejewski, W., Jedrzejewska, B., Zub, K., and Nowakowski, W.K. 2000. Activity patterns of radio-tracked weasels *Mustela nivalis* in Bialowieza National Park (E Poland). *Ann. Zool. Fenn.* **37**(3): 161–168.
- Jensen, P.G., Demers, C.L., McNulty, S.A., Jakubas, W.J., and Humphries, M.M. 2012. Marten and fisher responses to fluctuations in prey populations and mast crops in the northern hardwood forest. *J. Wildl. Manage.* **76**(3): 489–502. doi:10.1002/jwmg.322.
- Kenagy, G.J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology*, **54**(6): 1201–1219. doi:10.2307/1934184.
- Kenagy, G.J., Nespolo, R.F., Vasquez, R.A., and Bozinovic, F. 2002. Daily and seasonal limits of time and temperature to activity of degus. *Rev. Chil. Hist. Nat.* **75**(3): 567–581.
- Kenagy, G.J., Sharbaugh, S.M., and Nagy, K.A. 1989. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologia*, **78**(2): 269–282. doi:10.1007/BF00377166.
- Kitchen, A.M., Gese, E.M., and Schauster, E.R. 2000. Changes in coyote activity patterns due to reduced exposure to human persecution. *Can. J. Zool.* **78**(5): 853–857. doi:10.1139/cjz-78-5-853.

- Kohli, M., Sankaran, M., Suryawanshi, K.R., and Mishra, C. 2014. A penny saved is a penny earned: lean season foraging strategy of an alpine ungulate. *Anim. Behav.* **92**: 93–100. doi:10.1016/j.anbehav.2014.03.031.
- Kortner, G., and Geiser, F. 2000. The temporal organization of daily torpor and hibernation: Circadian and circannual rhythms. *Chronobiol. Int.* **17**(2): 103–128. doi:10.1081/CBI-100101036.
- Kozakai, C., Yamazaki, K., Nemoto, Y., Nakajima, A., Umemura, Y., Koike, S., Goto, Y., Kasai, S., Abe, S., Masaki, T., and Kaji, K. 2013. Fluctuation of daily activity time budgets of Japanese black bears: relationship to sex, reproductive status, and hard-mast availability. *J. Mammal.* **94**(2): 351–360. doi:10.1644/11-MAMM-A-246.1.
- Kuhn, K.M., and Vander Wall, S.B. 2008. Linking summer foraging to winter survival in yellow pine chipmunks (*Tamias amoenus*). *Oecologia*, **157**(2): 349–360. doi:10.1007/s00442-008-1072-4.
- Lacki, M.J., Gregory, M.J., and Williams, P.K. 1984. Spatial response of an eastern chipmunk population to supplemented food. *Am. Midl. Nat.* **111**(2): 414–416. doi:10.2307/2425338.
- Landry-Cuerrier, M., Munro, D., Thomas, D.W., and Humphries, M.M. 2008. Climate and resource determinants of fundamental and realized metabolic niches of hibernating chipmunks. *Ecology*, **89**(12): 3306–3316. doi:10.1890/08-0121.1.
- Larimer, S.C., Fritzsche, P., Song, Z., Johnston, J., Neumann, K., Gattermann, R., McPhee, M.E., and Johnston, R.E. 2011. Foraging behavior of golden hamsters (*Mesocricetus auratus*) in the wild. *J. Ethol.* **29**(2): 275–283. doi:10.1007/s10164-010-0255-8.
- Larivière, S., Huot, J., Samson, C., and Lariviere, S. 1994. Daily activity patterns of female black bears in a northern mixed-forest environment. *J. Mammal.* **75**(3): 613. doi:10.2307/1382508.
- LaZerte, S.E., and Kramer, D.L. 2011. Using thermosensitive radiotelemetry to document rest and activity in a semifossorial rodent. *Wildl. Soc. Bull.* **35**(4): 481–488. doi:10.1002/wsb.74.

- Leighton, P.A., Horrocks, J.A., and Kramer, D.L. 2010. Conservation and the scarecrow effect: Can human activity benefit threatened species by displacing predators? *Biol. Conserv.* **143**: 2156–2163.
- Loevy, M., Skliba, J., and Sumbera, R. 2013. Spatial and temporal activity patterns of the free-living giant mole-rat (*Fukomys mechowii*), the largest social bathyergid. *PLoS One*, **8**(1). doi:10.1371/journal.pone.0055357.
- Lovegrove, B.G. 1988. Colony size and structure, activity patterns and foraging behavior of a colony of the social mole-rat *Cryptomys damarensis* (Bathyergidae). *J. Zool. (Lond.)*, **216**: 391–402.
- Mattisson, J., Andrén, H., Persson, J., and Segerström, P. 2010. Effects of species behavior on global positioning system collar fix rates. *J. Wildl. Manage.* **74**(3): 557–563.
- Montiglio, P.-O., Garant, D., Pelletier, F., and Réale, D. 2012. Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Anim. Behav.* **84**(4): 1071–1079. doi: 10.1016/j.anbehav.2012.08.010.
- Munro, D., Thomas, D.W., and Humphries, M.M. 2005. Torpor patterns of hibernating eastern chipmunks *Tamias striatus* vary in response to the size and fatty acid composition of food hoards. *J. Anim. Ecol.* **74**(4): 692–700.
- Munro, D., Thomas, D.W., and Humphries, M.M. 2008. Extreme suppression of aboveground activity by a food-storing hibernator, the eastern chipmunk (*Tamias striatus*). *Can. J. Zool.* **86**(5): 364–370. doi:10.1139/Z08-008.
- Nunes, S., Muecke, E.M., Ross, H.E., Bartholomew, P.A., and Holekamp, K.E. 2000. Food availability affects behavior but not circulating gonadal hormones in maternal Belding's ground squirrels. *Physiol. Behav.* **71**(5): 447–455. doi:10.1016/S0031-9384(00)00366-8.

- Osgood, D.W., and Weigl, P.D. 1972. Monitoring activity of small mammals by temperature-telemetry. *Ecology*, **53**(4): 738–740. doi:10.2307/1934794.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Development Core Team. 2014. nlme: Linear and nonlinear mixed effects models. Available from <http://CRAN.R-project.org/package=nlme>.
- R Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/>.
- Roll, U., Dayan, T., and Kronfeld-Schor, N. 2006. On the role of phylogeny in determining activity patterns of rodents. *Evol. Ecol.* **20**(5): 479–490. doi:10.1007/s10682-006-0015-y.
- Ryan, D.A., and Larson, J.S. 1976. Chipmunks in residential environments. *Urban Ecol.* **2**(2): 173–178. doi:10.1016/0304-4009(76)90022-X.
- Schwagmeyer, P.L. 1988. Scramble-competition polygyny in an asocial mammal: Male mobility and mating success. *Am. Nat.* **131**(6): 885–892. doi:10.1086/284828.
- Sikes, R.S., Gannon, W.L., and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* **92**(1): 235–253. doi:10.1644/10-MAMM-F-355.1.
- Snyder, D.P. 1982. *Tamias striatus*. *Mamm. Species No.* **168**: 1–8. doi:10.2307/3503819.
- Strumwasser, F. 1959. Factors in the pattern, timing and predictability of hibernation in the squirrel, *Citellus beecheyi*. *Am. J. Physiol.* **196**(1): 8–14.
- Wasserberg, G., Kotler, B.P., and Abramsky, Z. 2006. The role of site, habitat, seasonality and competition in determining the nightly activity patterns of psammophilic gerbils in a centrifugally organized community. *Oikos*, **112**(3): 573–579. doi:10.1111/j.0030-1299.2006.14302.x.

- Wauters, L.A. 2000. Squirrels — medium-sized granivores in woodland habitats. *In* Activity Patterns in Small Mammals. *Edited by* S. Halle and N.C. Stenseth. Springer Berlin Heidelberg. pp. 131–143.
- Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer, New York.
- Williams, C.T., Wilsterman, K., Kelley, A.D., Breton, A.R., Stark, H., Humphries, M.M., Mcadam, A.G., Barnes, B.M., Boutin, S., and Buck, C.L. 2014. Light loggers reveal weather-driven changes in the daily activity patterns of arboreal and semifossorial rodents. *J. Mammal.* **95**(6): 1230–1239. doi:10.1644/14-MAMM-A-062.
- Wrazen, J.A. 1980. Late summer activity changes in populations of eastern chipmunks (*Tamias striatus*). *Can. Field-Nat.* **94**(3): 305–310.
- Yahner, R.H. 1977. Activity lull of *Tamias striatus* during the summer in southeast Ohio USA. *Ohio J. Sci.* **77**(3): 143–145.

Table 1. Activity levels and diurnality of eastern chipmunks (*Tamias striatus* (L., 1758)) in relation to year, period, day and night, and provisioning.

Year	Period	<i>n</i> total	<i>n</i> prov.	Diurnality	24-h activity	Daytime activity	Nighttime activity	24-h unprovisioned	24-h provisioned
2007	3 Late Summer (Jul-24 to Aug-14)	10	0	0.65 ± 0.36	0.11 (0.09 - 0.12)	0.15 (0.1 - 0.2)	0.03 (0.01 - 0.08)	0.11 (0.09 - 0.12)	
	4 Early Autumn (Aug-20 to Sep-14)	9	0	0.39 ± 0.48	0.07 (0.05 - 0.11)	0.07 (0.05 - 0.13)	0.06 (0.03 - 0.08)	0.07 (0.05 - 0.11)	
	5 Autumn (Sep-22 to Oct-03)	9	0	0.31 ± 0.37	0.06 (0.04 - 0.08)	0.09 (0.04 - 0.1)	0.03 (0.02 - 0.06)	0.06 (0.04 - 0.08)	
	Total (Jul-24 to Oct-03)	10	0	0.46 ± 0.42	0.08 (0.06 - 0.11)	0.10 (0.07 - 0.15)	0.04 (0.01 - 0.08)	0.08 (0.06 - 0.11)	
2008	1 Early Summer (Jun-26 to Jul-12)	3	3	0.82 ± 0.1	0.27 (0.24 - 0.36)	0.37 (0.34 - 0.52)	0.03 (0.03 - 0.04)		0.27 (0.24 - 0.36)
	2 Midsummer (Jul-17 to Jul-22)	5	3	0.55 ± 0.52	0.07 (0.03 - 0.17)	0.12 (0.03 - 0.24)	0.03 (0.01 - 0.03)	0.11 (0.07 - 0.15)	0.07 (0.05 - 0.12)
	3 Late Summer (Jul-28 to Aug-08)	6	3	0.85 ± 0.15	0.14 (0.07 - 0.30)	0.22 (0.10 - 0.47)	0.02 (0.01 - 0.03)	0.06 (0.05 - 0.08)	0.33 (0.26 - 0.39)
	4 Early Autumn (Aug-26 to Sep-14)	6	3	0.94 ± 0.06	0.35 (0.27 - 0.44)	0.65 (0.51 - 0.77)	0.02 (0.01 - 0.04)	0.25 (0.24 - 0.28)	0.45 (0.43 - 0.46)
	5 Autumn (Sep-22 to Oct-03)	6	3	0.82 ± 0.09	0.32 (0.29 - 0.42)	0.57 (0.51 - 0.76)	0.05 (0.04 - 0.08)	0.28 (0.22 - 0.31)	0.46 (0.38 - 0.46)
	Total (Jun-26 to Oct-03)	6	3	0.8 ± 0.26	0.26 (0.16 - 0.39)	0.48 (0.25 - 0.65)	0.03 (0.01 - 0.05)	0.19 (0.08 - 0.27)	0.33 (0.20 - 0.45)

Note: The date range and name for each period, the number of chipmunks recorded (n total), and the number that used supplementary provisioning (n prov) are shown. Diurnality is the mean diurnality index $\pm$ SD. Activity levels are medians of the individual proportions of time active, with 25th and 75th percentiles in parentheses.

Draft

Table 2. Linear mixed model examining the effects of year, period, and use of supplementary provisioning on mean 24-h activity of eastern chipmunks (*Tamias striatus* (L., 1758)), using custom independent contrasts.

Parameter	Estimate	SE	d.f.	t	P
(Intercept)	0.361	0.016	26	22.742	<0.0001 ***
Provisioned	0.231	0.039	26	5.939	<0.0001 ***
2008 vs. 2007	0.466	0.094	26	4.941	<0.0001 ***
2007: Avg(P4 + P5) vs. P3	-0.069	0.032	26	-2.188	0.038 *
2008: Avg(P4 + P5) vs. P3	0.191	0.040	26	4.750	0.0001 ***
2007: P5 vs. P4	-0.040	0.038	26	-1.066	0.296
2008: P5 vs. P4	-0.019	0.046	26	-0.417	0.680

Note: P3, P4 and P5 represent periods 3 (Late summer), 4 (Early autumn) and 5 (Autumn), respectively. * $P \leq 0.05$, *** $P \leq 0.001$.

Table 3. Post-hoc analysis of pair-wise differences in 24-h activity of eastern chipmunks (*Tamias striatus* (L., 1758)) between periods in 2008.

Paired periods	Estimate	SE	<i>z</i>	<i>P</i>
2 vs. 1	-0.109	0.039	-2.78	0.011 *
3 vs. 1	-0.035	0.039	-0.92	0.399
4 vs. 1	0.065	0.039	1.68	0.132
5 vs. 1	0.055	0.039	1.43	0.190
3 vs. 2	0.074	0.032	2.31	0.034 *
4 vs. 2	0.174	0.032	5.45	<0.0001 ***
5 vs. 2	0.165	0.032	5.15	<0.0001 ***
4 vs. 3	0.100	0.030	3.32	0.003 **
5 vs. 3	0.091	0.030	3.00	0.007 **
5 vs. 4	-0.010	0.030	-0.32	0.749

Note: *P*-values were adjusted for multiple tests using the Benjamini and Hochberg method.

Periods are 1 (Early summer), 2 (Midsummer), 3 (Late summer), 4 (Early autumn) and 5 (Autumn). * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 4. Linear mixed model examining the effects of year, period, and the use of supplemental provisioning on diurnality in eastern chipmunks (*Tamias striatus* (L., 1758)), using custom independent contrasts.

Parameter	Estimate	SE	df.	t	P
(Intercept)	0.653	0.045	26	14.501	<0.0001 ***
Provisioned	0.024	0.061	26	0.399	0.693
2008 vs. 2007	1.206	0.265	26	4.556	0.0001 ***
2007: Avg(P4 + P5) vs. P3	-0.301	0.160	26	-1.886	0.071
2008: Avg(P4 + P5) vs. P3	0.025	0.050	26	0.498	0.623
2007: P5 vs. P4	-0.080	0.191	26	-0.418	0.680
2008: P5 vs. P4	-0.120	0.058	26	-2.071	0.048 *

Note: P3, P4 and P5 represent periods 3 (Late summer), 4 (Early autumn) and 5 (Autumn), respectively. * $P \leq 0.05$, *** $P \leq 0.001$

Table 5. Torpor diurnality (mean diurnality index $\pm$ *SD*) and level (median proportion of time with 25th - 75th percentile in parentheses) over 24-h, day, and night of eastern chipmunks (*Tamias striatus* (L., 1758)).

Period	<i>n</i>	Diurnality of torpor	24-h torpor	Daytime torpor	Nighttime torpor
3	10		0.00 (0.00 - 0.00)	0.00 (0.00 - 0.00)	0.00 (0.00 - 0.00)
4	9	-0.32 $\pm$ 0.25	0.21 (0.16 - 0.36)	0.12 (0.09 - 0.38)	0.28 (0.19 - 0.31)
5	9	-0.29 $\pm$ 0.14	0.39 (0.34 - 0.60)	0.34 (0.29 - 0.60)	0.50 (0.40 - 0.61)
Total	10	-0.31 $\pm$ 0.19	0.20 (0.00 - 0.36)	0.12 (0.00 - 0.35)	0.25 (0.00 - 0.41)

Note: Periods are 3 (Late Summer), 4 (Early Autumn) and 5 (Autumn).

Figure Captions

Figure 1. Population medians of individual proportions of time per period or year spent either Active (black), Resting (grey) or Torpid (white). 2007 contains only unprovisioned eastern chipmunks (*Tamias striatus* (L., 1758)), while 2008 is split by unprovisioned and provisioned chipmunks. ND indicates that there were No Data for periods 1 and 2 in 2007 and for period 1 in unprovisioned chipmunks in 2008. Samples sizes are provided in Table 1.

Figure 2. Daily activity patterns of eastern chipmunks (*Tamias striatus* (L., 1758)) in 2007 (left) and 2008 (right) for 5 seasonal periods (1 - 5, top to bottom). The number of chipmunks sampled (n) is shown in the upper left of each panel. Grey areas indicate night (sunset to sunrise). Solid black lines indicate daily activity patterns (mean proportion of time active at each 15-min interval). Horizontal lines indicate population median activity levels for daytime (dashed red), and nighttime (dashed blue). ND indicates that there were no data for periods 1 and 2 in 2007.

Figure 1. Population medians of individual proportions of time per period or year spent either Active (black), Resting (grey) or Torpid (white). 2007 contains only unprovisioned chipmunks, while 2008 is split by unprovisioned and provisioned chipmunks. ND indicates that there were No Data for periods 1 and 2 in 2007 and for period 1 in unprovisioned chipmunks in 2008. Samples sizes are provided in Table 1.

Fig. 1

96x86mm (300 x 300 DPI)

Figure 2. Daily activity patterns of eastern chipmunks (*Tamias striatus*) in 2007 (left) and 2008 (right) for 5 seasonal periods (1 - 5, top to bottom). The number of chipmunks sampled (*n*) is shown in the upper left of each panel. Grey areas indicate night (sunset to sunrise). Solid black lines indicate daily activity patterns (mean proportion of time active at each 15-min interval). Horizontal lines indicate population median activity levels for daytime (dashed red), and nighttime (dashed blue). ND indicates that there were no data for periods 1 and 2 in 2007.

Fig. 2
149x167mm (300 x 300 DPI)