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Cache Selection by Arctic Ground Squirrels Inhabiting Boreal-steppe Meadows of Southwest Yukon Territory, Canada

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Abstract

We examined food items cached by arctic ground squirrels (*Spermophilus parryii*) from boreal-steppe meadows of southwest Yukon Territory, Canada. Caches recovered from two sites are dominated by fruits and seeds of either northern comandra (*Geocaulon lividum*) or prickly rose (*Rosa acicularis*). These two taxa are relatively rare in the local flora at the study sites (Site 1: ≥32 available taxa, and Site 2: ≥39 available taxa), suggesting they are selectively cached as preferred items. Cache selectivity may be related to perishability, fruit size/seed abundance, and predation risk. These caches are of significantly different composition than caches from present tundra sites and Pleistocene fossil arctic ground squirrel nests and caches (middens) recovered from central Yukon. These findings suggest that although arctic ground squirrels evolved in open tundra, they can subsist on a variety of cache items and may have the ability to adapt to and select a profitable cache within a variety of boreal and tundra habitats.

Introduction

Northern environments are characterized by winters with limited forage access and low food abundance. To cope with predictable forage scarcity, northern herbivores have adapted various strategies, such as migration, hibernation, fat accumulation, and food storage (Marchand, 1996). Hibernating mammals enter a state of highly reduced body temperatures and metabolic activity, and rely on fat reserves when energy requirements cannot be met through foraging (Galster and Morrison, 1976; Barnes, 1996; Buck and Barnes, 1999a, 1999b). Food caching is a common strategy for many non-hibernating mammals living in the north, including red squirrels (*Tamiasciurus hudsonicus*; Hurly and Robertson, 1987), collared pikas (*Ochotona collaris*; Morrison et al., 2004), and voles (*Microtus* spp. and *Clethrionomys* spp.; Vander Wall, 1990). Fat and food caches enable animals to store reserves when food availability is high for use during periods when food availability is low (Vander Wall, 1990).

Arctic ground squirrels (*Spermophilus parryii*) inhabit tundra and boreal habitats of northern North America and have adopted a mixed hibernation and food cache strategy that differs between sexes (McLean and Towns, 1981; Buck and Barnes, 1999b). Female arctic ground squirrels are not known to cache food (McLean and Towns, 1981; Buck and Barnes, 1999b), an observation consistent with other species of ground dwelling sciurids (*S. saturatus*; Kenagy et al., 1989; *S. richardsonii*; Michener, 1993; *S. columbianus*; Shaw, 1926). Males enter hibernation in late August–early September and emerge in late March to early April (McLean and Towns, 1981). Males sequester themselves underground for a one- to two-week pre-emergence euthermic interval (Buck and Barnes, 1999b) where they feed on seeds cached during the previous summer and autumn (McLean and Towns, 1981; Gillis et al., 2005b). Cache consumption by males replaces the 30–48% body mass lost during hibernation (Galster and Morrison, 1976; Gillis, 2003; Buck and Barnes, 1999a) and facilitates post-torpor sexual maturation (Barnes, 1984, 1996; Barnes et al., 1987). The sexual differences in cache behavior are related to intense male-vs.-male competition for females during the 3–4 week spring mating season in which competitive advantage correlates positively with body size and foraging opportunities are limited (Carl, 1971; Green, 1977; Buck and Barnes, 1999b; Gillis, 2003). Thus, the size and quality of a male's cache plays an important role in its reproductive fitness (Barnes, 1996).

Few studies have documented arctic ground squirrel forage preferences for consumption or for caching (Table 1). *S. parryii* are considered generalist foragers that consume a wide variety of graminoids and forbs with some species taken preferentially, such as legumes (Batzli and Sobaski, 1980; McLean, 1985; Frid and Turkington, 2001). McLean and Towns (1981) observed increased seed foraging by males in late summer and autumn to accumulate food caches. Mayer (1953) documented a food cache dominated by bulbils (fruits) of alpine bistort (*Polygonum viviparum*) from a site near Point Barrow, Alaska. Krog (1954) documented a nest recovered near Kotzebue, Alaska, that contained discreet caches of green willow leaves (*Salix* sp.), spikes of wheatgrass (*Agropyron latiglume*), and capsules containing ripe seeds of rush (*Juncus balticus*). The most detailed study on cache selection is from an alpine tundra site in southwest Yukon Territory in which cached food was inferred from cheek pouches contents (Gillis et al., 2005b). At least 25 cached plant taxa were documented, dominated by *Polygonum viviparum* rhizomes and fruits, from within a local community of at least 100 available vascular plant taxa (Gillis et al., 2005b).

We describe results from a preliminary study of *Spermophilus parryii* food caches from boreal-steppe meadows near Kluane Lake, southwestern Yukon Territory. We analyze cache contents from two sites and compare these with local vegetation to examine cache forage selectivity. Since limited work has been conducted on arctic ground squirrel cache foraging, the intent of this paper is to present these data, compare them with others, and hypothesize tentative explanations for cache forage selection. These are the first data on arctic ground squirrel cache contents from the boreal forest and add to the limited knowledge of foraging behavior for this herbivore. An objective of this study is to supplement ongoing investigation of Pleistocene arctic ground squirrel fossils nests and caches (middens)

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TABLE 1

Vascular plant species recorded in caches of arctic ground squirrels. Plant parts: A = achene, B = rhizome, C = seed capsule, F = floret or flower, L = leaf, P = perigynia, S = seeds, SC = silicle, SP = spikelet, and SQ = silique.

Taxon	Mayer (1953)	Krog (1954)	Gillis et al. (in 2005b)
Salicaceae			
Salix sp.		L	
Salix arctica			L
Salix polaris			L
Salix reticulata			C
Poaceae			
Agropyron latiglume		SP	
Festuca brachyphylla			F
Hierochloë alpina			F
Poa arctica			SP
Trisetum spicatum			SP
Cyperaceae			
Carex spp.			A,P
Kobresia myosuroides			A,P
Juncaceae			
Juncus balticus		C	
Luzula spp.			C
Polygonaceae			
Polygonum viviparum	B		B,R
Caryophyllaceae			
Cerastium beeringianum			C
Silene uralensis			C
Brassicaceae			
Cardamine sp.			S,SQ
Draba spp.			S,SC
Eutrema edwardsii			S,SC
Ranunculaceae			
Ranunuculus sp.			A
Anemone parviflora			A
Rosaceae			
Potentilla sp.			A
Dryas octopetala			L
Saxifragaceae			
Saxifraga sp.			C
Gentianacae			
Gentiana prostrata			C
Scrophulariaceae			
Pedicularis sp.			C,F,L,S

recovered from permafrost sediments in west-central Yukon (Zazula et al., 2005). These fossil middens have yielded diverse cache assemblages that include seeds, fruits, and leaves from at least 60 tundra and steppe taxa dating to the last glaciation, ca. 25,000 radiocarbon years ago (Zazula et al., 2005, in review). However, their efficacy for paleoecological reconstruction relies on some understanding of modern *S. parryii* foraging ecology.

Study Area and Methods

STUDY SITES

Arctic ground squirrel nests and caches were excavated by G. Zazula and R. Mathewes from two sites on the east side of Kluane Lake, southwest Yukon Territory on 10, 16, and 17 August 2004. The study area consists of vegetation dominated by white spruce forests (*Picea glauca*), with an understory of willow shrubs (*Salix* sp.), shrub birch (*Betula glandulosa*) and various forbs, and trembling aspen stands (*Populus tremuloides*) (Krebs et al., 2001). Grassland or steppe meadows form pockets of azonal vegetation within the boreal forest of southwest Yukon, and are restricted to dry hills or ridges and south-facing slopes (Laxton et al., 1996). The study was conducted in the latter part of the growing season when many of the graminoid and forb plant taxa were in fruit. The boreal-steppe in southwest Yukon was chosen for study because some aspects of arctic ground squirrel ecology have been studied previously in the region (McLean and Towns, 1981; McLean, 1985; Karels et al., 2000; Hubbs and Boonstra, 1997; Karels and Boonstra, 1999; Hik et al., 2001; Boonstra et al., 2001; Krebs et al., 2001). Furthermore, these steppe meadows are considered by many researchers to contain refugial vegetation that may be analogous to communities that were widespread in central Yukon and Alaska during Pleistocene glaciations (Laxton et al., 1996).

FIELD AND LABORATORY METHODS

The study sites are meadows, 15 and 19 km north of the Alaska Highway on the Cultus Bay Road, respectively (61°08.361′N, 138°25.690′W, 813 m a.s.l.; and 61°09.401′N, 138°25.008′W, 799 m a.s.l.). The study sites were chosen because we noted physical signs of recent burrow use. Burrow systems were excavated using garden shovels by following burrows from their entrances. At each site, we defined vegetation types based on visually determined dominant plant cover and structure and all species found in that type were assigned a cover value using the Braun-Blanquet (1927) approach (Appendix A). Nests and caches were collected in the field, placed in sample bags, air dried, and examined in the laboratory with a dissecting microscope. Plant nomenclature follows Cody (2000).

Results

SITE 1

Site 1 is a crescent-shaped meadow bordered by the Cultus Bay road to the east and spruce forest to the north, west, and south (Fig. 1). We observed freshly excavated soil surrounding at least 2 of 12 burrow entrances at the ground squirrel colony. Five vegetation types were recognized with 32 plant taxa recorded (Appendix A).

A hibernaculum was recovered approximately 75 cm below surface within silt, immediately above the underlying gravel (Fig. 2a). The hibernaculum consisted of a main spherical chamber (25 cm wide, 25 cm deep, 25 cm high) that housed a nest, and a small antechamber (10 cm wide, 10 cm deep, 10 cm high) with a food cache (Site 1, Cache 1). A side burrow next to the nest contained a latrine with wet feces. The "grassy" nest was built upon an old nest that contained moldy, wet material and decaying remains of eight juvenile arctic ground squirrel carcasses. A small food cache was also found associated with the moldy nest (Site 1, Cache 2). Several beetles were observed in the hibernacula. Further excavations within the colony failed to yield additional nests or caches.

The nest weighs 209 g and is composed primarily of graminoid foliage, with foxtail (*Hordeum jubatum*), wild rye (*Elymus trachycaulus* ssp. *subsecunduns*), reed bent grass (*Calamagrostis purpurescens* var. *purpurescens*), sedge (*Carex filifolia*), and prairie crocus (*Pulsatilla ludoviciana*), lichen, moss, and horse hair.

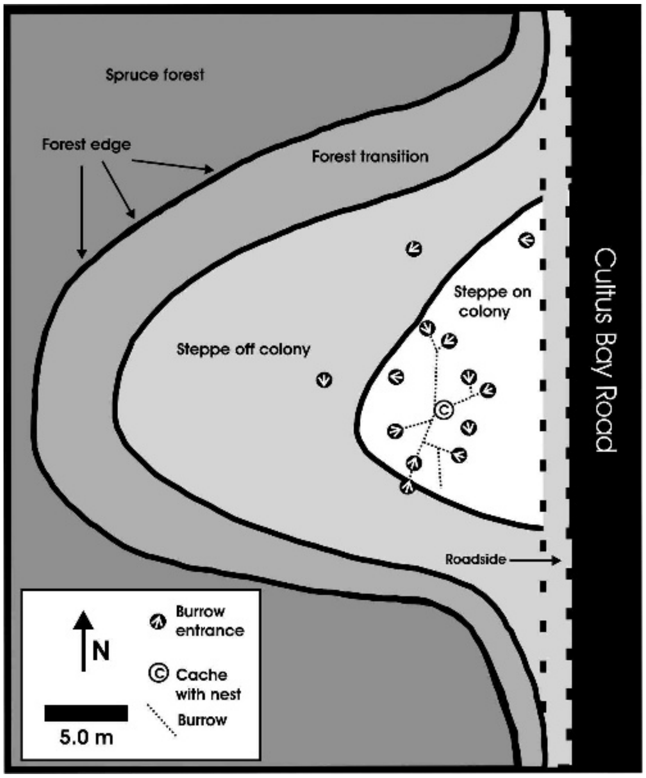

FIGURE 1. Map of Site 1 with vegetation types.

Cache 1 contains seeds, fruits, and other remains from 12 vascular plant species and weighs 13.86 g (Appendix B). *Geocaulon lividum* berries dominate the cache, representing 92.7% of the total mass. Cache 2 weighs 5.52 g and is of similar composition, with 11 plant species dominated by *Geocaulon lividum* berries (60.1%). In total, *Geocaulon lividum* berries account for 83.4% of the total dry mass of cached food at Site 1 (Fig. 3).

Although the fresh nest was built on what may be a former female natal nest, we think the seeds and fruits (dominated by fresh *Geocaulon lividum* berries; Fig. 2a) represent a recent male cache because females are not known to cache seeds and fruits (Buck and Barnes, 1999a; Gillis et al., 2005b), and the study was conducted when females have typically already entered hibernation (McLean and Towns, 1981; McLean, 1985).

SITE 2

Site 2 is on a ca. 150-m-long northwest-southeast–trending ridge that slopes down about 20° to the south. Burrow entrances were observed across the ridge, but dense colonies were at the northwest end and near the middle (Fig. 4). Six vegetation types were recognized with 39 plant taxa recorded (Appendix A).

Several of the burrow entrances at Site 2 had small piles or scatters of partially eaten *Rosa acicularis* hips (fruits *sensu lato*), rose achenes (seeds *sensu lato*), and/or bastard-toadflax (*Comandra umbellatus*) berries (Fig. 2b). Excavation was attempted at several of these entrances but many tunnels ended abruptly, suggesting these were temporary duck holes (Carl, 1971). We partially excavated a colony near the middle of the study site, yielding one nest with cache and two other individual caches. The three caches were recovered in the burrow system within a ca. 3-m radius of each other (Fig. 4). Cache 1 was 25 cm below the surface within an oval chamber (25 cm wide, 25 cm deep, and 15 cm high) located alongside a main tunnel (Fig. 2c). Cache 1 consisted of two discreet piles; one with unopened rose fruits and the other dominated by rose seeds and milk-vetch (*Astragalus williamsii*) legumes, both resting on a small nest (Fig. 2d). Both Cache 2 and Cache 3 were found in small round chambers (50 cm and 40 cm below surface, respectively) along side main burrows.

The nest associated with Cache 1 weighs 29.5 g and is dominated by graminoid foliage, with some *Populus tremuloides* leaves, lichen, moss, deciduous woody twigs, nylon string and plastic wrap. Cache 1 is the most diverse with 17 vascular plant species and weighs 37.05 g (Appendix B). *Rosa acicularis* fruits (63.4%) and seeds (31%) dominate the mass of Cache 1. Although less diverse in composition, Cache 2 (17.96 g; 9 species, 8 families) and Cache 3 (30.23 g; 11 species, 8 families) were similar in that they are also dominated by rose hips (89.6% and 96.2%, respectively). *Rosa acicularis* fruits and seeds account for 95.5% of the combined mass of the three caches at Site 2 (Fig. 5).

Discussion

SELECTION OF FOOD CACHE ITEMS

Although our study is limited to caches recovered from two sites, these data suggest *Geocaulon lividum* and *Rosa acicularis* are preferred cache items for male arctic ground squirrels in the boreal-steppe meadows of southwest Yukon. Because these taxa were relatively rare in the local flora and there were abundant potential forage plants available (Site 1: $\geq$32 available taxa, and Site 2: $\geq$39 available taxa), the overwhelming dominance of these two cache items suggests high cache forage selectivity.

Because our data is limited, and little is known about arctic ground squirrel foraging behavior, our discussion of potential forage selection factors can only be considered tentative. Unfortunately, we did not obtain or are not aware of any nutritional data for *Geocaulon lividum* or *Rosa acicularis* fruits. Thus, we refer to some aspects of foraging theory to hypothesize several factors that may be important for cache selection at our study sites. In general, forage selectivity is influenced by intrinsic characteristics of food items, such as caloric value, specific nutrients, perishability, or size, and extrinsic factors of the forage, such as the spatial distribution of vegetation, predation risk, or social environment (Stephens and Krebs, 1986; Vander Wall, 1990).

For many food cachers, perishability is a key factor in a forager's assessment of food cacheability and determines whether an animal will immediately consume a food item or cache it for later (Eshelman and Jenkins, 1989; Vander Wall, 1990; Gendron and Reichmann, 1995; Hadj-Chikh et al., 1996; Kotler et al., 1999; Gerber et al., 2004). Consumption of perishable fleshy fruits such as *Rosa acicularis* and *Geocaulon lividum* may enable arctic ground squirrels to meet current water or nutrient requirements while the enclosed seed can be cached over-winter. No other available plants (with the exception of *Arctostaphylos uva-ursi*) at our sites produce fleshy fruits with cacheable seeds. Thus, perishability may offer a plausible explanation for the dominance of *Geocaulon lividum* and *Rosa acicularis* fruits and seeds in our caches. Cache preparation to increase storability (Vander Wall, 1990) is suggested by separate piles of *Rosa acicularis* fleshy fruits and seeds in Cache 1 at Site 2 (Figs. 2c, 2d) and scattered partial fruits and seeds near some tunnel entrances (Fig. 2b).

The size and/or quantity of cacheable seeds on a particular plant are important for cache foraging decisions because they directly affect feeding rates and handling times (Hurly and Robertson, 1987; Vander Wall, 1990; Garb et al., 2000; Gerber et al., 2004). Plants that produce abundant fruits and/or large cacheable food items minimize foraging cost and exposure to

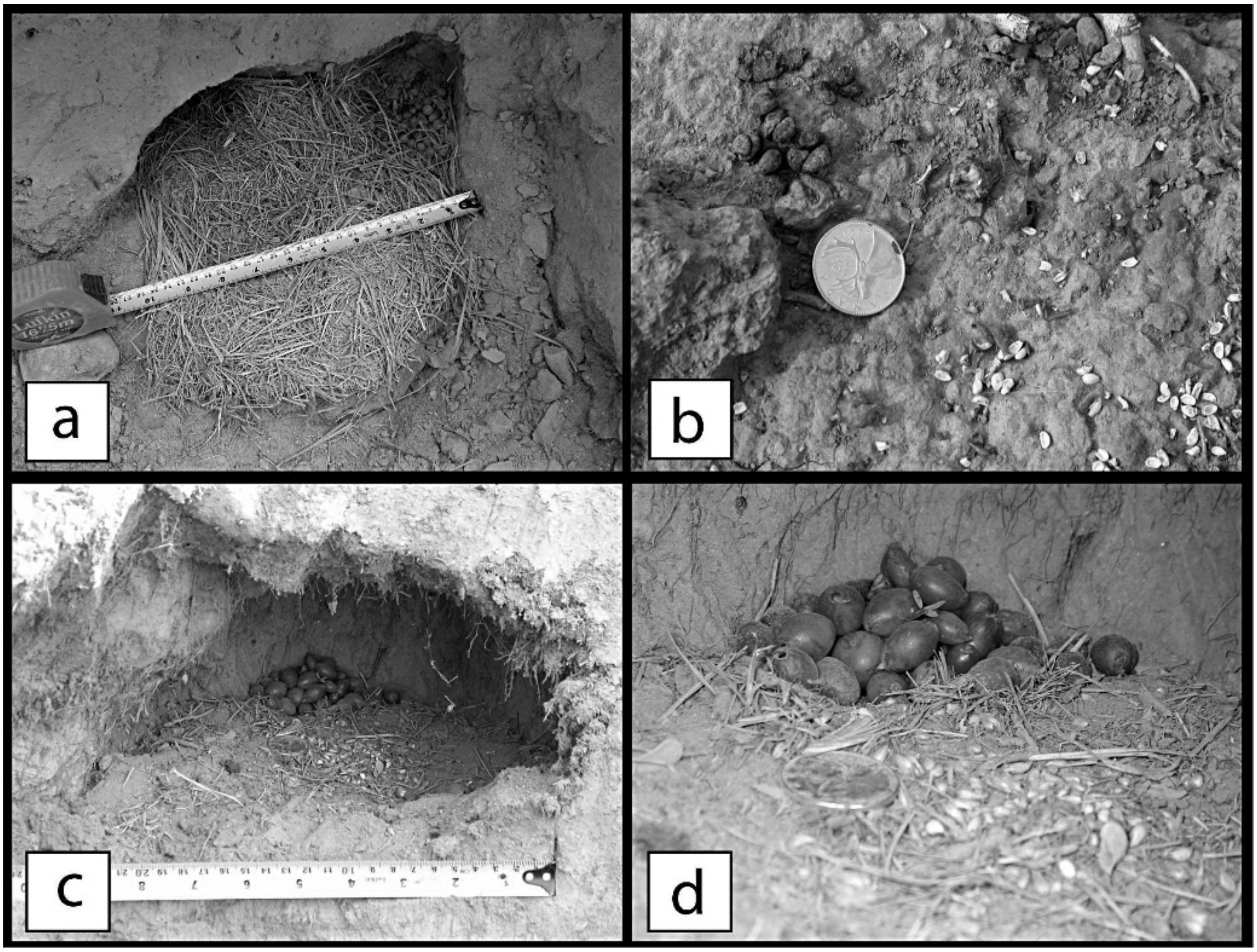

FIGURE 2. (a) Nest and cache in hibernaculum at Site 1. (b) Scattered partial *Rosa acicularis* fruits and seeds near burrow entrance at Site 2. (c) Cache 1 in hibernaculum at Site 2. (d) Close-up of Cache 1 with discreet piles of *Rosa acicularis* fruits and seeds at Site 2.

predators because sufficient forage can be obtained in one excursion without the need to travel between several plants or patches. Our site vegetation data suggest *Geocaulon lividum* and *Rosa acicularis* are the largest fruits with the largest or most abundant enclosed seeds available. Individual *Rosa acicularis* stems typically produce one large fruit which encloses many seeds (15–30), while *Geocaulon lividum* plants produce 2–4 individual berries that each contains a single large seed. Thus, fruit size and seed abundance may be factors affecting selectivity for cache items at our study sites.

Varying levels of risk and security from predators associated with different vegetation types should influence foraging decisions and cache contents (Ivins and Smith, 1983; Brown, 1988; Andrusiak and Harestad, 1989; Vasquez et al., 2002; Brown and Kotler, 2004). Because *Geocaulon lividum* and *Rosa acicularis* do not occur directly on the colonies at our sites, ground squirrels

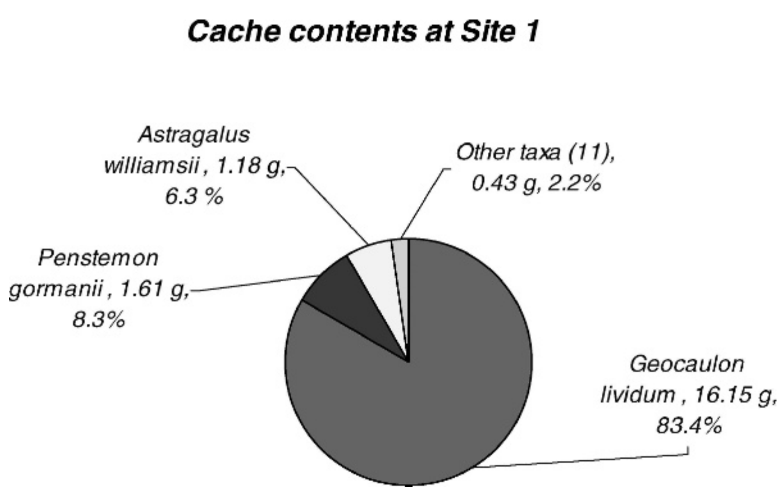

FIGURE 3. Summarized contents for two caches at Site 1 based on dry weight.

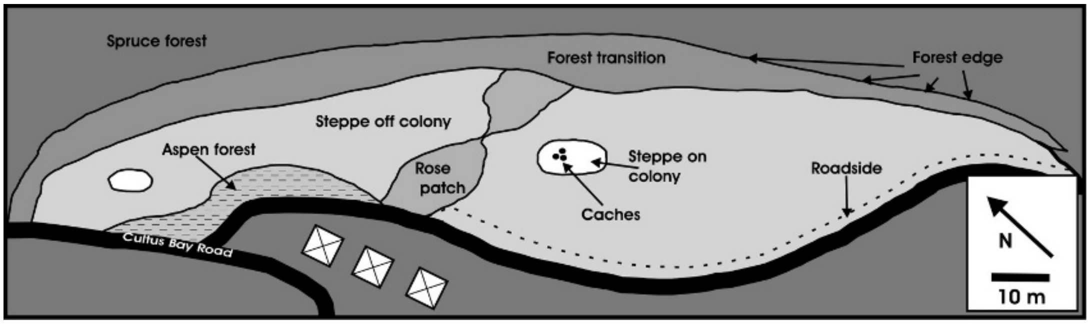

FIGURE 4. Map of Site 2 with vegetation types.

must accept greater foraging distances and exposure to predators to obtain these cache items (Figs. 1, 4; Appendix A). However, *Geocaulon lividum* and *Rosa acicularis* occur in vegetation types of higher stature (shrubby vegetation) and denser ground cover than steppe vegetation; hence these forage patches provide increased security cover and reduced predation risk. The possible reduction in predation risk while collecting *Geocaulon lividum* and *Rosa acicularis* may be an important factor for their dominance of caches contents.

ARCTIC GROUND SQUIRREL CACHE FORAGING ADAPTATIONS

Cache contents at our two study sites and between those from previously published studies (e.g. Mayer, 1953; Krog, 1954; Gillis et al., 2005b), have markedly different contents. These results suggest that cache foraging strategies for arctic ground squirrels may be site or habitat specific based on local plant availability and distribution. The principal difference between our study and others is that we examined cache contents from low elevation boreal-steppe meadows, while others are from high latitude arctic tundra (Mayer, 1953; Krog, 1954) or high elevation alpine tundra (Gillis et al., 2005a, 2005b). Potential forage items differ substantially between tundra and boreal meadows. Because both *Geocaulon lividum* and *Rosa acicularis* are boreal plants that do not occur within tundra habitats, they are not potentially available forage items in those habitats (e.g. Mayer, 1953; Krog, 1954; Gillis et al., 2005b). Also, these plants probably did not occur within Pleistocene habitats in Beringia occupied by arctic ground squirrels (Zazula et al., 2005). Thus, modern caches excavated from the boreal-steppe meadows cannot be considered good analogues for preferred plant taxa cached by Pleistocene arctic ground squirrels in Beringia (Zazula et al., 2005; Zazula, unpublished data), although some selective factors (e.g., seed abundance) may apply during both periods. Furthermore, the similarity of dominant food items between fossil Pleistocene caches from Beringia (Zazula et al., 2005, in review) and modern tundra caches (Mayer, 1953; Gillis et al., 2005b) support other hypotheses (Hik et al., 2001; Gillis et al., 2005a) that suggest arctic ground squirrels evolved in and are adapted to open steppe-tundra habitats. However, because arctic ground squirrels can subsist on a variety of cache items in both tundra and boreal forest, they may have the ability to adapt to and select a profitable cache within a variety of northern habitats.

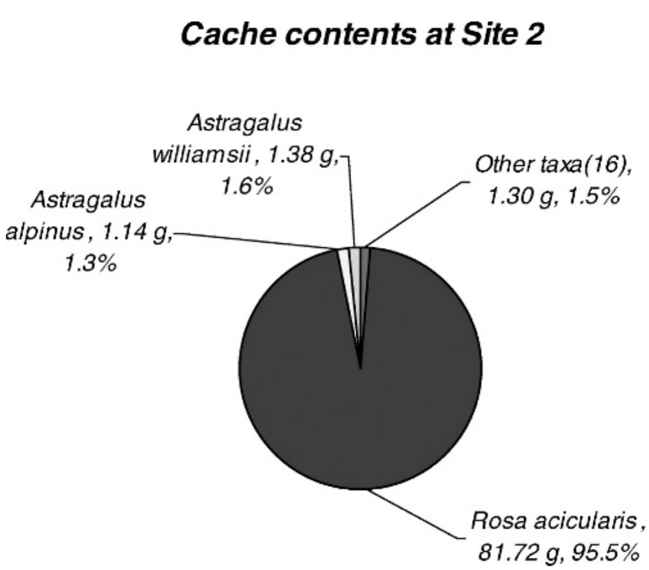

FIGURE 5. Summarized contents for three caches at Site 2 based on dry weight.

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References Cited

Andrusiak, L. A., and Harestad, A. S., 1989: Feeding behaviour and distance from burrows of Columbian ground squirrels. *Canadian Journal of Zoology*, 67: 381–384.

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.

Barnes, B. M., 1996: Relationships between hibernation and reproduction in male ground squirrels. *In* Geiser, F. H., and Nicol, S. C. (eds.), *Adaptations to the cold: Tenth international hibernation symposium*. Armidale: University of New England Press, 71–80.

Barnes, B. M., Licht, P., and Zucker, I., 1987: Temperature dependence of in vitro androgen production in testes from hibernating ground squirrels, *Spermophilus lateralis*. *Canadian Journal of Zoology*, 65: 3020–3023.

Batzli, G. O., and Sobaski, S. T., 1980: Distribution, abundance and foraging patterns of ground squirrels near Atkasook, Alaska. *Arctic and Alpine Research*, 12: 501–510.

Boonstra, R., McColl, J., and Karels, T. J., 2001: Reproduction at all costs: the adaptive stress response of male arctic ground squirrels. *Ecology*, 82: 1930–1946.
Braun-Blanquet, J., 1927: *Pflanzensoziologie*. Wien: Springer.
Brown, J. S., 1988: Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology*, 22: 37–47.
Brown, J. S., and Kotler, B. P., 2004: Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, 7: 999–1014.
Buck, C. L., and Barnes, B. M., 1999a: Annual cycle of body condition and hibernation in free-living arctic ground squirrels. *Journal of Mammalogy*, 80: 430–442.
Buck, C. L., and Barnes, B. M., 1999b: Temperatures of hibernacula and changes in body composition of arctic ground squirrels over winter. *Journal of Mammalogy*, 80: 1264–1276.
Carl, E. A., 1971: Population control in arctic ground squirrels. *Ecology*, 52: 395–413.
Cody, W. J., 2000: *Flora of the Yukon Territory*, 2nd edition. Ottawa: National Research Council of Canada, NRC Press.
Eshelman, B. D., and Jenkins, S. H., 1989: Food selection by Belding's ground squirrels in relation to plant nutritional features. *Journal of Mammalogy*, 70: 846–852.
Frid, L., and Turkington, R., 2001: The influence of herbivores and neighbouring plants on risk of browsing: a case study using arctic lupine (*Lupinus arcticus*) and arctic ground squirrels (*Spermophilus parryii plesius*). *Canadian Journal of Zoology*, 79: 874–880.
Galster, W., and Morrison, P., 1976: Seasonal changes in body composition of the arctic ground squirrel, *Citellus undulatus*. *Canadian Journal of Zoology*, 54: 74–78.
Garb, J., Kotler, B. P., and Brown, J. S., 2000: Foraging and community consequences of seed size for coexisting Negev Desert granivores. *Oikos*, 88: 291–300.
Gendron, R. P., and Reichman, O. J., 1995: Food perishability and inventory management: a comparison of three caching strategies. *American Naturalist*, 145: 948–968.
Gerber, L. R., Reichman, O. J., and Roughgarden, J., 2004: Food hoarding: future value in optimal foraging decisions. *Ecological Modeling*, 175: 77–85.
Gillis, E. A., 2003: Breeding dispersal, mating tactics, and population dynamics of arctic ground squirrels. Ph.D. dissertation. University of British Columbia.
Gillis, E. A., Hik, D. S., Boonstra, R., Karels, T. J., and Krebs, C. J., 2005a: Being higher is better: effects of elevation and habitat on arctic ground squirrel demography. *Oikos*, 108: 231–240.
Gillis, E. A., Morrison, S. F., Zazula, G. D., and Hik, D. S., 2005b: Evidence for selective caching by arctic ground squirrels living in alpine meadows in the Yukon. *Arctic*, 59: 354–360.
Green, J. E., 1977: Population regulation and annual cycles of activity and dispersal in the arctic ground squirrel. M.Sc. thesis. University of British Columbia.
Hadj-Chikh, L. Z., Steele, M. A., and Smallwood, P. D., 1996: Caching decisions by grey squirrels: a test of the handling time and perishability hypotheses. *Animal behavior*, 52: 941–948.
Hik, D. S., McColl, C. J., and Boonstra, R., 2001: Why are arctic ground squirrels more stressed in the boreal forest than in alpine meadows? *Ecoscience*, 8: 275–288.
Hubbs, A. H., and Boonstra, R., 1997: Population limitation in arctic ground squirrels: effects of food and predation. *Journal of Animal Ecology*, 66: 527–541.
Hurly, T. A., and Robertson, R. J., 1987: Scatter-hoarding by territorial red squirrels: a test of the optimal density model. *Canadian Journal of Zoology*, 65: 1247–1252.
Ivins, B. L., and Smith, A. T., 1983: Responses of pikas (*Ochotona princes*, Lagomorpha) to naturally occurring terrestrial predators. *Behavioral Ecology and Sociobiology*, 13: 139–148.
Karels, T. J., and Boonstra, R., 1999: The impact of predation on burrow use by arctic ground squirrels in the boreal forest. *Proceedings of the Royal Society of London, B*, 266: 2117–2123.
Karels, T. J., Byrom, A. E., Boonstra, R., and Krebs, C. J., 2000: The interactive effects of food and predators on reproduction and overwinter survival of arctic ground squirrels. *Journal of Animal Ecology*, 69: 235–247.
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: 1432–1939.
Kotler, B. P., Brown, J. S., and Hickey, M., 1999: Food storability and the foraging behavior of fox squirrels (*Sciurus niger*). *American Midland Naturalist*, 142: 77–86.
Krebs, C. J., Boutin, S., and Boonstra, R. (eds.), 2001: *Ecosystem dynamics of the boreal forest*. Oxford: Oxford University Press.
Krog, J., 1954: Storing of food items in the winter nest of the Alaskan ground squirrel, *Citellus undulatus*. *Journal of Mammalogy*, 35: 586.
Laxton, N. F., Burn, C. R., and Smith, C. A. S., 1996: Productivity of Loessal Grasslands in the Kluane Lake Region, Yukon Territory, and the Beringian "Production Paradox." *Arctic*, 49: 129–140.
Marchand, P. J., 1996: *Life in the cold: an introduction to winter ecology*. Hanover: University Press of New England.
Mayer, W. V., 1953: A preliminary study of the barrow ground squirrel, *Citellus parryi barrowensis*. *Journal of Mammalogy*, 34: 334–345.
McLean, I. G., 1985: Seasonal patterns and sexual differences in the feeding ecology of arctic ground squirrels (*Spermophilus parryii plesius*). *Canadian Journal of Zoology*, 63: 1298–1301.
McLean, I. G., and Towns, A. J., 1981: Differences in weight changes and the annual cycle of male and female arctic ground squirrels. *Arctic*, 34: 249–254.
Mitchener, G. R., 1993: Sexual differences in hibernaculum contents of Richardson's ground squirrels: males store food. *In* Carey, C., Florant, G. L., Wunder, B. A., and Horwitz, B. (eds.), *Living in the Cold: Ecological Physiological, and Molecular Mechanisms*. Boulder: Westview Press, 109–118.
Morrison, S., Barton, L., Caputa, P., and Hik, D. S., 2004: Forage selection by collared pikas, *Ochotona collaris*, under varying degrees of predation risk. *Canadian Journal of Zoology*, 82: 533–540.
Shaw, W. T., 1926: Age of the animal and slope of the ground surface, factors modifying the structure of hibernating dens of ground squirrels. *Journal of Mammalogy*, 7: 81–96.
Stephens, D. W., and Krebs, J. R., 1986: *Foraging theory*. Princeton: Princeton University Press.
Vander Wall, S. B., 1990: *Food hoarding in animals*. Chicago: University of Chicago Press.
Vasquez, R. A., Ebensperger, L. A., and Bozinovic, F., 2002: The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. *Behavioral Ecology*, 13: 182–187.
Zazula, G. D., Froese, D. G., Westgate, J. A., La Farge, C., and Mathewes, R. W., 2005: Paleoecology of Beringia "packrat" middens from central Yukon Territory. *Quaternary Research*, 63: 189–198.
Zazula, G. D., Froese, D. G., Elias, S. A., Kuzmina, S., and Mathewes, R. W., (in review): Arctic ground squirrels of the mammoth-steppe: paleoecology of middens from the last glaciation, Yukon Territory, Canada. *Quaternary Science Reviews*.

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APPENDIX A

Cover (abundance) (after Braun-Blanquet, 1927) of vascular plant species recorded in each vegetation type at study sites near Kluane Lake. Numerical scale: first number designates cover value, second number designates measure of grouping. Cover value: * = sparsely or very sparsely present with cover very small; 1 = plentiful but of small cover value; 2 = very numerous or covering up to 5% of area; 3 = any number of individuals covering 25–50% of area; 4 = any number of individuals covering 50–75% of area; 5 = covering more than 75% of area. Grouping value: 1 = growing singly or isolated individuals; 2 = group or tufted; 3 = in small patches or cushions; 4 = in small cushions. ***Trees present but not quantified.

	Roadside		Steppe on colony		Steppe off colony		Forest transition		Rose patch	Forest edge	
Taxon	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 2	Site 1	Site 2
Pinaceae											
Picea glauca (trees)										***	***
Poaceae											
Bromus pumpellianus var. *arcticus*							1,1	*,1		1,1	*,1
Calamagrostis purpurescens var. *purpurescens*					*,1		2,2	2,1		2,2	2,1
Elymus calderii						2,2					
Elymus sp. (clipped)				1,1		1,2		2,2	2,1		
Elymus trachycaulus ssp. *subsecunduns*	1,1		1,2		1,2						
Hordeum jubatum		2,2									
Poa glauca	*,2				1,2	1,2		2,2	2,2		
Cyperaceae											
Carex filifolia			3,3	1,2	3,3	2,2		1,2	1,2		
Liliaceae											
Maianthemum stellatum								1,1			1,1
Zygadenus elegans							1,1			1,1	
Salicaceae											
Salix sp. (trees)										***	***
Populus tremuloides (saplings)								1,1		***	***
Santalaceae											
Comandra umbellata ssp. *pallida*					*,1	2,1		*,1	1,1		
Geocaulon lividum							2,1	*,1		2,2	2,2
Caryophyllaceae											
Silene taimyrensis										*,1	
Ranunculaceae											
Anemone multifida					*,1		2,1	*,1		1,1	*,1
Pulsatilla ludoviciana			*,1		3,1	*,1		2,1	2,1		
Brassicaceae											
Arabis holboellii var. *retrofracta*								*,1			
Lepidium densiflorum		2,2				*,1					
Rosaceae											
Potentilla pensylvanica	2,1		1,1		2,1	1,1					
Rosa acicularis						*,1		2,2	4,3	1,1	1,1
Fabaceae											
Astragalus alpinus						1,1		*,1			
Astragalus williamsii							2,1	*,1		2,1	*,1
Hedysarum alpinus								1,1			1,1
Oxytropis campestris var. *varians*								*,1			
Oxytropis splendens	*,1				2,1		2,1	*,1			
Linaceae											
Linum lewisii	*,1		*,1	*,1	*,1	*,1		*,1	*,1		
Elaeagnaceae											
Shepherdia canadensis							2,3	*,1		3,3	3,3
Onagraceae											
Epilobium angustifolium										1,1	1,1
Ericaceae											
Arctostaphylos uva-ursi							4,4	2,4		3,4	2,4
Primulaceae											
Androsace septentrionalis			*,1		*,1			*,1			

APPENDIX A
(Continued)

Taxon	Roadside		Steppe on colony		Steppe off colony		Forest transition		Rose patch	Forest edge	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 2	Site 1	Site 2
Boraginaceae											
Lappula squarrosa	1,1	1,1		*,1		*,1					
Mertensia paniculata										*,1	*,1
Scrophulariaceae											
Castilleja hyperborea					*,1						
Penstemon gormanii	1,1		1,1		1,1	1,1		*,1			
Plantaginaceae											
Plantago canescens	1,1	1,1									
Rubiaceae											
Galium boreale								*,1		*,1	*,1
Asteraceae											
Achillea millefolium							*,1	*,1			
Artemisia frigida	3,3	2,2	3,3	4,3	1,2	3,2		1,1	2,1		
Erigeron caespitosa					*,1	1,1	*,1	*,1			
Solidago multiradiata	*,1						2,1	*,1			
Bare ground or bryophyte crust	4	4	3	4	1	2	0	3	0	0	0

APPENDIX B

Vascular plant taxa recovered from caches near Kluane Lake. % represents percent of total mass of cache. Plant parts: A = achene, B = berry, C = seed capsule, CS = cone scale, F = floret or flower, H = hip (fleshy hypanthium or "fruit"), L = leaf, LG = legume, N = needle, S = seed, SC = silicle, and T = twig.

Taxon	Part	Site 1, Cache 1		Site 1, Cache 2		Site 2, Cache 1		Site 2, Cache 2		Site 2, Cache 3	
		(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)
Picea glauca	N, CS, T	0.0334	<1	0.0611	1.1	0.2990	<1	0.0021	<1	0.0022	<1
Carex filifolia	A	0.0620	<1	0.0688	1.2	0.1167	<1			0.0044	<1
Betula glandulosa	S					0.0007	<1				
Zygadenus elegans	S	0.0013	<1	0.0758	1.4						
Comandara umbellatus	B					0.2173	<1	0.2223	1.2		
Geocaulon lividum	B	12.831	92.7	3.3205	60.1						
Silene taimyrensis	S, C	0.0278	<1	0.0050	<1						
Anemone multifida	A			0.0008	<1	0.0001	<1				
Pulsatilla ludoviciana	A	0.0020	<1								
Arabis holboellii	S									0.0002	<1
Lepidium densiflorum	SL, S					0.0345	<1			0.0003	<1
Linum lewisii	S	0.0080	<1			0.0014	<1				
Potentilla pensylvanica	A					0.0358	<1	0.0003	<1	0.0098	<1
Rosa acicularis	H					23.5000	63.4	16.1000	89.6	29.1000	96.2
Rosa acicularis	A					11.481	31.0	0.59	3.3	0.9491	3.1
Astragalus alpinus	L					0.0463	<1	1.0218	5.7	0.0763	<1
Astragalus williamsii	LG, S	0.5862	4.2	0.5952	10.8	1.3483	3.6	0.0093	<1	0.0182	<1
Oxytropis splendens	LG			0.0260	<1						
Lupinus arcticus	LG					0.0182	<1				
Shepherdia canadensis	B, S					0.1883	<1	0.0089	<1	0.0369	<1
Arctostaphylos uva-ursi	S, L					0.0102	<1	0.0034	<1	0.0280	<1
Androsace septentrionalis	S, C	0.0036	<1	0.0079	<1						
Lappula squarrosa	S					0.0039					
Penstemon gormanii	S, C	0.2668	1.9	1.3439	24.3	0.047	<1				
Plantago canescens	S					0.0018	<1				
Galium boreale		0.0098	<1								
Artemisia frigida	L, F	0.0241	<1	0.0168	<1			0.0001	<1	0.0087	<1
Total mass		13.8560		5.5180		37.0510		17.9600		30.2340	
Total # vascular taxa		12		11		17		9		11	