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Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments

Shawn F. Morrison · Graeme Pelchat · Aaron Donahue · David S. Hik

Abstract Food hoarding is a behavioral adaptation of some herbivores to manage food availability through time and space. In strongly seasonal environments, where summer growing seasons are short relative to winter, an earlier start to hoarding should increase the amount of vegetation stored for winter and improve subsequent survival. We examined hoarding behavior ('haying') and its impact on survival for a small alpine lagomorph, the collared pika (*Ochotona collaris*) in Yukon, Canada. We used a combination of video surveillance, haypile measurements, and survival data from marked individuals of known age and sex. Annual haypile initiation was strongly influenced by age and year. Adult pikas began haying an average of 16 days earlier in 2004 relative to 2005, whereas young of the year (juveniles) did not vary in the timing of haypile initiation. The mean haying rate per hour increased monthly from 3.7 ± 0.7 trips in June to 6.6 ± 0.8 trips in August. Simulation analysis estimated the median haypile mass (dry weight) by mid-September to be 5.5 kg. At least 75% of simulated haypiles had a minimum of 90 days (3 months) of food reserves, and 50% of simulated haypiles had a minimum of 177 days (5.9 months) of food reserves by mid-September, supporting the hypothesis that haypiles serve as the primary source of food during winter. Survival was greatest for pikas in 2005 when they began haying prior to 31 July, but the benefits of earlier accumulation of vegetation on survival also varied between years. The implications of earlier spring snowmelt are discussed with respect to pika foraging and overwinter survival.

Keywords Alpine · Classification tree · Lagomorph · *Ochotona collaris* · Yukon

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Introduction

Food hoarding is an adaptive behavior used by herbivores to manage food availability through time and space (Andersson and Krebs 1978; Vander Wall 1990). For many species, food may become scarce or unavailable due to factors such as competition (Keddy 2001), seasonality (Owen-Smith 2002), or perceived risk of predation (Hik 1995; Morrison et al. 2004). A food cache allows individuals to meet their nutritional requirements despite unfavorable conditions (Vander Wall 1990). For many herbivores, plant protein content is higher at the beginning of the growing season and declines as plants reach maturity (e.g., Greenwood and Barnes 1978; Millar 1971; Sinclair 1975). Caching, therefore, allows individuals to partially escape the potentially adverse consequences of seasonally reduced forage availability and quality.

Caching may have implications for fitness by influencing survival (Rusch and Reeder 1978; Wauters et al. 1995), body mass (Buck and Barnes 1999; Rusch and Reeder 1978), and weaning rates (Wauters et al. 1995). Even

hoards that supply only a small portion of the individual's energetic needs can have important influences on survival (Hitchcock and Houston 1994). For herbivores in strongly seasonal environments, where summer growing seasons are short relative to winter, the initiation of hoarding is likely determined by vegetation phenology and moisture content (Smith 1974). Under such conditions, an earlier start to hoarding should increase the amount of vegetation stored for winter. If a cache represents most of an individual's winter food reserves, then an earlier start should translate into improved survival, and therefore increased fitness. Vegetation caching is known for several hibernating and non-hibernating northern mammals such as singing voles (*Microtus miurus*; Batzli and Henttonen 1993), arctic ground squirrels (*Spermophilus parryii*; Buck and Barnes 1999; Gillis et al. 2005), red squirrels (*Tamiasciurus hudsonicus*; Hurly and Robertson 1990; Smith 1968), and pikas (*Ochotona* spp.; MacDonald and Jones 1987), among others (Humphries et al. 2003; Vander Wall 1990).

In this study, we examined hoarding behavior ('haying') and its impact on survival for a small (~160 g) alpine lagomorph, the collared pika (*Ochotona collaris*). The haying behavior of collared pikas, and the closely related American pika (*O. princeps*), are well documented (Barash 1973; Broadbooks 1965; Conner 1983; Dearing 1996; Hudson et al. 2008; Huntly et al. 1986; Krear 1965; Millar and Zwickel 1972; Morrison and Hik 2008a). Both species make numerous foraging trips each summer to accumulate vegetation in haypiles for consumption during winter (Dearing 1997b). The timing of when pikas begin haying each summer appears to be a function of vegetation maturity and moisture content (Smith 1974; Smith and Weston 1990). Earlier snowmelt in spring should advance vegetation phenology and allow pikas to accumulate greater amounts of vegetation relative to a spring with delayed snowmelt. The initiation of haying may also vary by age, such that juveniles are delayed relative to adults and therefore have less time to accumulate vegetation for haypiles (Huntly et al. 1986; Krear 1965; Millar 1971; Smith 1974; Smith and Ivins 1984). Millar (1971) also suggested that adult males began haying before adult females.

The ecological significance of haypiles has been the subject of some debate (Dearing 1997b). Both Conner (1983) and Millar and Zwickel (1972) reported that haypiles did not contain sufficient vegetation to be the sole source of winter food and concluded that haying was a 'bet hedging' strategy to be used during inclement weather or delayed snowmelt in spring. Millar (1971) reported that haypile mass had no effect on *O. princeps* reproduction and supplementing haypiles with 1 kg of vegetation did not affect subsequent weaning rates in the following spring. Dearing (1997b), however, argued that Millar and Zwickel

(1972) underestimated haypile mass because of difficulties in extracting all vegetation from the many deep crevices within boulderfields. Using time–budget data, Dearing (1997b) reported that pikas in Colorado collected sufficient vegetation to sustain themselves during an entire winter, and that haypiles were more than a 'bet hedging' strategy. Kreuzer and Huntly (2003) studied *O. princeps* populations in Colorado and concluded that birth rates and survivals were associated with the timing of snowmelt such that areas with delayed snowmelt were sink populations.

Within this context, we tested three hypotheses regarding pika haying behavior and its relation to survival. First, we examined the hypothesis that *O. collaris* haypiles are sufficiently large to serve as the sole source of food during winter. Second, we tested whether the timing of hoarding behavior was age- and sex-dependant. Based on previous work on *O. princeps* described above, we predicted (1) adult pikas would initiate haying earlier than juveniles (young of the year), and (2) adult males would begin haying prior to adult females, and (3) we tested the hypothesis that earlier initiation of hoarding behavior improved over-winter survival.

Materials and methods

Study area

The study was conducted in a 4-km^2 alpine valley within the Ruby Range, east of Kluane Lake, Yukon, Canada (61°13′N, 138°16′W; 1,600–2,200 m a.s.l). The valley was a mosaic of meadow and tundra vegetation interspersed with patches of boulderfields (pika habitat). Vegetation communities were dominated by *Dryas octopetala*, *Salix* spp. *Cassiope tetragona* and several graminoids (e.g., *Carex consimilis*) (Hik et al. 2001; McIntire and Hik 2005). Collared pikas, hoary marmots (*Marmota caligata*) and arctic ground squirrels (*Spermophilus parryii*) were the dominant mammalian herbivores. Our study was conducted over 3 years (2004–2006), and we provide weather and climate data to facilitate comparisons and interpretations among years (Table 1). In addition to site-specific data, some weather data were obtained from the Environment Canada weather station at Burwash Landing (61°22′N, 139°3′W). This weather station is at lower elevation (807 m) than our site, but weather data collected there should reflect regional weather patterns because it is approximately 40 km northwest of our alpine study site.

Annual initiation of haying activity

Since 1995, each haypile within our study site has been marked with a wooden stake, so all haypile locations were

Table 1 Comparison of weather and climate characteristics in southwest Yukon during 2004–2006

Characteristic	2004	2005	2006
Pacific decadal oscillation (mean from November to May)[a]	0.546	0.671	0.189
Estimated snow-free day of year[b] (mean ± 95% CI)	173 (167–178)	171 (165–177)	176 (172–181)
Mean June temperature at site[c] (°C)	12.0	7.5	7.0
Mean spring temperature[d] (°C)	4.7	4.7	1.5
Mean summer temperature[e] (°C)	13.3	12.4	11.7
Total summer precipitation[f] (mm)	119.8	201.6	133.2

[a] The November–May mean is negatively correlated to the date of snowmelt at our study site (Morrison and Hik 2007). The value for year t is the mean from 1 November in year $t-1$ to 31 May in year t

[b] Derived from Fig. 4 in Morrison and Hik (2007)

[c] Mean air temperature collected at the center of our alpine study site

[d] Mean air temperature during March and April measured at Burwash Landing, YT (61°22′N, 139°3′W, elevation 807 m)

[e] Mean air temperature from June to August measured at Burwash Landing, YT

[f] Total precipitation from June to August measured at Burwash Landing, YT

known. Haypile locations were used in successive years (D.S. Hik, unpublished data), and therefore we were able to monitor all possible haypile locations. These haypile locations were checked weekly from 11 June (day 162) to 14 August (day 226) in 2004, and from 22 June (day 173) to 20 August (day 232) in 2005 for the presence of freshly collected vegetation that indicated the initiation of haying activity for that year. The proportion of active haypiles at the start of our monitoring period did not appear to differ between years (Fig. 1). Therefore, annual differences cannot be attributed to variation in our monitoring protocol. Weekly monitoring allowed estimation of the annual onset of haying for 44 pikas in 2004 and 64 pikas in 2005 (Table 2).

Freshly collected vegetation was easily distinguishable from brown and decomposing vegetation collected during previous years. Pikas in North America are asocial and each individual accumulates and defends a haypile for personal use (Millar 1971; Smith et al. 1990; Smith and Ivins 1984). Therefore, data from each territory represented the activities of a single individual.

Haying rates

In 2004, we used two Sentinal™ video cameras (Models HWB-2 5A6 and AC 2002-1; Sandpiper Technologies, Manteca, CA) to record the rate at which pikas delivered vegetation to their haypile, measured as the number of trips per hour. This is the most direct method for determining the amount of food collected by pikas during the summer. We obtained 220, 282, and 294 h of video data for June, July, and August, on 7, 6, and 5 individual pikas, respectively (Fig. 2). Only actively haying pikas were selected for observation. For each recording session, one camera was

deployed per haypile allowing us to simultaneously record activity within two pika territories. Cameras were placed at vantage points where movements of pikas to and from the haypiles were easily detected. Cameras were programmed to record images at a rate of 2.5 frames per second throughout the entire 24-h period. Because of the high-latitude of our site, there was adequate ambient light to record nighttime activity during June. However, 1–4 h of darkness in July and August limited our nighttime data collection to one camera that was equipped with 12 onboard infrared lights and a day–night sensor (Model AC 2002-1). The infrared lights illuminated an area within 3–4 m of the camera, and we positioned the camera accordingly.

Mammalian predators (e.g., weasels (*Mustela* spp.) or red foxes (*Vulpes vulpes*)) were never observed at haypiles. Hoary marmots, arctic ground squirrels, and ptarmigan (*Lagopus* spp.) broods were observed in the vicinity of haypiles, but at no time did any of these species forage from haypiles or have direct interactions with pikas. Pikas deposited vegetation directly onto the surface of the haypile with no apparent attempt to air dry plants prior to storage.

Load size

Pikas are classical multiple prey loaders, such that they collect multiple parts of several plant species during each haying trip. These loads were deposited on the haypile as discrete bundles and churned into the haypile over time through the movements of the pika. We inspected active haypiles 1–2 times weekly and collected all deposited loads (generally 1–3 per visit) before they had been mixed into the rest of the haypile. Loads were oven-dried and weighed to the nearest 0.1 g.
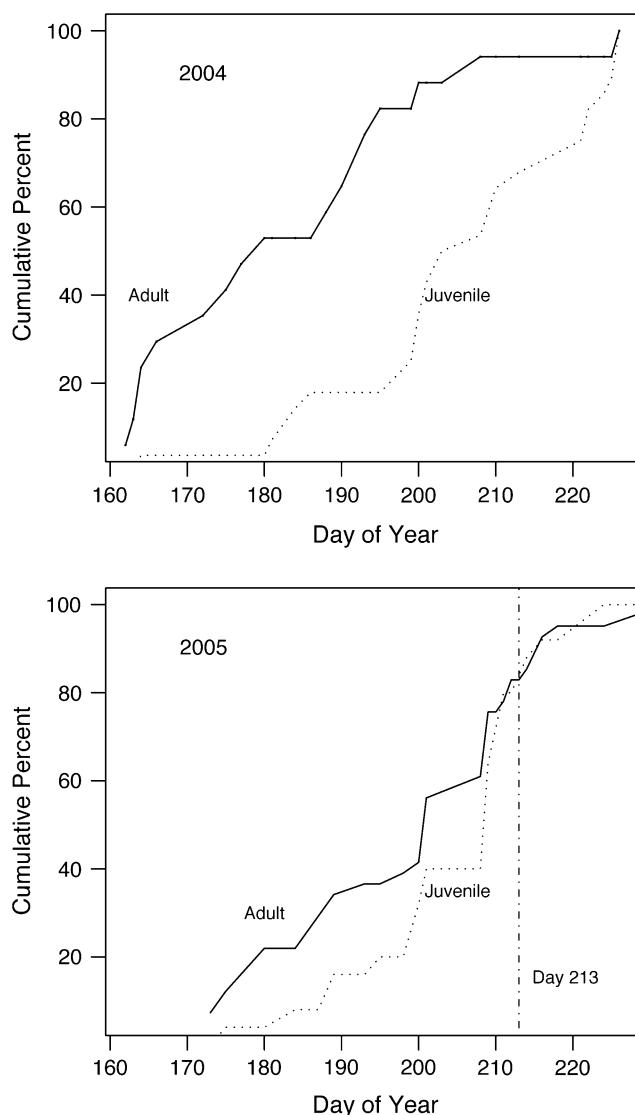
converted to mass per month by multiplying by 15, 31, 31, and 15 days for June, July, August, and September, respectively. Total summer mass (dry mass) was the sum of the four monthly estimates.

$$\frac{\text{mass}}{\text{day}} = \frac{\text{trips}}{\text{hour}} \times \frac{\text{mass}}{\text{trip}} \times \frac{24\,\text{h}}{\text{day}} \tag{1}$$

In mid-September 2006, all visible and accessible vegetation was excavated from 27 pika haypiles, placed in large plastic bags, and weighed to the nearest 100 g. All vegetation was returned to the haypiles following weighing.

We estimated food reserves by dividing haypile mass by daily consumption rates obtained from the literature (Dearing 1997a, b; Millar and Zwickel 1972). Dearing (1997a, b) and Millar and Zwickel (1972) used captive *O. princeps* provided with a known amount of haypile material to estimate daily consumption rates. The caloric content of haypile vegetation was assumed be 4.5 kcal per g of dried vegetation (Johnson and Maxwell 1966).

Survival

We monitored the fates (lived or died) of all individuals for which we knew the date of haypile initiation (Table 2). As part of a long-term study of pika ecology (Franken and Hik 2004a; Morrison and Hik 2007, 2008b), pikas were captured each summer using Tomahawk live-traps baited with fresh native vegetation. Individuals trapped for the first time were marked with numbered metal ear tags (Monel #1) and a unique color combination of thin wire to allow for later re-identification. We followed Duke (1951) in assigning gender and classified individuals as juveniles or adults based on body mass and molt pattern (Franken and Hik 2004b).

Because of their high visibility (Smith 1974, 1980), extreme adult philopatry (Smith and Ivins 1983), and data from our site indicating the recapture probability was approximately one (Morrison and Hik 2007), we did not have to account for overlooked individuals when determining survival.

Statistical analyses

We used a three-way analysis of variance (ANOVA) to examine the effects of pika age, sex, and year on the timing of haying behavior initiation. Age was classified as either juvenile or adult, sex was classified as male or female, and year was either 2004 or 2005. The response variable was the day of year when haypile accumulation began (e.g., day 1 = 1 January). Age, sex, and year were treated as fixed effects.

We used classification and regression trees (CARTs; Breiman et al. 1984) to model pika over-winter survival

Fig. 1 Cumulative percentage of active haypiles collected by collared pika (*Ochotona collaris*) throughout a summer growing season stratified by year (2004 and 2005) and age. *Solid lines* represent adult pikas, and *dotted lines* represent juveniles. Day of year is the number of days elapsed since 1 January of a given year. The *vertical dotted line* indicates the threshold date (estimated to be day 213, or 31 July, by classification tree analysis in Fig. 4), by which pikas needed to begin haying in order to survive the subsequent winter

Haypile mass and estimation of food reserves

For the months of June, July, and August, we simulated haypile mass by randomly selecting, with replacement, an hourly haying rate and a load size (dry mass) in order to calculate the mass of vegetation delivered to the haypile each day (Eq. 1). Haying at our site began approximately mid-June and continued to mid-September. We did not have video data for September, so we substituted observations from August. Accumulated mass per day was

Table 2 Number of active collared pika (*Ochotona collaris*) haypiles for which the date of haypile initiation was known and the mean (±SE) day of year (i.e., day 1 = 1 January) when pikas initiated haying behavior, stratified by sex, age, and year

Sex–age class	No. of haypiles		Haypile initiation (mean day of year ±SE)		
	2004	2005	2004	2005	Years pooled
Males	15	28	198.4 (3.9)	203.7 (2.5)	201.5 (2.2)
Juveniles	9	12	206.0 (4.2)	207.8 (3.1)	206.8 (2.6)
Adults	6	16	189.2 (6.1)	201.8 (3.4)	197.7 (3.2)
Females	22	31	191.7 (6.0)	198.9 (2.9)	196.4 (2.8
Juveniles	12	10	204.4 (6.6)	201.7 (3.5)	202.9 (3.4)
Adults	10	21	172.7 (5.3)	196.8 (4.4)	190.2 (4.2)
Unknown Sex	7	5	–	–	–
Juveniles	6	1	–	–	–
Adults	1	4	–	–	–
Sex–age pooled	44	64	196.8 (3.0)	200.9 (1.8)	199.3 (1.6)

Fig. 2 Number of vegetation deliveries to collared pika haypiles (trips per hour) according to month and time of day in southwest Yukon during June, July, and August 2004. For each *boxplot*, the *horizontal line* represents the median value, the *top and bottom of each box* indicates the 25th and 75th percentile, and the whiskers represent the 10th and 90th percentiles. The *horizontal bars* for each month indicate daylight hours
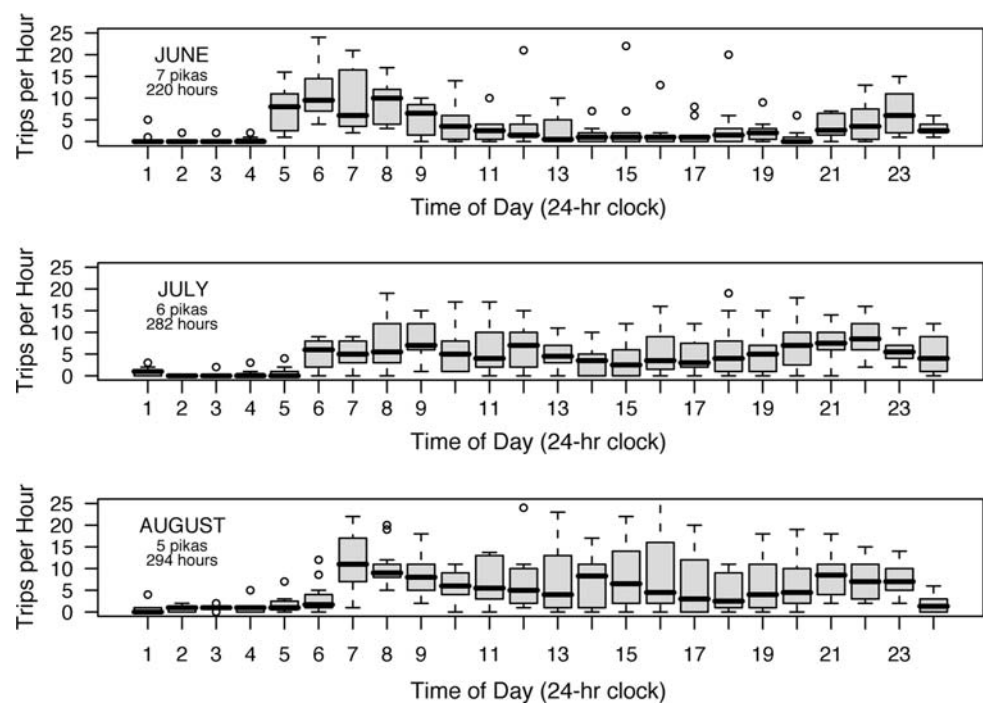
(survived or died) during the winters of 2004–2005 and 2005–2006. The independent variables were pika age (juvenile or adult), year (2004–2005 or 2005–2006), sex, and when haying behavior was initiated in the preceding summer measured as the day of year (i.e., day 1 = 1 January).

CARTs are becoming increasingly common for addressing a variety of ecological issues such as predicting species occurrence (De'ath and Fabricius 2000; Morrison et al. 2003), age classification (classified as young-of-the-year, juveniles, or adults; Karels et al. 2004), survival (survived or died; Franken 2002), and the response of populations to climate variability (Crozier and Zabel 2006). In essence, classification trees are a regression technique that allows the use of categorical and continuous data, non-linear relationships, missing values, and implicitly include

interactions among predictor variables (Faraway 2006). Trees are created using recursive partitioning to separate the response observations into increasingly homogenous subsets. Each split (node) in the tree is based on a threshold value of the predictor variable that produces the greatest within-group similarity for the response variable. The entire dataset may be partitioned until each observation is explained or according to pre-specified stopping criteria. The optimal tree size (i.e., number of nodes) is a balance between explanatory ability and generality to other datasets. We determined the optimal tree size through a k-folds cross-validation pruning procedure as described by Faraway (2006). We measured the ability of the pruned tree to predict known observations and calculated misclassification rates accordingly.

Results

Effects of age, sex, and year on onset of haying

There was no significant 3-way interaction of age, sex, and year ($F_{1,88} = 1.40$, $P = 0.24$), allowing us to consider 2-way interactions. Haypile initiation was significantly related to an age × year interaction ($F_{1,88} = 6.80$, $P = 0.011$) in which adult pikas began haying an average of 16 days earlier in 2004 (mean day of year = 183.3 ± 4.4 SE.) relative to 2005 (199.3 ± 2.5). Juveniles in 2004 lagged behind adults for the entire monitoring period (Fig. 1). Juveniles in 2005, however, initially lagged behind adults but had caught up by the end of July (Fig. 1). There was no sex × year interaction ($F_{1,88} = 0.26$, $P = 0.61$), nor was there an age × sex interaction ($F_{1,88} = 0.21$, $P = 0.65$). There was a significant effect of age ($F_{1,88} = 10.17$, $P = 0.002$) and year ($F_{1,88} = 6.59$, $P = 0.01$) when considered as main effects. However, interpretation of age and year as main effects is cautioned, because they occur in significant 2-way interactions and are therefore not independent of other factors (Zar 1999). The influence of sex as a main effect was inconclusive (day of year = 201.5 ± 2.2 days for males and 196.4 ± 2.8 for females; $F_{1,88} = 3.34$, $P = 0.071$).

Haying rates, load size, and daily activity

Pikas actively collected vegetation for haypiles throughout the entire 24-h day although peaks of activity were noted (Fig. 2). Haying rates in June appeared to peak twice daily at approximately 0500–0900 hours and again at 2100–2400 hours. Similar peaks of activity were less obvious in July and August, although haying seemed to be more common between 0600–1300 and 2000–2300 hours. The mean haying rate per hour increased monthly from 3.7 ± 0.7 (95% CI, $n = 223$) trips in June, 5.0 ± 0.5 (95% CI, $n = 283$) trips in July, and 6.6 ± 0.8 (95% CI, $n = 307$) trips in August. The maximum rate did not appear to vary monthly, but the amount of midday activity increased sharply during July and August relative to June (Fig. 2). Haying activity was reduced between 0100–0400 hours for all months; however, pikas were occasionally observed haying during these hours. Pikas carried a mean of 0.62 ± 0.06 g (dry weight, 95% CI, range = 0.01–3.77 g, $n = 213$) of vegetation per haying trip.

Haypile mass via simulations, excavations, and estimated reserves

Our simulations provided estimates of median haypile mass (dry weight) by mid-September of 5.5 kg (25th and 75th quartiles = 2.8 and 9.8 kg, respectively; mean = 7.4 kg).

Mean haypile mass based on the excavation of 27 pika haypiles in mid-September 2006 was estimated to be 3.1 ± 0.82 kg (95% CI, $n = 27$).

The amount of food represented by the median 5.5-kg haypile differed according to the consumption rate (Fig. 3). However, for both consumption rates, at least 75% of simulated haypiles had a minimum of 90 days (3 months) of food reserves, and 50% of simulated haypiles had a minimum of 177 days (5.9 months) of food reserves by mid-September. Based on Dearing's (1997b) estimate, the median haypile at our site had 251 days (8.3 months) of food reserves (based on a 22 g/day rate of consumption; Dearing 1997a). Pikas had a median of 178 days (5.9 months) of food reserves based on Millar and Zwickel's (1972) maximum estimate of 31 g/day.

Effects of haying onset, age, sex, and year on survival

Classification tree analysis using year, age, sex, and day of year as predictor variables, indicated that survival was greatest for pikas in 2005–2006 when they began haying prior to day 213 (31 July) (Fig. 4). Over-winter survival during 2004–2005 was less than half that observed in 2005–2006 (25% survival in 2004–2005 ($n = 44$), and 56% survival in 2005–2006, $n = 64$)). Haying dates in 2004 and pika age did not appear in the pruned tree
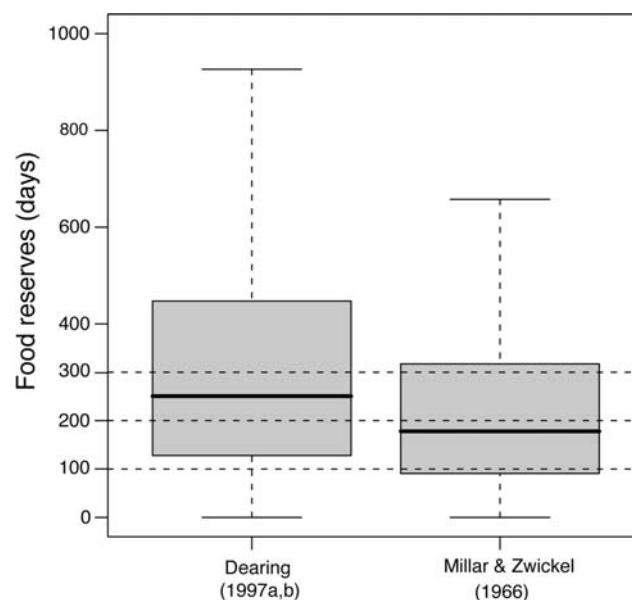

Fig. 3 Number of days of food reserves contained within pika haypiles as estimated by delivery rates and load size for two published rates of consumption. For each *box*, the *horizontal line* represents the median value, the *top and bottom of each box* indicates the 25th and 75th percentile, and the *whiskers* represent the 10th and 90th percentiles. The *horizontal lines* represent 100, 200, and 300 days of food reserves
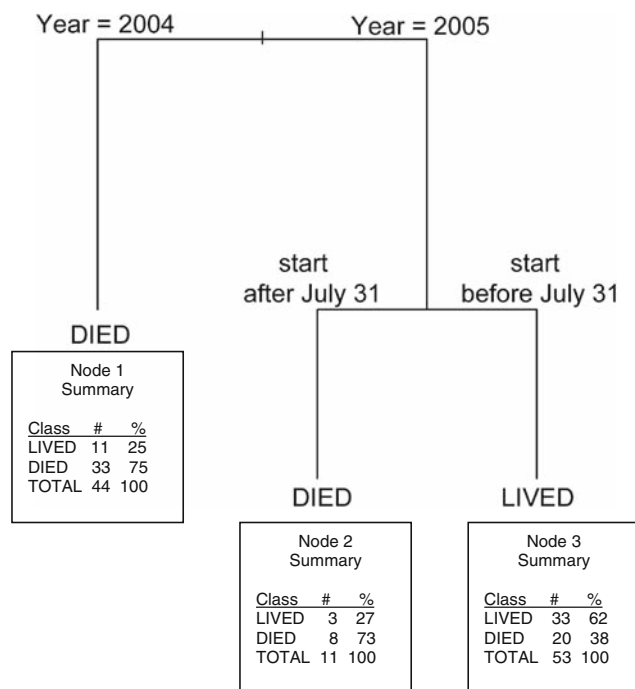
Fig. 4 Classification tree predicting pika overwinter survival (classified as lived or died) during winters of 2004–2005 and 2005–2006. Independent variables included age (juvenile or adult), sex, and when haypile accumulation began (measured as day of year). Each *node* (split) displays the split variable and its splitting (or threshold) value. *Nodes branching to the left and right* contain observations that correspond to the splitting value indicated. The *terminal nodes* (leaves) present the number and percentage of observations that were classified correctly and incorrectly. *Vertical line* length is proportional to the amount of deviance explained by the preceding node

suggesting that neither influenced survival in that year. The pruned tree correctly classified 67.2% of known deaths and 70.2% of known survival events for an overall misclassification rate of 31.5%.

Discussion

Our study evaluated the factors affecting when collared pikas began hoarding vegetation for winter consumption and its effect on subsequent survival. Our first hypothesis, that the onset of haying behavior was related to pika age, was supported in 1 of the 2 years of our study. Specifically, our results suggested that the annual onset of haying behavior was related to an interaction between pika age and year (Hypothesis 1). Juveniles did not vary in their onset of haying behavior; however, adults started haying 16 days earlier in 2004 than in 2005. Similar age-specific patterns were observed by Krear (1965) and Millar (1971). The occurrence of a year effect for adults at our site does not appear to be explained by differences in the date of

snowmelt or seasonal temperatures (i.e., Table 1). Instead, the effect may be related to increased pika abundance on east- and west-facing slopes and decreased abundance on south-facing slopes in 2005 relative to 2004 (Morrison and Hik 2007, 2008b). East- and west-facing slopes at our site typically had delayed snowmelt and lower vegetation biomass relative to south-facing slopes (D.S. Hik and T.J. Karels, unpublished data). These finer-scale patterns of snowmelt and vegetation characteristics may have contributed to the year effect observed in our analysis.

Because adult females must nurse their young, and therefore have greater time and energetic constraints relative to adult males, we expected adult females to start haying later than adult males (Hypothesis 2). Millar (1971) suggested similar timings for *O. princeps*, although that was based on anecdotal observations and not structured data collection. However, we observed no sex-based differences among adults, perhaps due to (1) the time and energetic costs of nursing and tending offspring on adult females are reduced or absent before haying begins for adult males, and therefore both sexes have approximately equal opportunity to begin haying, or (2) adults females compensate by increasing haying effort following weaning of offspring. Contrary to our prediction, adult females began haying approximately 11 days earlier (all years pooled) than adult males, but this difference was not statistically significant. The reasons for this pattern are unclear, but may reflect the need for females to ensure adequate food supplies during the following winter to allow them to recover from the energetic costs associated with gestation and rearing of young. However, additional data would be required to determine if this pattern is biologically meaningful.

Our third hypothesis, that over-winter survival was related to the initiation of haying behavior, was supported by our data, providing additional support for a direct link between foraging behavior and survival for pikas. The effect of this timing, however, was conditional on the year of observation and the age of the individual. The 2005 date threshold (day 213 or 31 July) selected by the classification tree analysis closely corresponded to the date juveniles and adults had approximately the same cumulative percentage of active haypiles. In 2004, and before 31 July in 2005, juveniles lagged behind adults in the initiation of haypile activity. However, by 31 July 2005, adults and juveniles had approximately the same proportion of active haypiles. In some years, therefore, juveniles appear able to emerge from the natal nest, disperse, find and claim a vacant territory, and begin haying without any delay relative to adults by the end of the growing season. Earlier haying did not affect over-winter survival in 2004–2005 suggesting that, in some years, other factors may over-ride the amount of vegetation contained within a haypile. For example,

mid-winter freeze–thaw events may have important effects on pika survival that are independent of food reserves (Smith et al. 2004).

Peak vegetation biomass near talus occurs in late July at our site and senescence begins soon thereafter (McIntire and Hik 2005). Thus, pikas that begin haying in late July have access to maximum vegetation biomass and can therefore quickly accumulate vegetation for haypiles. However, in doing so, they also assume the risk of collecting vegetation of steadily declining biomass (McIntire and Hik 2005) and quality (Millar 1971). Therefore, starting late in the season will affect both the amount and quality of vegetation contained within haypiles and may affect pika nutrition during winter with implications for survival.

The southwest Yukon has experienced rapid warming since instrumental record keeping began (Zhang et al. 2000). This trend is expected to continue (ACIA 2005; Laprise et al. 2003), resulting in longer growing seasons in this region due to earlier spring snowmelt (ACIA 2005). Our results from 2 years of observations suggest this may allow pikas to begin haying earlier and improve their subsequent over-winter survival. However, this positive effect of warming must be evaluated with respect to the known negative effects of warming such as increased frequency of mid-winter freeze–thaw events (ACIA 2005; IPCC 2007) that may increase pika mortality (Smith et al. 2004). Earlier snowmelt will also affect vegetation life history (Hoye et al. 2007; Post et al. 2008) and community composition (Chapin et al. 1995; De Valpine and Harte 2001), with currently unknown effects on pika foraging behavior and population dynamics.

The timing of parturition may affect survival in that individuals born earlier in a summer are expected to have better over-winter survival (Gillis 1998; Roff 1992). However, over-winter survival of juveniles at our site was unaffected by parturition date, because their rapid growth rate allowed most individuals to achieve adult mass before winter irrespective of parturition date (Franken and Hik 2004b).

Haypile mass based on simulations (median = 5.5 kg, mean = 7.4 kg) and excavations (median = 2.2 kg, weighted mean = 3.1 kg) were similar to masses based on excavations reported for *O. princeps* (5.7–7.7 kg by Dearing 1997b, 4.8 kg by Sundby 2002, and 0.4–6.0 kg by Millar 1971) and *O. rufescens* (5 kg in Smith et al. 1990). Our estimates based on simulations are based on dry weight, whereas vegetation from excavated haypiles may not be completely dry. Thus, the dry weight difference between simulated and excavated haypiles may be slightly greater than reported. Millar (1971) further reported differences among sex and age classes in which adult males had larger haypiles (2.9 ± 0.3 kg) by the end of September than adult

females (2.0 ± 0.3 kg), and juveniles, in turn, had significantly smaller haypiles (1.1 ± 0.2 kg) than adult females.

Collared pikas at our site tended to make more haying trips in the early morning and again from 2100–2300 hours during June, similar to the patterns described for *O. himalayana* (Smith et al. 1990) and *O. princeps* (Severaid 1950). Pikas increased their haying rate in July and August by increasing their midday activity such that peak activity times became less obvious. Broadbooks (1965) also noted that *O. collaris* was actively haying throughout the day with no major lulls in midday activity. Activity was reduced considerably from 2400–0400 hours in all months; however, pikas were observed haying during these times. Therefore, it cannot be assumed that pikas are inactive during these times and time budgets should be based on the entire 24-h period to capture the full range of behaviors. Smith (1974) reported elevation differences in the daily activity of *O. princeps* and attributed the increased levels of nocturnal activity at lower elevations due to higher daytime temperatures that restricted activity. We hesitate to attribute nocturnal activity to inhospitable daytime temperatures, because pikas were very active during the day. Rather, nocturnal activity could be due to atypical circadian rhythms recently discovered in high-latitude reindeer (*Rangifer tarandus*; van Oort et al. 2005), or a relatively shorter growing season that forces pikas to harvest at a maximum rate to obtain enough vegetation for their haypiles.

Collared pikas at our site carried less vegetation (by mass) per haying trip than reported for *O. princeps* (Dearing 1997b). The reasons for this are unknown, but likely reflect differences in plant species composition and plant morphology. Vegetation carried by haying pikas typically extends out of both sides of their mouth, enabling them to carry multiple stems simultaneously (i.e., multiple prey loaders; Stephens and Krebs 1986). In other words, they are less constrained by mouth volume than other herbivores. Plants in the subarctic Ruby Range meadows may be of smaller stature then plants in Rocky Mountain meadows where previous observations have been made (e.g., Dearing 1997b), requiring more trips to collect the same amount of cached vegetation.

Simulations showed pikas accumulated sufficient vegetation in haypiles to serve as a sole source of food for at least 5.9 months. Millar and Zwickel (1972) concluded that *O. princeps* required 6 kg by the end of September to survive 6 months, the mean length of the non-growing season in southern Alberta. Of 105 haypiles excavated at that site only 3 (2.9%) were ≥6 kg, the minimum required to provide the sole source of winter nutrition. At our site, only 1 of 27 (3.7%) excavated haypiles had ≥6 kg of vegetation by mid-September when haying activity was largely completed. Excavated haypiles at our site were

smaller than simulated haypiles; however, haypile vegetation may be located out of reach within the talus, and therefore haypile masses based on excavations underestimated what was actually available to pikas (Dearing 1997b; Krear 1965).

Pikas foraged in meadows outside of the growing season until snow cover greatly reduced accessibility (K. O'Donovan, unpublished observations), and therefore collared pikas may not be completely reliant on their haypiles for the entire non-growing season. Snow cover at our site lasts approximately 6–7 months (Danby and Hik 2007), and therefore pikas appear to accumulate sufficient food reserves for this period, supporting Dearing's (1997b) argument that pikas collected sufficient haypile reserves to improve survival during winter. Foraging in meadows during the non-growing season may be a strategy to ensure sufficient reserves remain in the haypile for use when meadow vegetation is snow-covered.

To conclude, food hoarding, such as haying by pikas, provides a buffer against variable environmental conditions, and often is critical to a species ability to maintain persistent populations in harsh environments (Vander Wall 1990). The day of year that pikas begin haying varied between years for adults but not for juveniles. The survival benefits of earlier accumulation of vegetation varied between years suggesting the factors influencing pika behavior and survival are not consistent over time. Increased variability in spring snowmelt patterns, as predicted to occur due to global climate change (ACIA 2005; IPCC 2007), could have important implications for the population dynamics of alpine mammals, like pikas, whose survival partially depends on their ability to acquire food resources for use during winter. Haying may also confer a competitive advantage to pikas over other sympatric herbivores that store energy as body fat reserves for use during hibernation (such as hoary marmots or arctic ground squirrels), because pikas are not affected by digestive constraints (such as passage time) at the time of collection. Further, the relocation of vegetation from the meadow to haypiles may enhance nutrient cycling (Aho et al. 1998) and alter plant species diversity (Huntly 1987; Roach et al. 2001). Therefore, the large amount of time spent haying each summer has broader implications for vegetation biomass, community structure, and biodiversity.

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