



10-8-2009

Formation and contents of yellow-pine chipmunk (*Tamias amoenus*) winter larders

Kellie M. Kuhn

University of Nevada, Reno, kellie.kuhn@uconn.edu

Stephen B. Vander Wall

University of Nevada, Reno, sv@unr.edu

Follow this and additional works at: <https://scholarsarchive.byu.edu/wnan>

Recommended Citation

Kuhn, Kellie M. and Vander Wall, Stephen B. (2009) "Formation and contents of yellow-pine chipmunk (*Tamias amoenus*) winter larders," *Western North American Naturalist*. Vol. 69 : No. 3 , Article 4. Available at: <https://scholarsarchive.byu.edu/wnan/vol69/iss3/4>

This Article is brought to you for free and open access by the Western North American Naturalist Publications at BYU ScholarsArchive. It has been accepted for inclusion in Western North American Naturalist by an authorized editor of BYU ScholarsArchive. For more information, please contact scholarsarchive@byu.edu, ellen_amatangelo@byu.edu.

FORMATION AND CONTENTS OF YELLOW-PINE CHIPMUNK (*TAMIAS AMOENUS*) WINTER LARDERS

Kellie M. Kuhn^{1,3} and Stephen B. Vander Wall²

ABSTRACT.—Despite much attention to the foraging habits and hibernation patterns of food-storing mammals, little is known about the contents of winter larders under natural conditions or how animals prepare a winter larder. Here we describe the contents of 15 yellow-pine chipmunk (*Tamias amoenus*) winter larders from 3 different years and describe the movement of scatter-hoarded seeds into larders. We found larders by locating 14 radio-collared chipmunks in their winter dens. One additional larder was found by tracking the movement of seeds labeled with radioactive scandium-46 from scattered caches into the larder. Chipmunks formed winter dens and rapidly provisioned winter larders in the fall, just before the onset of winter. Surface caches were dynamic, with seeds residing in 1–6 cache sites ($\bar{x} = 2.6$, $s = 1.1$) before being found in the larder. Distances from scattered caches to the winter larder were 34.5 m ($s = 17.1$). Contents of winter larders consisted of pine and shrub seeds. In 14 of the 15 larders, pine seeds contributed most to the size and caloric content of larders. Pine seeds and other seeds found in winter larders were produced by plants 2–4 months before the onset of winter. We conclude that if yellow-pine chipmunks did not scatter-hoard seeds during summer and autumn, seeds would not have been available for use in winter larders.

Key words: caloric content, larder-hoarding, scatter-hoarding, *Tamias amoenus*, *Sciuridae*, winter larder, yellow-pine chipmunk.

Many small mammals are seasonally dormant (e.g., hibernators) and use metabolic depression to reduce energy consumption during periods of food scarcity (Lyman et al. 1982, Tauber et al. 1986, Ultsch 1989). Animals become dormant when the cost associated with being active is higher than the cost of hibernating (Michener 1984, Bucks and Barnes 1999, Neuhaus et al. 1999, Humphries et al. 2003). Mammals that hibernate store food, accumulate body fat, or do both during the active season to provide themselves sufficient energy to survive the winter. Some small mammals circumvent possible energy storage limitations by storing food rather than fat (French 1988, McNab 2002). For food-storing species, the contents of winter larders are critical for winter survival and can influence body condition in the spring (e.g., Barnes 1984, Place et al. 2002).

Sciurid rodents are a group of small mammals for which hibernation has been well studied (e.g., Stebbins and Orich 1977, MacLean 1981, Wrazen and Wrazen 1982, Barnes 1984, Michener 1984, Geiser and Baudinette 1990, Geiser et al. 1990, French 2000, Humphries

et al. 2001, 2003, Hut et al. 2002, Place et al. 2002, Landry-Cuerrier et al. 2008). Despite much research on the physiology of hibernation and the importance of the winter larder in overwinter survival, few studies have described the contents of larders (summer larders: Allen 1938, Hawbecker 1940, Jennings 1975, Elliott 1978, Kawamichi 1989; winter larders: Broadbooks 1958, Kuhn and Vander Wall 2008), and little is known about how these animals prepare a winter larder. In order to fully understand hibernation patterns and the physiology of hibernation in food-storing hibernators, it is important to know how much food is stored in winter larders under natural conditions.

Yellow-pine chipmunks (*Tamias amoenus*, 40–50 g) are scatter-hoarding sciurid rodents that are seasonally dormant. In the active season, yellow-pine chipmunks gather seeds as they become available and store them in many scattered cache sites (Broadbooks 1958). To survive the winter, chipmunks sharply decrease their activity and food consumption and conserve energy by using intermittent bouts of torpor (Stebbins and Orich 1977, French 2000). Yellow-pine chipmunks do not accumulate

¹Department of Biology, University of Nevada, Reno, Reno, NV 89557.

²Department of Biology and the Program of Ecology, Evolution and Conservation Biology, University of Nevada, Reno, Reno, NV 89557.

³Present address: University of Connecticut, Department of Ecology and Evolutionary Biology, 75 North Eagleville Road, Unit 3043, Storrs, CT 06269-3043. E-mail: kellie.kuhn@uconn.edu

body fat before hibernation (Tevis 1952). Instead they collect a large number of scattered food items and store them in a single winter larder (Broadbooks 1958, this study). While in their winter dens, chipmunks arouse periodically to eat and excrete waste. Without stored food, chipmunks could not survive the winter (Aunfried and Arkhipov 2004). Here we describe temporal and spatial movement of scatter-hoarded seeds into larders and document contents of winter larders of yellow-pine chipmunks.

METHODS

Study Site

We conducted this study in the Whittell Forest and Wildlife Area (39°15'64"N, 119°52'49"W) on the east slope of the Carson Range in western Nevada at an elevation of 1975–2000 m, about 30 km south of Reno. Vegetation at the site consisted of open Jeffrey pine (*Pinus jeffreyi*) forest with lodgepole pine (*Pinus contorta*) and a shrub understory of antelope bitterbrush (*Purshia tridentata*), greenleaf manzanita (*Arctostaphylos patula*), tobacco brush (*Ceanothus velutinus*), and Sierra bush chinquapin (*Castanopsis sempervirens*). Seven species of sciurid rodents are found on the study site: yellow-pine chipmunks, long-eared chipmunks (*Tamias quadrimaculatus*), lodgepole chipmunks (*Tamias speciosus*), golden-mantled ground squirrels (*Spermophilus lateralis*), California ground squirrels (*Spermophilus beecheyi*), Douglas squirrels (*Tamiasciurus douglasii*), and western gray squirrels (*Sciurus griseus*). Among all rodent species found on the study site, yellow-pine chipmunks, deer mice (*Peromyscus maniculatus*: Muridae), and golden-mantled ground squirrels are most abundant.

Larder Formation from Scatter-hoarded Caches

It is rare to observe seeds being recovered and then recached. Therefore, to demonstrate the movement of seeds among scatter-hoarded caches and the movement of seeds from scattered cache sites into a winter larder, we include data collected as part of a broader study on the scatter-hoarding behavior of yellow-pine chipmunks (Vander Wall 2002, 2003). To track the movements of seeds, we located 1036 seed caches labeled with radioactive

scandium-46 in the fall of 2000. We used 3 species of pine seeds (sugar pine, *Pinus lambertiana*; Jeffrey pine; and ponderosa pine, *Pinus ponderosa*). Sugar pine and ponderosa pine are native to the area, but they did not occur on our study site. Each seed was uniquely numbered with indelible ink, which allowed us to follow the fates of individual seeds. Few other pine seeds were produced by trees in the vicinity in autumn 2000.

Radioactive seeds were deployed under a single Jeffrey pine tree (hereafter referred to as the source tree) between 9 and 11 September 2000 (methods detailed in Vander Wall 2002, 2003). On 12 September, we began surveying the area around this source tree with Geiger counters to locate cached and eaten seeds. When we located a cache, we excavated the seeds, recorded the numbers on them, buried them at the cache site at the original depth, and mapped the cache location relative to the source tree using cardinal directions as x- and y-axes. Care was taken to not touch seeds and to leave no indication of our digging visible to the human eye. To detect whether cached seeds were being moved and recached, we conducted 3 separate surveys over the following 2 months (until 11 November) of the area extending out over 60 m from the source tree, covering approximately 0.75 ha for each survey.

As a result of the long-term tracking, we located a large number of radio-labeled seeds in a chipmunk den on 15 November 2000. We used these labeled seeds to reconstruct the spatial and temporal dynamics of seeds moved from scatter-hoarded caches into a larder. We excavated and collected the nest and its contents on 18 November. We separated the labeled pine seeds in the field and recorded the numbers on each seed. The rest of the larder was taken to a laboratory at the University of Nevada in Reno, where other seeds were separated, counted, and weighed. We used the numbers on seeds to reconstruct spatial and temporal patterns of scatter-hoarding behavior and larder formation. Using map coordinates, we calculated the minimum distance chipmunks moved seeds from the source tree to cache sites, between successive cache sites occupied by the same seed, and from cache sites to the winter larder. If rodents moved 2 or more seeds together, only 1 distance was recorded.

TABLE 1. Caloric contents and sizes of seeds found in yellow-pine chipmunk larders.

Species of seed	$\text{kJ} \cdot \text{g}^{-1}$ (edible mass)	Kernels $\cdot \text{g}^{-1}$	Source
<i>Pinus jeffreyi</i>	25	11	Vander Wall 1995
<i>Pinus albicaulis</i>	27	12	Smith 1968
<i>Pinus contorta</i>	26	216	Smith 1968
<i>Pinus lambertiana</i>	27	7	this study
<i>Pinus ponderosa</i>	32	31	Smith 1968
<i>Purshia tridentata</i>	36	136	Jenkins 1988
<i>Arctostaphylos patula</i>	31	218	this study
<i>Ceanothus velutinus</i>	29	457	this study
<i>Phacelia heterophylla</i>	27	828	this study
<i>Elymus</i> spp.	12	300	Roundy et al. 1983
<i>Castanopsis sempervirens</i>	22.5	2	Roth and Vander Wall 2005
<i>Helianthus annuus</i> ^a	27	32	Hullar et al. 1999
<i>Panicum miliaceum</i> ^a	18 ^b	202 ^b	Hullar et al. 1999
<i>Sorghum</i> spp. ^a	16	36	Hullar et al. 1999

^aSeeds obtained from traps^bMean for red and white millet

Larder Contents

To find larders, it was necessary to locate chipmunks inside their winter dens. To do so, we fitted chipmunks with 2.0-g radio-telemetry collars (Holohil Systems Ltd., Carp, Ontario, Canada; model #BD-2C) in mid-October 2003 and 2004. Collared animals were located on a nearly daily basis between 26 October and 9 December 2003 and between 5 October and 29 November 2004. We located chipmunks by homing and marking their location with a global positioning system coordinate. When an animal was located underground in the same location on at least 3 consecutive days, we assumed that the animal had finished provisioning its larder and was dormant. At that time, we excavated its winter den and removed the animal and its winter larder. Chipmunks were taken into captivity and housed in accordance with Institutional Animal Care and Use Committee guidelines at the University of Nevada–Reno.

After the nest and larder were removed, we measured the dimensions of the nest chamber and the depth of the nest. We collected the soil surrounding nest chambers to ensure that seeds cached in the wall of the den were also collected. Larder contents and soil were spread onto cafeteria trays and allowed to air-dry. We separated seeds from soil and sorted them to species. To separate smaller seeds from the soil, we sifted samples through 5 sieves, the smallest with a pore size of 712 μm that prevented loss of tiny seeds and seed fragments. All food items were weighed and counted. For the smallest seed type, we estimated the number

of seeds by dividing total mass by mean seed mass, based on a sample of 100 seeds of each species. We estimated the number of eaten seeds in larders from seed shells, and we estimated the edible mass of eaten seeds before they were consumed by multiplying the estimated number of eaten seeds by mean edible seed mass.

To determine the caloric values of seeds, we reviewed the literature (Table 1). Seed species for which the caloric contents could not be found were sent to the Washington State University Wildlife Habitat and Nutrition Lab for gross caloric content analysis. We used edible mass (g) and caloric values ($\text{kJ} \cdot \text{g}^{-1}$) of each seed type to calculate caloric contents of larders. Results are presented as means with one standard deviation unless otherwise noted.

RESULTS

Larder Formation from Scatter-hoarded Caches

Of the 209 labeled pine seeds found in the larder on 18 November 2000, 174 had legible numbers. We traced the 174 seeds to 263 scattered cache sites (Fig. 1). There were more caches than seeds because rodents frequently excavated cached seeds and moved them to new cache sites. Figure 2 illustrates the dynamics of labeled pine seeds as chipmunks moved them from the source tree to caches and eventually into the winter larder. The average seed was found at 2.6 ± 1.1 cache sites, with 7 seeds found at 5 cache sites and 1 seed found at 6 different cache sites. Although caches

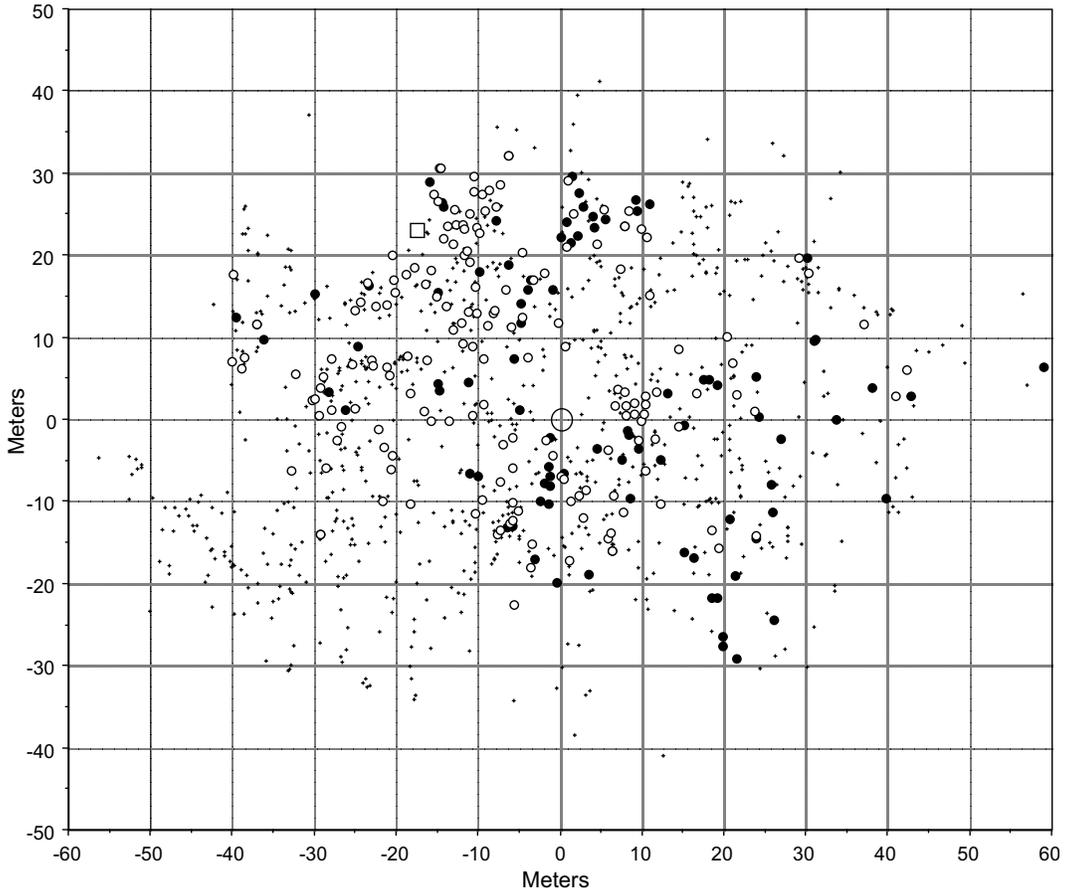


Fig. 1. A map of the study area showing source tree (large circle at origin) and winter nest and larder (square). All other symbols are cache sites: closed circles are the 94 caches from which labeled pine seeds were taken to form the winter larder; open circles are the 142 interim cache sites where larder-hoarded seeds resided temporarily during the autumn before being taken to the final 94 caches; small crosses are 800 other caches created by chipmunks using labeled seeds taken from beneath the source tree and found over a period of 2 months. Seeds from these latter caches were either eaten during autumn or they germinated in spring 2001.

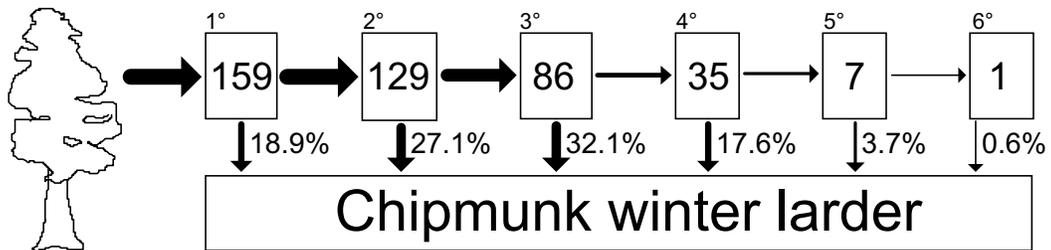


Fig. 2. Fate of labeled pine seeds taken from a source tree in 2000 that eventually were found in a yellow-pine chipmunk winter larder. Small rectangles are cache sites: primary (1°) caches contain seeds taken from the source tree and located for the first time, and secondary (2°) caches are those containing seeds taken from primary caches, etc. The size and direction of arrows show the movement of labeled seeds (numbers) between different-order cache sites. Percentages represent the contribution of labeled pine seeds from different-order caches to the winter larder.

TABLE 2. Composition and caloric content (Joules) of the larders of 15 yellow-pine chipmunks. The larder from 2000

Year	Animal number	Sex	Seed species									
			<i>Pinus albicaulis</i>		<i>Pinus contorta</i>		<i>Pinus jeffreyi</i>		<i>Pinus lambertiana</i>		<i>Pinus ponderosa</i>	
			Count	J	Count	J	Count	J	Count	J	Count	J
2000 ^a	1	Unk.	4	9000	0	0	78	175,500	54	208,278	77	79,464
2003	156	M	0	0	0	0	1680	3,780,000	0	0	0	0
	105	M	0	0	0	0	1651	3,714,750	0	0	0	0
	294	M	0	0	0	0	1624	3,654,000	0	0	0	0
	336	M	0	0	0	0	1123	2,526,750	0	0	0	0
	236	M	0	0	0	0	1691	3,804,750	0	0	0	0
	369	F	0	0	0	0	767	1,725,750	0	0	0	0
Mean			0	0	0	0	1423	3,201,000	0	0	0	0
2004	009	F	282	634,500	0	0	315	708,750	0	0	0	0
	268	F	283	636,750	14	1666	137	308,250	0	0	0	0
	554	F	97	218,250	81	9639	240	540,000	0	0	0	0
	716	M	220	495,000	291	34,629	267	600,750	0	0	0	0
	604	M	23	51,750	666	79,254	137	308,250	0	0	0	0
	395	F	29	65,250	0	0	12	27,000	0	0	0	0
	049	M	300	675,000	294	34,986	32	72,000	0	0	0	0
	359	M	157	353,250	39	4641	295	663,750	0	0	0	0
	Mean			174	401,655	173	20,602	179	301,826	0	0	0

^a209 pine seeds were given to animals by researchers.

seeds (Table 2). In 2003, larders contained 5 native species of seeds and bait seed. Bait seed was mixed birdseed that animals removed from traps during summer trapping sessions and later stored in winter larders. In addition to the seed species found in Table 2, chipmunk #236's larder also contained a single white fir (*Abies concolor*) seed. In 2004, larders contained 8 species of native seeds, bait seed, and whitebark pine (*Pinus albicaulis*) seeds. Whitebark pine trees do not occur in the study area. Clark's Nutcrackers (*Nucifraga columbiana*) gather whitebark pine seeds at higher elevations and cache them in Little Valley. All whitebark pine seeds found in larders were the result of chipmunks pilfering the caches of Clark's Nutcrackers. Larders had a mean energy content of 2108 kJ (2000), 2516 ± 684 kJ (range 1344–2972 kJ; 2003), and 997 ± 509 kJ (range 90–1685 kJ; 2004). Additionally, some larders in 2003 and 2004 contained small quantities of insect egg cases, insect body parts, moss, bitterbrush leaves, and rabbit feces.

DISCUSSION

Food stored in scattered caches that were made during summer and early autumn was essential for construction of winter larders by yellow-pine chipmunks. Winter larders were

formed in late autumn when little unstored food was available. This pattern of behavior is clear from observations of foraging chipmunks (Kuhn and Vander Wall 2008) and from our study of radio-labeled pine seeds, which were scatter-hoarded more than 7 weeks before the winter larder was formed (Fig. 3). Many species of seeds found in larders were from shrubs and herbaceous plants that ripen in summer (Roth and Vander Wall 2005, Kuhn and Vander Wall 2008). These seed crops were depleted within 2–3 weeks of maturity. Yellow-pine chipmunks scatter-ward these seeds as they ripen, placing food items in countless cache sites from spring until autumn. Scatter-hoarded seeds are important food sources for yellow-pine chipmunks during the summer and autumn, but if these seeds were not scatter-hoarded, they would not have been available in November, when chipmunks were constructing their winter larders (Kuhn and Vander Wall 2008).

In the radioactive-seed study, we found that between initial scatter-hoarding and eventual construction of the winter larder, seed caches were not static. The average seed was recorded at 2.6 cache sites, but this is surely an underestimate of the frequency of recaching. For example, primary caches made on 9–11 September were found for the first

was found using radio-labeled seeds; those from 2003 and 2004 were found using radio-telemetry to track chipmunks.

Seed species													
<i>Purshia tridentata</i>		<i>Arctostaphylos patula</i>		<i>Castanopsis sempervirens</i>		<i>Ceanothus velutinus</i>		<i>Phacelia heterophylla</i>		<i>Elymus</i> spp.		Bait	Total
Count	J	Count	J	Count	J	Count	J	Count	J	Count	J	J	J
3846	1,019,190	2211	313,962	31	348,750	3022	120	0	0	0	0	0	2,154,264
144	38,160	15	3	0	0	7	0.3	0	0	0	0	43,872	3,862,035
334	90,261	32	7	0	0	61	3	0	0	0	0	54,507	3,859,528
123	32,595	9	2	0	0	26	2	0	0	0	0	167,247	3,853,846
394	104,410	97	25	0	0	3132	125	0	0	0	0	11,304	2,642,614
131	34,715	15	4	0	0	1	0.1	0	0	0	0	87,458	3,926,927
48	12,720	23	6	0	0	0	0	0	0	0	0	39,092	1,777,568
196	52,144	33	8	0	0	538	22	0	0	0	0	67,247	3,320,420
89	23,585	157	14	0	0	33	3	0	0	0	0	167,832	1,534,684
150	39,750	90	9	0	0	0	0	0	0	0	0	374,880	1,361,305
122	32,330	8	1	0	0	0	0	0	0	0	0	426,955	1,227,175
91	24,115	0	0	1	11,250	0	0	8281	270	213	8	684,222	1,850,244
328	86,920	10	1	0	0	0	0	2622	85	8	0.4	80,032	606,292
0	0	3134	309	1	11,250	1	0.1	0	0	0	0	7269	111,078
13	3445	4386	543	0	0	95	10	0	0	0	0	24,300	810,284
594	157,410	770	45	0	0	0	0	3657	119	173	6	49,242	1,228,463
173	45,944	1069	115	0	2813	16	2	1820	59	49	2	226,842	1,091,191

time sometime between mid-September and mid-October (Fig. 3), providing ample opportunity for rodents to move cached seeds one or more times before we first found them. Further, some of the seeds found in the larder disappeared from cache sites in late October (Fig. 3) but must have been scatter-hoarded elsewhere because the larder was not constructed until after 4 November. The frequent movement of cached seeds probably represents pilferage and recaching of seeds by other chipmunks and even other species such as deer mice (Vander Wall 2000, 2002). The caches of eastern chipmunks (*T. striatus*) are also dynamic, but in that species, seeds from the short-lived caches are often moved into burrows by the cache makers (Elliott 1978, Clarke and Kramer 1994).

We found that in the eastern Sierra Nevada, yellow-pine chipmunks constructed new winter dens each year and that these larders were not constructed until late autumn, just prior to winter dormancy. Only a single excavated den (1 of 15) showed evidence of being used for more than one winter. Siberian chipmunks (*Tamias sibiricus*) also excavate a new winter den each year (Kawamichi 1996). This behavior is in contrast to eastern chipmunks, which actively defend and occupy a single den year-round and frequently use the same burrow for multiple years (Elliott 1978).

We found no evidence that yellow-pine chipmunks made larders in spring, summer, or early fall. In the semiarid region of western Nevada, the availability of food resources is patchy. In order to find food resources, chipmunks spend the majority of their time foraging and searching for food (Kuhn and Vander Wall 2008). Yellow-pine chipmunks have been observed moving as much as 425 m between food patches (Kuhn unpublished data). This pattern of activity precludes chipmunks from defending food cached in larders. Previous work in our study site showed that unprotected larders were raided by pilferers and received catastrophic losses to food stores (Vander Wall et al. 2005). Radio-collared animals were seldom found in the same locations (burrows and rock and tree crevices) on the same day or on consecutive days and nights prior to immergence. If animals were larder-hoarding food prior to winter provisioning, we would have expected to find chipmunks in the same locations on numerous occasions. Moreover, during >520 hours of observation in 2003 and 2004, yellow-pine chipmunks were never observed carrying nest material or seeds into a burrow from late summer to early autumn. In contrast, in late autumn, chipmunks were frequently observed carrying nest material and food items. It is unlikely that

yellow-pine chipmunks provision more than one larder. In fact, one chipmunk that escaped after its winter den was excavated was never located in a new den, even after repeated snow events.

Some chipmunk species store much more food in winter larders than they could consume during the period of winter dormancy. For example, Elliott (1978) found over 20,000 kJ of food remaining in eastern chipmunk larders in the spring. This is nearly 10 times greater than the size of yellow-pine chipmunk larders at the beginning of winter (Table 2). Siberian chipmunks, like eastern chipmunks, store large quantities of acorns in their winter larders (average 596 acorns; Kawamichi 1989). If we assume that acorns average approximately 5 kCal · g⁻¹ (Ivan and Swihart 2000), the average Siberian chipmunk larder contains approximately 1192 kCal (approximately 4991 kJ) in acorns (excluding all other seed types). In general, excess winter food stores are likely to be important for increasing spring survival, increasing reproductive success, and may also provide food in the case of future mast failures (Elliott 1978, Kawamichi 1980, Barnes 1984, Place et al. 2002). In contrast with these other species, yellow-pine chipmunks in our study area did not have larders with any significant quantity of seeds remaining in spring. We observed yellow-pine chipmunks in spring and early summer recovering scatter-hoarded caches of bitterbrush and Jeffrey pine seeds from the previous year. Chipmunks recovered Jeffrey pine seeds as late as 21 July in 2003. Seed species that remain viable in the seed bank for long periods, such as manzanita and tobacco brush (Dremann and Shaw 2002), may also be important sources of food in the spring. Chipmunk species that extensively scatter-hoard, such as yellow-pine chipmunks, likely rely less on the remnants of a winter larder during spring and more on scatter-hoarded food items stored the previous year than species that primarily larder-hoard, such as eastern chipmunks.

Seed abundance influenced the sizes and contents of winter larders (Kuhn and Vander Wall 2008). Sizes and contents of larders, however, were not influenced by the chipmunks' size or sex (Kuhn and Vander Wall 2008). Abundance of Jeffrey pine seeds at our site was high in 2003 (257.1 ± 182.7 cones · tree⁻¹, $n = 23$ [for all 3 years]), but low in 2000 (12.6 ± 32.2 cones · tree⁻¹) and 2004 (22.3 ± 23.3

cones · tree⁻¹; Vander Wall 2002, Kuhn and Vander Wall 2008). When Jeffrey pine seeds were available, yellow-pine chipmunks stored pine seeds almost to the exclusion of all other seed types. Jeffrey pine seeds are large and are calorically profitable (Table 1), and when these seeds are available, chipmunks seem able to acquire adequate food stores to survive the winter (Kuhn and Vander Wall 2008). When Jeffrey pine seeds were less abundant, chipmunks stored more species of seed, many of which were small-seeded species that ripen in early and mid-summer. In 2004 overall seed production on our study site was low (Kuhn and Vander Wall 2008). During this period, it appears that chipmunks had a difficult time obtaining adequate winter provisions. Kuhn and Vander Wall (2008) estimated that these larders contained enough food stores to allow the occupants to survive only approximately 6–83 days (an average winter lasts 140 days). In addition to the small seed crops, the winter of 2004 was longer than average (approximately 158 days) with large snow accumulations.

Years with low seed production coupled with long winters may exert the greatest selective pressure on food-storing hibernators. Such times of “ecological crunch” should act to reduce the variation observed in a population in favor of a phenotype that increases over-winter survival (Wiens 1977). Chipmunks' ability to recover food items cached by other animals, such as whitebark pine seeds, may have significant implications for larder contents and winter survival. Vander Wall and Jenkins (2003) predicted that successful pilferers could gradually increase the amount of food they control if they are better than average at gaining more cached food than they lose. In addition to favoring foraging ability, long winters should also select for individuals with high digestive efficiencies and individuals that optimize the use of torpor (Humphries et al. 2001).

ACKNOWLEDGMENTS

We thank Salvatore Agosta, Jennifer Armstrong, Maurie Beck, Jenny Briggs, Laura Colgin, W. Scott Hampton, Matthew Johnson, Morgan Lind, Christopher Mattson, and Julie Roth for their help in the field. We are especially grateful to Jack Hayes for the use of his telemetry equipment and Cheryl Nowak who assisted in seed identification. Sal Agosta and

Rob Colwell made useful comments on earlier versions of this manuscript. Parts of this research were supported by NSF grant DEB-9708155.

LITERATURE CITED

- ALLEN, E.G. 1938. The habits and life history of the eastern chipmunk, *Tamias striatus lysteri*. New York State Museum Bulletin 314:1-122.
- AUNFRIEV, A.I., AND G.G. ARKHIPOV. 2004. Influence of body weight and size on the mode of wintering in hibernators of the family Sciuridae in northeastern Russia. *Russian Journal of Ecology* 35:189-193.
- BARNES, B.M. 1984. Influence of energy stores on activation of reproductive function in male golden-mantled ground squirrels. *Journal of Comparative Physiology B* 154:421-425.
- BROADBOOKS, H.E. 1958. Life history and ecology of the chipmunk, *Eutamias amoenus*, in eastern Washington. University of Michigan, The Museum of Zoology, Miscellaneous Publications 103:1-48.
- BUCK, C.L., AND B.M. BARNES. 1999. Annual cycle of body composition and hibernation in free-living arctic ground squirrels. *Journal of Mammalogy* 80:430-442.
- CLARKE, M.F., AND D.L. KRAMER. 1994. The placement, recovery, and loss of scatter hoards by eastern chipmunk *Tamias striatus*. *Behavioral Ecology* 5:353-361.
- DREMANN, C.C., AND M. SHAW. 2002. Releasing the native seed bank: an innovative approach to restoring a coastal California ecosystem. *Ecological Restoration* 20:103-107.
- ELLIOTT, L. 1978. Social behavior and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack Mountains. *Smithsonian Contributions in Zoology* 265:1-107.
- FRENCH, A.R. 1988. The pattern of mammalian hibernation. *American Scientist* 76:569-575.
- _____. 2000. Interdependency of stored food and changes in body temperature during hibernation of the eastern chipmunk, *Tamias striatus*. *Journal of Mammalogy* 81:979-985.
- GEISER, F., AND R.V. BAUDINETTE. 1990. The relationship between body mass and rate of rewarming from hibernation and daily torpor in mammals. *Journal of Experimental Biology* 151:349-359.
- GEISER, F., S. HIEBERT, AND G.J. KENAGY. 1990. Torpor bout duration during the hibernation season of two sciurid rodents: interrelationship with temperature and metabolism. *Physiological Zoology* 63:489-503.
- HAWBECKER, A.C. 1940. The burrowing and feeding habits of *Dipodomys venustus*. *Journal of Mammalogy* 21:388-396.
- HULLAR, I., I. MELEG, S. FEKETE, AND R. ROMVARI. 1999. Studies on the energy content of pigeon feeds I. Determination of digestibility and metabolizable energy content. *Poultry Science* 78:1757-1762.
- HUMPHRIES, M.M., D.W. THOMAS, AND D.L. KRAMER. 2001. Torpor and digestion in food-storing hibernators. *Physiological and Biochemical Zoology* 74:283-292.
- _____. 2003. The role of energy availability in mammalian hibernation: a cost-benefit approach. *Physiological and Biochemical Zoology* 76:165-179.
- HUT, R.A., B.M. BARNES, AND S. DAAN. 2002. Body temperature patterns before, during, and after semi-natural hibernation in the European squirrel. *Journal of Comparative Physiology B* 172:47-58.
- IVAN, J.S., AND R.K. SWIHART. 2000. Selection of mast by granivorous rodents of the central hardwood forest region. *Journal of Mammalogy* 81:549-562.
- JENKINS, S.H. 1988. Comments on relationship between native seed preferences of shrub-steppe granivores and seed nutritional characteristics. *Oecologia* 75:481-482.
- JENNINGS, T.J. 1975. Notes on the burrow systems of woodmice (*Apodemus sylvaticus*). *Journal of Zoology, London* 177:500-504.
- KAWAMICHI, M. 1980. Food, food hoarding and seasonal changes of Siberian chipmunks. *Japanese Journal of Ecology* 30:211-220.
- _____. 1989. Nest structure dynamics and seasonal use of nests by Siberian chipmunks (*Eutamias sibiricus*). *Journal of Mammalogy* 70:44-57.
- _____. 1996. Ecological factors affecting annual variation in commencement of hibernation in wild chipmunks (*Tamias sibiricus*). *Journal of Mammalogy* 77:731-744.
- KUHN, K.M., AND S.B. VANDER WALL. 2008. Linking summer foraging to winter survival in yellow-pine chipmunks (*Tamias amoenus*). *Oecologia* 157:349-360.
- LANDRY-CUERRIER, M., D. MUNRO, D.W. THOMAS, AND M.M. HUMPHRIES. 2008. Climate and resource determinants of fundamental and realized metabolic niches of hibernating chipmunks. *Ecology* 89:3306-3316.
- LYMAN, C.P., J.S. WILLIS, A. MALAN, AND L.C.H. WANG. 1982. Hibernation and torpor in mammals and birds. Academic Press, New York.
- MACLEAN, G.S. 1981. Torpor patterns and microenvironment of the eastern chipmunk, *Tamias striatus*. *Journal of Mammalogy* 62:64-73.
- MCNAB, B.K. 2002. The physiological ecology of vertebrates. Cornell University Press, Ithaca, NY.
- MICHENER, G.R. 1984. Age, sex and species differences in the annual cycle of ground-dwelling sciurids: implications of sociality. Pages 81-107 in J.O. Murie and G.R. Michener, editors, *The biology of ground-dwelling squirrels*. University of Nebraska Press, Lincoln.
- NEUHAUS, P., R. BENNETT, AND A. HUBBS. 1999. Effects of a late snowstorm and rain on survival and reproductive success in Columbian ground squirrels (*Spermophilus columbianus*). *Canadian Journal of Zoology* 77:879-884.
- PLACE, N.J., C. VELOSO, G.H. VISSER, AND G.J. KENAGY. 2002. Energy expenditure and testosterone in free-living male yellow-pine chipmunks. *Journal of Experimental Zoology* 292:460-467.
- ROTH, J.K., AND S.B. VANDER WALL. 2005. Primary and secondary seed dispersal of bush chinquapin (Fagaceae) by scatter-hoarding rodents. *Ecology* 86:2428-2439.
- ROUNDY, B.A., G.J. CLUFFE, J.A. YOUNG, AND R.A. EVANS. 1983. Treatment of inland saltgrass and greasewood sites to improve forage production. USDA General Technical Report INT-157, Ogden, UT.
- SMITH, C.C. 1968. The adaptive nature of social organization in the genus of three tree squirrels, *Tamiasciurus*. *Ecological Monographs* 38:31-64.
- STEBBINS, L.L., AND R. ORICH. 1977. Some aspects of overwintering in the chipmunk, *Eutamias amoenus*. *Canadian Journal of Zoology* 55:1139-1146.

- TAUBER, M.J., C.A. TAUBER, AND S. MASAKI. 1986. Seasonal adaptations of insects. Oxford University Press, New York.
- TEVIS, L.P. 1952. Autumn foods of chipmunks and golden-mantled ground squirrels in the northern Sierra Nevada. *Journal of Mammalogy* 33:198–205.
- ULTSCH, G.R. 1989. Ecology and physiology of hibernation and overwintering survival among freshwater fishes, turtles and snakes. *Biological Reviews* 64:435–516.
- VANDER WALL, S.B. 1995. The effects of seed value on the caching behavior of yellow pine chipmunks. *Oikos* 74:533–537.
- . 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology* 11:544–549.
- . 2002. Masting in animal-dispersed pines facilitates seed dispersal. *Ecology* 83:3508–3516.
- . 2003. Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. *Oikos* 100:25–34.
- VANDER WALL, S.B., E.C. HAGER, AND K.M. KUHN. 2005. Pilfering of stored seeds and the relative costs of scatter-hoarding versus larder-hoarding in yellow pine chipmunks. *Western North American Naturalist* 65:248–257.
- VANDER WALL, S.B., AND S.H. JENKINS. 2003. Reciprocal pilferage and the evolution of food-hoarding behavior. *Behavioral Ecology* 14:656–667.
- WIENS, J.A. 1977. On competition and variable environments. *American Scientist* 65:590–597.
- WRAZEN, J.A., AND L.A. WRAZEN. 1982. Hoarding, body mass dynamics, and torpor as components of the survival strategy of the eastern chipmunk. *Journal of Mammalogy* 63:63–72.

Received 24 May 2008

Accepted 8 May 2009