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The energetics of autumn mast hoarding in eastern chipmunks

Received: 6 August 2001 / Accepted: 18 June 2002 / Published online: 9 August 2002
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Abstract The timing and basis of the transition from energy reserve accumulation to reserve utilization in autumn may be a key determinant of winter survival in endotherms, but has rarely been examined directly in the field. In the present study we quantify the energetics of autumn mast hoarding in eastern chipmunks (*Tamias striatus*) to document the degree to which larder hoarding permits capitalizing on brief pulses of resource abundance and to evaluate the basis of the decision to stop hoarding and initiate hibernation. Daily energy expenditure, measured with the doubly labeled water technique, increased significantly with date and decreasing ambient temperature, eventually exceeding 3× resting metabolic rate in late autumn. Simultaneous documentation of food delivery to burrow larder hoards revealed that delivery rates were low in early autumn, extremely high for a brief period in mid-autumn, then low again in late autumn. Combining estimates of energy expenditure, consumption, and delivery yielded net energy surpluses of 1,320–4,600 kJ day⁻¹ during the peak hoarding period, meaning total hibernation energy requirements could be acquired in 1–2 days. These results, together with measures of food availability and ambient temperature, suggest that chipmunk activity in late autumn may be affected by both the extent of hoard accumulation and thermoregulatory constraints on sustained energy expenditure.

We speculate that both state-dependency and energetic ceilings on autumn hoarding behavior may enhance the capacity of the mast seeding strategy of trees to effectively swamp the foraging efforts of larder-hoarding granivores.

Keywords Energetics · Food hoarding · Forest ecology · Hibernation · Thermoregulation

Introduction

Winter is widely believed to represent a major energetic challenge to temperate and arctic endotherms because snow cover and low ambient temperatures simultaneously reduce resource availability and elevate resource requirements (King and Murphy 1985; Davenport 1992; Messier 1995; Speakman 2000). Many endotherms ameliorate this challenge by accumulating food or fat reserves in autumn and using these to support negative energy balances during winter (Vander Wall 1990; Robbins 1993). If the transition from reserve accumulation to the onset of reserve depletion is imposed by environmental conditions, its timing should be a direct determinant of winter survival (Murie and Boag 1984; Clutton-Brock et al. 1997); a later transition results in more reserve accumulation and a shorter winter period during which the reserve is used. Frequently, however, the transition from reserve accumulation to reduction coincides with a seasonal shift in habitats, foraging mode, and/or physiological status (e.g., migration, Dingle 1996; hibernation, Lyman et al. 1982) and its timing is likely to be influenced by individual state as well as environmental conditions (Houston and McNamara 1999). As a result, individuals with the largest reserves may undergo the transition first and survival may be independent of, or even diminish with, the latency of the transition.

Autumn immergence by hibernating mammals provides an extreme example of a transition between reserve accumulation and reserve reduction that coincides with changes in habitat occupation, behavior, and physiology.

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Following termination of above-ground activity in late summer or autumn, many hibernators rely completely on stored energy until spring emergence (Lyman et al. 1982; French 1992). Most hibernation research has been conducted on species that store energy in the form of body fat, but many hibernating species accumulate food in larder hoards during autumn then consume this food during periodic winter arousals (Humphries et al. 2001). The timing of autumn immergence by food- and fat-storing hibernators is partly influenced by circannual rhythms (Kenagy 1985), but in the field varies substantially between years and thus appears to be influenced by environmental conditions and/or individual state (e.g., Kawamichi 1996; Milesi et al. 1999). Although age and sex class differences and inter-annual variability in immergence dates have been documented in many fat-storing (e.g., Schooley et al. 1994; Michener 1984; Kunz et al. 1998) and some food-storing hibernators (O'Farrell et al. 1975; Kawamichi 1996), the role of environmental factors and individual state in determining the timing of immergence remain poorly understood.

The decision to terminate activity and initiate hibernation could depend on the energetic costs and benefits of additional activity as well the size of the energy reserve that has been accumulated. Hibernators might remain active in autumn as long as resource availability and thermoregulatory requirements permit additional reserve accumulation. For example, low ambient temperatures could cause termination of above-ground activity independent of resource availability, if maximum sustained energy expenditure is constrained by physiological ceilings (Hammond and Diamond 1997; Speakman 2000). Conversely, individuals might terminate activity as soon as a reserve of a given size has been acquired, if accumulating a larger reserve is associated with diminishing returns or made impossible by constraints on maximum storage capacity (Clark 1993; Witter and Cuthill 1993; Clarke and Kramer 1994).

The eastern chipmunk (*Tamias striatus*) is a hibernating rodent that specializes on mast seed produced by oak (*Quercus* spp.), beech (*Fagus grandifolia*), and maple (*Acer* spp.) trees throughout much of eastern North America (Elliot 1978; Snyder 1982). The major mast crops exploited by eastern chipmunks in northern deciduous forests ripen and fall to the ground in autumn and during this period individuals establish a larder hoard of seed in their burrow through intensive central place foraging (Elliot 1978; Giraldeau et al. 1994) and there is considerable spatial overlap in the foraging sites used by individual chipmunks (Getty 1981). Mast seeding by trees involves synchronous production of large amounts of seed in some years and little or none in others, and is speculated to increase seed survival by providing more seeds than predators can consume in one season (Janzen 1971; Silvertown 1980; Curran and Leighton 2000). Thus, chipmunks experience extreme inter-annual variation in food availability and their capacity to accumulate large hoards prior to hibernation may have direct relevance to the effectiveness of the mast seeding strategy.

In the present study, we document the energetics of autumn hoarding in eastern chipmunks during an acorn mast year by quantifying temporal patterns in food hoarding and energy expenditure between early and late autumn. This permits us to quantify the net energetic gain that can be achieved by larder hoarding and to evaluate the role of energy expenditure and resource availability in the decision to terminate above-ground activity and initiate hibernation.

Materials and methods

We studied eastern chipmunks in autumn 1997 at McGill University's Gault Nature Reserve, Mont Saint Hilaire, Québec, Canada (45.5°N, 73.1°W). The 25-ha study site consists of mature hardwood forest, with sugar maple (*A. saccharum*), American beech (*F. grandifolia*), and red oak (*Q. rubra*) representing the predominant canopy trees. Because the site is located within a public park, chipmunks are well habituated to humans; feeding animals is prohibited and actively discouraged throughout the park, but limited feeding does occur. Additional mast feeding mammals present in the study site include gray squirrels (*Sciurus carolinensis*), deer mice (*Peromyscus maniculatus*), and white-tailed deer (*Odocoileus virginianus*).

Chipmunks have been studied at this site for more than a decade using general methodology described by Clarke and Kramer (1994). Briefly, all chipmunks present in the study site are ear-tagged, have a known burrow location, and are individually marked for visual identification by clipping a unique pattern in their rump guard hairs. Individuals are live-captured using Longworth traps baited with sunflower seeds and set at burrow entrances. At each capture, body mass is measured to the nearest gram using a 200-g Pesola spring balance. Chipmunks forage diurnally on the forest-floor and occupy an extensive underground burrow at night and during inactive periods (Elliot 1978). In the northern portion of their range, chipmunks remain in their burrows throughout winter, expressing repeated bouts of prolonged torpor (Humphries et al., unpublished manuscript). We did not measure torpor patterns in this study, but consider the onset of hibernation to represent the commencement of winter inactivity (Nedergaard and Cannon 1990; Lyman et al. 1982) rather than the initiation of torpor expression.

We monitored population activity patterns from 7 September to 8 November 1997 with visual transect sampling, radio telemetry, and focal behavioral sampling. The transect consisted of a 1.5-km path that traversed the study site. The width of the transect was marked with flagging tape every 25 m, and varied between 3 and 25 m according to visibility. One of two observers slowly walked the transect and recorded the number and identity (via hair-clipped marks) of the chipmunks seen within the transect. Sampling effort was distributed systematically between 0800 and 1700 hours, and any multiple daily transects were condensed into a daily average. For radio tracking of activity patterns, ten adult male chipmunks were fitted with radio collars (Holohil Systems, Carp, Ontario, Canada; transmitter model Md-2c) in early summer under light anesthesia (Halothane). We then visited their burrow locations throughout autumn, two times per day between sunrise and sunset, and recorded whether they were in or out of their burrow. Based on these observations we calculated the proportion of individuals seen above ground each day and the last day each individual was observed. Two radio-collared chipmunks were killed by an unidentified predator in late summer, reducing this sample to eight individuals by autumn immergence.

From 17 September to 8 November 1997, we quantified the amount of food 15 focal chipmunks delivered to their burrow during a 2–4-day period coinciding with measurement of their daily energy expenditure. This sample did not include any of the radio-collared individuals used to monitor activity patterns. During each

individual's sampling interval, 2-h focal sessions were distributed systematically between sunrise and sunset, with the total observation time averaging 48% (range 18–72%, $n=15$ chipmunks) of daylight hours during the interval. Between sunrise and sunset, chipmunks do not express detectable periodicity in activity patterns (M.M. Humphries, C.L. Hall, unpublished data). Observations were conducted from 2-m-high towers situated 10 m from the focal chipmunk's burrow entrance. Each time a focal chipmunk entered its burrow, we attempted to identify the type and amount of food that was delivered to the burrow. Our ability to do this was greatly enhanced by red oak being the only autumn mast species producing a seed crop at our site in 1997. Red oak acorns are sufficiently large that chipmunks can load only one into each of their cheek pouches and their presence in a pouch forms a clearly visible, distinctly shaped, bulk. Thus, it was possible to identify when a chipmunk was delivering acorns to its burrow, and discern whether the load consisted of one, two, or three acorns (one in each cheek pouch plus one in the mouth; Kawamichi 1996). Approximately 8% of observed deliveries consisted of unidentified food items other than acorns. In these cases, the fullness of each cheek pouch was qualitatively scored from 0 (empty) to 3 (completely full).

The energetic value of the loads delivered to the burrow was estimated based on their average mass and energy content. Average dry mass of shelled acorns was assumed to be 1.57 g, based on measurements made on a subsample ($n=30$) of acorns collected during the study period for another project (Humphries et al. 2001), and was multiplied by red oak acorn energy content (22.13 kJ/g dry mass; Chung-MacCoubrey et al. 1997) and digestibility (80%; Humphries et al. 2001). In the rare instances when food other than acorns was delivered to the burrow, loads likely consisted of mushrooms, bulbs, and other miscellaneous items (Elliot 1978; C.L. Hall and M.M. Humphries unpublished data). Thus, we assumed a full cheek pouch (score=3) would approximate the dry mass of a single acorn and that its energy content would be 50% that of acorns (Robbins 1993). This is likely an over-estimate, but because the occurrence of the unknown items was sufficiently rare and the observed patterns sufficiently divergent (see Results), altering these assumptions has no effect on the trends reported. We calculated an hourly rate of energy delivery from the deliveries observed during focal observations, then converted this to a daily rate based on the number of daylight hours during the sampling interval.

We did not quantify the behavior of focal chipmunks when they were outside their burrows, and thus were unable to directly evaluate the extent to which food consumption away from the burrow contributed to their energy budgets. However, we estimated this contribution to be 30 kJ h⁻¹ above-ground (equivalent to one acorn per hour), based on behavioral observations of the radio-collared chipmunks used to monitor activity patterns. Observations consisted of 75, 30-min behavioral sampling sessions between 15 September and 21 October, and involved continuous recording of the amount of time individuals spent feeding and, whenever possible, the identity and number of food items ingested. Recording the number of items ingested was almost always possible for acorn feeding, which represented 83% of identified-item feeding time. Based on the mass, energetic value, and digestibility of acorns (see above), we converted feeding observations into estimated ingestion rates (kJ h⁻¹). Similarly, we assumed non-acorn food items yielded half the energy intake rate of acorns. Estimated ingestion rates did not change significantly with date ($r^2=0.01$, $F_{1,72}=0.92$, $P=0.34$). Because chipmunks do not accumulate sizeable fat reserves in autumn (Wrazen and Wrazen 1982), the contribution of feeding to the daily energy budget can be assumed to not exceed daily energy expenditure. Accordingly, we multiplied the time focal chipmunks spent above-ground by the average ingestion rate (30 kJ h⁻¹) and credited their daily energy balance accordingly, up to a maximum of their measured daily energy expenditure.

Daily energy expenditure was measured using the doubly labeled water method (Speakman 1997). Chipmunks were lightly anesthetized with Halothane and injected intraperitoneally with 150 μ l of ¹⁸O (95 atom %) and H₂ (5 ml 99.9% in 100 ml). Fol-

lowing injections, individuals were returned to Longworth traps for a 1-h equilibration period, then duplicate blood samples were collected with heparinized microhematocrit tubes from a clipped toenail. Chipmunks were recaptured 48 h ($n=3$, range 46.0–49.5), 72 h ($n=2$, 71.9–74.1), 96 h ($n=6$, 96.0–97.1), or 120 h ($n=1$, 120.0) later, and a second, duplicate blood sample was taken. Blood samples were frozen until stable isotope analyses were conducted at the Department of Zoology, University of Aberdeen, UK, using methodology described by Speakman (1997). CO₂ production was calculated using the single pool, plateau model, and converted to energy expenditure based on 21.9 J ml⁻¹ CO₂. Two previous studies have validated the doubly labeled water method in eastern chipmunks, having shown the technique to produce estimates of CO₂ production within 1–13% of values measured with flow-through respirometry (Little and Lifson 1975; Randolph 1980).

We documented air and soil temperature during each chipmunk's sampling interval with HOBO data loggers (Onset Computer Corporation, Pocasset, Mass., USA). One temperature probe was installed 2–3 cm above the leaf litter near the burrow entrance of the focal chipmunk and a second was inserted into the soil nearby to the approximate depth of chipmunk burrows (Elliot 1978) using a narrow, 1-m-long, soil probe. Temperatures were recorded at 2–10 min intervals, to the nearest 0.1°C. An index of the thermal environment experienced by each chipmunk was then calculated according to

$$T_{index} = [1 - L(A)]T_{soil} + [L(A)]T_{air}$$

where L is the proportion of daylight hours during the sampling interval, A is an activity index calculated from focal observations that reflects the proportion of time spent above-ground during daylight hours, and T_{soil} and T_{air} are average soil and average daytime air temperatures, respectively. This thermal index implicitly assumes activity during the day is independent of air temperature (see Results).

Finally, food availability on the forest floor was measured with belt transect sampling under the canopies of red oak, American beech, and sugar maple trees. Individual trees of each species within the study site were randomly selected, and 20-cm-wide belt transects running from the tree trunk to the canopy drip line were marked in two random compass directions. The number of acorns, beechnuts and maple seeds found within the belt transect, on top of or within the leaf litter, was recorded. Seeds were classified according to ripeness and opened to check for insect infestation; for the present analysis only ripe and uninfested seeds are considered. Sampling effort was concentrated during mid-October and just after snowmelt the following spring to permit documentation of resource availability during and after the period when most of the population terminated above-ground activity.

Results

Transect and telemetry sampling indicated medium to high levels of above-ground activity throughout September and early October, with levels generally increasing over-time. Activity patterns then changed abruptly in mid-October when most individuals in the population terminated above-ground activity (Fig. 1). All radio-collared chipmunks were last seen outside of their burrows 14–21 Oct (median date 20 October). This synchronous termination of above-ground activity coincided with a brief period of unseasonably low ambient temperatures (Fig. 2). Although temperatures soon increased to unseasonably warm levels, there was little reversion to above-ground activity, with only three individuals in the entire study site being characterized by above-ground activity. During the interval when most chipmunks disappeared

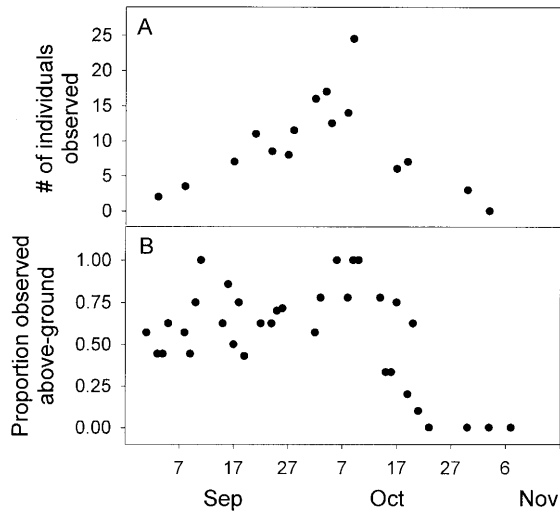


Fig. 1 Population activity patterns of eastern chipmunks (*Tamias striatus*) during an acorn mast year at Mont St Hilaire, Québec, Canada. **A** Number of individuals observed along a 1.5-km transect. **B** Proportion of radio-collared adult males ($n=10$) observed above ground daily

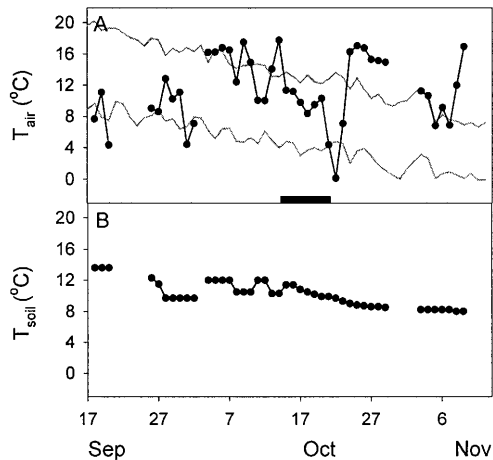


Fig. 2 Environmental temperature patterns during autumn 1997 at Mont St Hilaire. **A** Average daylight temperatures recorded outside the burrow entrances of focal chipmunks. *Gray lines* indicate 19-year average daily highs and lows for the region (Saint-Hyacinthe weather station, 45.6°N, 73.0°W; Direction des Réseaux Atmosphériques, Environment-Québec) and the *black bar* reflects the range in immersion dates of radio-collared chipmunks ($n=8$). **B** 24-h average soil temperatures recorded approximately 1 m below ground, adjacent to burrows of focal chipmunks

below ground, food availability remained favorable for additional hoard accumulation. Acorn density underneath oak trees averaged 5.6 ± 2.9 acorns m^{-2} (mean \pm SE; $n=14$ trees) between 10 and 18 October, and acorns remained readily available until snow cover as indicated by a density of 1.5 ± 0.5 acorns m^{-2} ($n=15$ trees) early the next spring (19 April–6 May 1998). Note that only intact acorns without evident mold or insect infestation upon opening were included in these counts.

Activity patterns of focal chipmunks were highly variable, with the percentage of 2-h focal sessions where

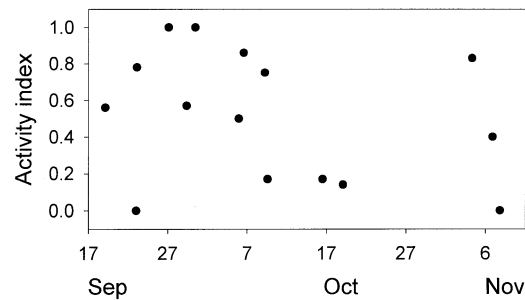


Fig. 3 Activity patterns of focal chipmunks during autumn. Each point represents a different chipmunk, observed for a 2–4-day sampling interval. The activity index indicates the proportion of 2-h focal sessions during which the individual was observed above-ground. The absence of data points between 19 October and 3 November and after 7 November results from no chipmunks being located above ground, despite intensive searching throughout the study site

above-ground activity was observed ranging from 0–100% (mean=51%, SE=10%, $n=15$; Fig. 3). Most animals studied prior to 10 October had relatively high levels of activity, but following this date activity was much lower (Fig. 3). During late October few additional chipmunks could be located despite intensive searching throughout the study site, including transect and telemetry sampling; two individuals were briefly observed in late October, but became inactive prior to live-capture. Three late-immersing chipmunks were then discovered in early November and their rates of energy delivery ($n=3$) and expenditure ($n=2$) were successfully documented. Following this period, no additional above-ground activity was detected.

Like activity, daily energy delivery to the burrow by focal chipmunks was highly variable (Fig. 4a). The highest delivery rates were observed in four individuals measured successively from 29 September to 9 October (89 ± 35 acorns day^{-1} , $2,464 \pm 962$ kJ day^{-1} ; mean \pm SE). The individual that realized the highest hoarding rate during this period delivered on average more than 14 acorns to its burrow each hour of observation, producing an estimated daily delivery rate of 165 acorns or 4,600 kJ day^{-1} . With the exception of these four individuals, delivery rates were generally low throughout autumn, ranging from 0 to 9 acorns (0–250 kJ) per day.

Measures of daily energy expenditure were successfully obtained for 12 of the 15 focal individuals, and averaged 163 kJ day^{-1} (range 70–345 kJ day^{-1} ; Fig. 4b). Inter-individual variation in body mass of chipmunks was very low (100.0 ± 1.7 g; CV=0.06; range 87–113 g), and, presumably as a result, energy expenditure was not significantly correlated with body mass ($r=0.11$, $P=0.74$). Because of this, and to facilitate direct comparison with energy delivery rates, whole animal rates of energy expenditure (rather than weight-specific measures) were used in all subsequent analyses. Daily energy expenditure increased significantly with date ($r^2=0.52$, $F_{1,10}=10.7$, $P=0.008$; Fig. 4b), and the relationship remained statistically significant if the two November values were omit-

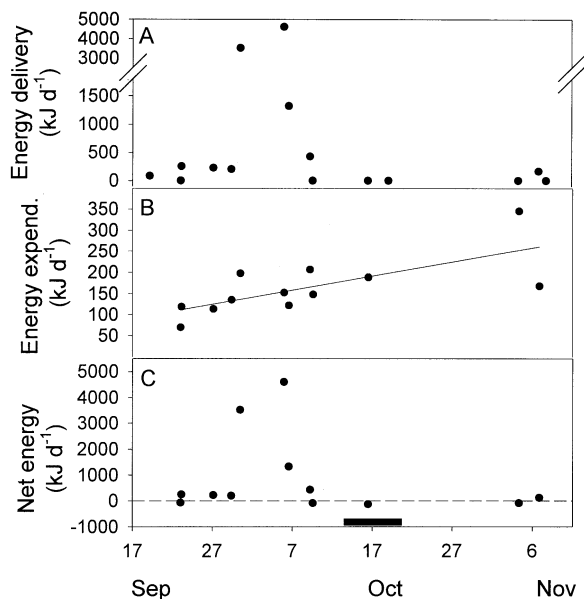


Fig. 4 Energy delivery, expenditure, and balance of focal chipmunks during autumn. **A** Daily energy delivery, based on the number and energetic value of food items larder hoarded to the burrow. **B** Daily energy expenditure, measured on the same individuals during the same sampling interval, using the doubly labeled water method. **C** Daily net energy balance, which combines observed rates of energy delivery (**A**) and expenditure (**B**), and estimated food consumption away from the burrow. The *black bar* indicates the range in immersion dates of radio-collared chipmunks ($n=8$). Otherwise, as stated in Fig. 3 caption

ted ($r^2=0.48$, $F_{1,8}=7.4$, $P=0.027$). This trend does not appear to be related to differences in activity as there was no relationship between energy expenditure and the proportion of focal sessions chipmunks were observed above ground ($r^2=0.087$, $F_{1,10}=1.0$, $P=0.35$). Instead, the increase appears related to declining ambient temperatures, as there was a significant, negative relationship between daily energy expenditure and ambient temperature during the sampling interval ($r^2=0.47$, $F_{1,10}=9.0$, $P=0.01$; Fig. 5). This relationship remains significant if the outlying, high expenditure value (345 kJ day^{-1}) is omitted from the analysis ($r^2=0.41$, $F_{1,9}=6.2$, $P=0.03$).

Despite the effect of ambient temperature on daily energy expenditure, chipmunk activity was not oriented to warmer portions of the day. Focal sessions with above-ground activity occurred at temperatures not significantly different from the average daily temperature on the day they occurred (mean difference $+0.62^\circ\text{C}$; paired $t_{36}=0.99$, $P=0.33$). Further, this temperature differential (temperature when active – average daily temperature) did not change with date ($r^2=0.003$, $F_{1,35}=0.11$, $P=0.75$), indicating that temperature discrimination did not increase as autumn advanced and ambient temperatures became cooler.

Combining estimates of above-ground ingestion, energy delivery, and energy expenditure reveals that 4 of 12 chipmunks had negative net energy balances (mean $=-97 \text{ kJ day}^{-1}$, range -70 to -133 kJ day^{-1}), 5 of 12 had slightly positive balances (mean $=243 \text{ kJ day}^{-1}$, range 116 – 427 kJ

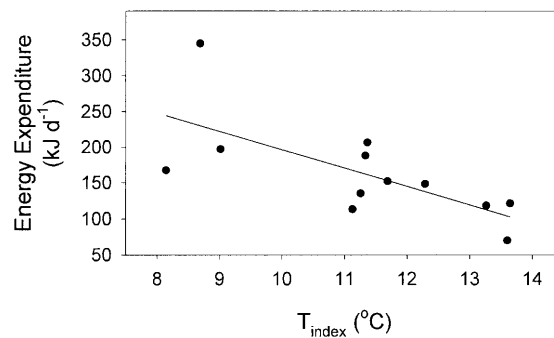


Fig. 5 Relationship between environmental temperature and daily energy expenditure. The temperature index reflects a combination of soil temperatures and daytime air temperatures, modified according to the proportion of daylight hours individuals spent outside the burrow

day^{-1}), and 3 of 12 had substantially positive balances (mean $=3,143 \text{ kJ day}^{-1}$, range $1,320$ – $4,598 \text{ kJ day}^{-1}$; Fig. 4c). The net accumulation rates attained by these latter three individuals translates into 20 days of average energy requirements (163 kJ day^{-1}) accumulated in a single day. Because energy delivery ($\text{CV}=1.96$) was substantially more variable than energy expenditure ($\text{CV}=0.42$), variation in net energy balances basically reflected variation in gross energy delivery (compare Fig. 4a and 4c).

Discussion

Our results demonstrate that larder hoarding is indeed a highly effective strategy for capitalizing on brief periods of resource abundance. The maximum observed rate of net daily energy delivery to the burrow ($4,600 \text{ kJ day}^{-1}$), indicates that nearly one month (~ 28 days) of average euthermic energy requirements (163 kJ) can be accumulated in a single day. Given that chipmunks are capable of expressing prolonged torpor bouts throughout winter, and that this reduces total energy requirements to 15% of average euthermic requirements (Wang and Hudson 1971), the gain of $4,600 \text{ kJ}$ in a single day could satisfy an entire winter's worth of energy requirements ($4,500 \text{ kJ}$, assuming a winter duration of 6 months). Kawamichi (1996) reported that Siberian chipmunks (*T. sibiricus*) hoarding acorns (*Q. mongolica* and *Q. dentata*) in autumn achieved a maximum daily delivery rate of 170 acorns day^{-1} , which represents approximately $3,010 \text{ kJ day}^{-1}$ (based on average acorn mass provided by Kawamichi, dry mass $=0.5$ wet mass, and a similar energetic value as *Q. rubra*).

Because food hoarding permits circumvention of the ingestive (Kersten and Visser 1996; Klaassen et al. 1997; Abrams and Schmitz 1999) and storage capacity constraints (Lindstedt and Boyce 1985) associated with fat storage, food-hoarding hibernators should have the capacity to accumulate more energy, more quickly than fat-storing species. Maximum energy accumulation by fat-storing hibernators in autumn appears limited to approximately 40% of body mass (Kunz et al. 1998; Buck and Barnes

1999). Thus a 100-g fat-storing hibernator could have a maximum of ~40 g fat or 1,440 kJ available at the onset of hibernation (assuming 36 kJ g⁻¹ fat; Blem 1990). Further, accumulating a reserve of this size typically requires weeks (e.g., *Myotis lucifugus*, 3–4 weeks, Kunz et al. 1998; *Zapus princeps*, 4–5 weeks, Cranford 1983; *Burramys parvus*, 4–5 weeks, Körtner and Geiser 1995) to months (e.g., *Spermophilus richardsoni*, 2–3 months, Bintz 1988; *Spermophilus parryi*, 2–3 months, Buck and Barnes 1999; *Marmota marmota*, 3–4 months, Körtner and Heldmaier 1995) of hyperphagia. In contrast, a 100-g food-storing hibernator can accumulate the energetic equivalent of 122 g of fat in a single day, given sufficient food availability. However, reliance on a food hoard is associated with disadvantages not experienced by fat-storing species, including hoard pilferage, perishability, and ingestion requirements (Vander Wall 1990; Humphries et al. 2001).

What determines the timing of autumn immergence?

Net energy balance

If chipmunks terminated activity when additional activity was energetically possible, but not energetically beneficial, we would expect expenditure and delivery rates to converge as autumn advanced and individuals to terminate above-ground activity when net energy balances approximated zero. Consistent with this, the termination of above-ground activity by most of the population coincided with net energy balances of focal chipmunks dramatically decreasing from highly positive to slightly positive or negative levels. These declines, however, appear due to reduced hoarding activity rather than resource shortage. During the 10–18 October interval when above-ground activity of the population as a whole (Fig. 1) and focal animals in particular (Fig. 3) rapidly declined, acorns remained readily abundant on the forest floor. We did not monitor temporal changes in acorn abundance throughout the autumn, and thus cannot exclude the possibility that the termination of above-ground activity coincided with a decrease in food availability. But the average density of nearly 6 acorns m⁻² present during mid-October, and even the 1.5 acorns m⁻² available the following spring, clearly should have been sufficient for chipmunks to achieve high rates of energy delivery to the burrow, had they continued active hoarding. Furthermore, since net energy budgets during autumn were much more dependent on delivery rates than energy expenditure, high food abundance should have permitted a positive energy balance despite the small increase in expenditure from early- to mid-October. Thus, we suggest that chipmunks terminated above-ground activity when resource abundance and climatic conditions still permitted energy accumulation.

Expenditure constraint

Physiological ceilings on sustained metabolism are speculated to occur at 3–4× resting metabolic rate (RMR),

although much higher metabolic scopes have been documented (Drent and Daan 1980; Hammond and Diamond 1997; Speakman 2000). If a constraint on sustainable expenditure led to the termination of above-ground activity, daily rates of expenditure would be expected to increase from early to late autumn and reach 3–4×RMR when individuals began disappearing below ground. Our results were generally consistent with these expectations as daily energy expenditure increased significantly with date and declining ambient temperature, and the predicted mass-specific rate of expenditure during early November (256 kJ day⁻¹) was 3.2–3.8× the RMR of this species (Neumann 1967, 67 kJ day⁻¹; Wang and Hudson 1971, 81 kJ day⁻¹). Expenditure levels were lower in mid-October when most of the population terminated above-ground activity (191 kJ day⁻¹; 2.4–2.9×RMR), but the short period of cold temperatures that followed soon after (Fig. 2) would have necessitated rates of expenditure in excess of 3.5×RMR (predicted from temperature data assuming 50% above-ground activity and Fig. 5 regression equation). Thus, limits to sustained metabolism resulting from thermoregulatory requirements may serve as both a general constraint on the potential duration of activity in autumn and a short-term cue prompting individuals to terminate above-ground activity.

Nevertheless, daily and seasonal variability in ambient temperature created opportunities for additional activity with sustainable thermoregulatory requirements that were not taken advantage of by chipmunks. Daily activity patterns may also be influenced by temporal changes in predation risk (Lima and Dill 1990) or competitive advantage (Getty 1981; Milinski and Parker 1991), but autumn activity by chipmunks did not vary with ambient conditions in a manner that permitted maximum hoard accumulation given an expenditure constraint. Thus, although energy expenditure was sufficiently high in late autumn to constrain late season activity by chipmunks, under the particular conditions we studied, there appeared to be opportunities for additional resource accumulation that were not exploited.

Extent of hoard accumulation

If there is a constraint on maximum reserve size or diminishing returns associated with large reserves, chipmunks could be expected to immerge once a reserve of a given size has been acquired, despite opportunities for additional hoard accumulation. Because chipmunks quickly accumulated large amounts of stored energy, then terminated activity while resource availability and thermal conditions still permitted additional hoard accumulation, we speculate that the decision to initiate hibernation was at least partly determined by the extent of hoard accumulation. The average rates of energy delivery we observed in late September and early October were sufficiently high that chipmunks required only a few days of sustained hoarding activity to accumulate the energy required to survive hibernation. Because chipmunks typically occupy

large, complex burrows (Elliot 1978), burrow capacity is not likely to constrain maximum hoard size (Clarke and Kramer 1994). Additional energy accumulation beyond the minimum requirement may be beneficial in reducing torpor requirements during hibernation (French 1988), supporting subsequent spring reproduction, and potentially even as a multi-annual energy reserve (Elliot 1978; Vander Wall 1990), but the benefits are likely to be characterized by diminishing returns due to the possibility of hoard perishability and pilferage. Thus, we suggest that the extent of hoard accumulation affected how closely activity patterns of different individuals approached constraints imposed by energetic ceilings.

The behavioral decisions made by animals are increasingly realized to depend on their current energetic state (Clarke 1993; Houston and McNamara 1999). Frequently state involves the level of internal fat reserves, but external food reserves represent an energetically analogous situation. If the survival and reproductive benefits of hoard accumulation are characterized by diminishing returns, chipmunks could be expected to terminate autumn activity while additional hoard accumulation remains energetically feasible. This decision could be entirely dependent on accumulated hoard size, or could involve an interaction between hoard size and increasing energetic costs or risk of predation.

Implications for mast seeding and the timing of autumn immergence

Many birds and mammals are known to hoard large amounts of seed during masting events (reviewed by Vander Wall 1990), and this capacity could reduce the effectiveness of masting for promoting seed germination. Larder hoarding permits the rapid accumulation of large amounts of seed and typically prevents the seed from successfully germinating even if it is not eventually consumed (Vander Wall 1990). Theoretical models that demonstrate a predator satiation benefit of masting assume seed consumers are characterized by a saturating functional response (Ims 1990; Lalonde and Roitberg 1992), and even with this assumption, high predator search efficiency combined with low handling times eliminate any benefits of masting (Lalonde and Roitberg 1992). Larder hoarding offers a granivore the potential of a non-saturating functional response, very low handling times and associated increases in search efficiency, and thus could plausibly eliminate the adaptive value of masting. Nevertheless, our data suggest that energy accumulation by larder hoarders may be influenced by seasonal energetic constraints and state-dependency, and both factors are capable of generating the saturating functional responses required for mast seed escape. Because many mast crops ripen in autumn, ceilings on sustainable metabolism may facilitate seed escape by constraining the late season activity of endotherm consumers. Accordingly, the optimal timing of seed fall for temperate-zone trees may represent a trade-off between the

benefits of late seed maturation in minimizing exploitation by seed predators and of early maturation in ensuring seed fall precedes snow cover (Young 1992). Similarly, state-dependency by seed consumers could generate the saturating functional responses necessary for seed escape. In this case, predation risk or other non-energetic costs of above-ground activity would cause food hoarders to immerse while seeds remained available on the forest floor. Interestingly, because prey are highly responsive to temporal and spatial variation in predation risk (Lima and Dill 1990; Lima and Bednekoff 1999), continued presence of predators in forest habitats may help to maintain this state-dependency and thus may indirectly contribute to successful forest regeneration.

Under the influence of state-dependency, the timing of autumn immergence by hibernators becomes difficult to predict. High ambient temperatures and abundant resources could prolong autumn activity by delaying the transition from positive to negative energy balances, but could also abbreviate autumn activity by facilitating rapid accumulation of large energy reserves. Thus, although some hibernators have shorter active seasons in years when resources are abundant (O'Farrell et al. 1975; Michener 1984), others respond to abundant resources by delaying immergence (Larivière et al. 1994; Schooley et al. 1994; Kawamichi 1996). In the year we studied eastern chipmunks, most of the population appeared to acquire a large food hoard in late September and early October then quickly terminated above-ground activity. The return of warmer temperatures combined with abundant resources made additional hoarding possible in late October and early November, but few individuals took advantage of the opportunity. Whether chipmunks would have immersed earlier or later in an autumn with lower resource abundance depends whether past reserve accumulation is more or less important than the potential for additional accumulation. Combining experimental manipulations of reserve size with the energy budget approach used in this study should permit direct evaluation of the role of past earnings and future potential in the energetic decisions animals make.

Acknowledgements We thank T. Low, S. Foster, and G. Kramer for assisting with the fieldwork, and M. Lechowicz and the staff at the Gault Nature Reserve for logistical support and permission to conduct the study. The research was financially supported by NSERC research grants to D.L.K. and D.W.T.

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