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THE FUNCTION OF HAYPILES OF PIKAS (*OCHOTONA PRINCEPS*)

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The pika, *Ochotona princeps*, spends a considerable amount of time during summer caching vegetation. These caches (haypiles) have been suggested to function as the mainstay of diet in winter, as a source of food for intermittent periods when the animal is unable to forage elsewhere, or in nonfood functions, e.g., nest sites. I investigated the haying behavior of a population of pikas on the West Knoll of Niwot Ridge, Colorado. In addition to directly measuring sizes of haypiles of pikas on West Knoll, I also estimated, using data from the literature, sizes of haypiles of another population of pikas. Haypiles that were excavated immediately after construction revealed that pikas from West Knoll stored 350 days of food, more than that required for winter. Initial contents of haypiles, discounted for decay and spring leftovers, indicated that pikas from West Knoll consumed at ≥ 175 days of food from their haypile during winter 1992–1993. Sizes of haypiles based on behavioral data collected on a different population of pikas corroborated the large size of haypiles found on West Knoll. Given these data, the primary function of haypiles appears to be to provide the major source of sustenance for pikas during winter.

Key words: *Ochotona princeps*, pika, cache, food hoarding, haypiles

The pika, *Ochotona princeps* (Lagomorpha), is a small herbivore known for its unusual haying behavior (Broadbrooks, 1965; Conner, 1983; Huntly et al., 1986; Millar and Zwickel, 1972). During the short alpine summer, pikas harvest and store plants in caches (haypiles) under rocks (Broadbrooks, 1965; Krear, 1965; Millar and Zwickel, 1972). From late July through mid-September, 25–55% of their surface activity is spent constructing winter caches (Conner, 1983; Smith and Ivins, 1984). Pikas may make up to 27 collecting trips/h and are most exposed to predation while foraging; thus, mortality from predation may be greatest during the haying season (Conner, 1983; Ivins and Smith, 1983; McKechnie, 1990). Despite the large energetic investment and enhanced risk of predation associated with haying, the primary purpose of haying has not been firmly established.

Because pikas are herbivores that inhabit regions where fresh vegetation is limited or absent during winter, haypiles initially were

believed to serve as the fundamental food resource consumed during winter. However, excavations of haypiles of pikas revealed that in many cases, the quantity of vegetation stored was not adequate to sustain an animal throughout winter and a significant fraction of the haypile was not consumed during winter (Krear, 1965; Millar and Zwickel, 1972; West, 1980). Additionally, size of haypiles was not a reliable indicator of mortality in winter or reproductive success of females the following spring (Millar, 1974; Millar and Zwickel, 1972). The discrepancy in sizes of haypiles, but not mortality or natality, implied that pikas must forage outside of the haypile during winter. Whereas data on foraging of pikas in winter is scarce, there is evidence that pikas forage outside of the haypile on lichens, tree bark, evergreen trees, and shrubs (Conner, 1983; Huntly et al., 1984; Johnson and Maxell, 1966; Krear, 1965; West, 1980). Collectively, these observations have led to the hypothesis that haypiles of pikas serve not as the principal source of food for winter, but

rather represent a short-term, food resource most critical to survival in years when pikas are unable to forage outside of their haypile (Conner, 1983; Millar and Zwickel, 1972).

Haypiles also have been proposed to serve non-food functions, such as nesting sites, insulation, or protection against predators (Ivins, 1984; Krear, 1965). Evidence of occupancy of haypiles during winter is apparent in leftovers of haypiles, as fecal accumulations typically are found adjacent to or in leftovers of haypiles. Moreover, collection and storage of non-edible items for their haypile suggests that the haypile may serve as more than just a food resource (Ivins, 1984; Severaid, 1955).

If pikas forage from their haypiles during winter, then the reduction in size of the haypile after winter should be significantly greater than that from decomposition alone. Additionally, initial size of the haypile may be suggestive of its importance to foraging in winter. If pikas construct haypiles for short-term food resources, then haypiles should not contain extensive quantities of vegetation. However, if haypiles provide the majority of diet in winter, then this should be reflected in their initial size. The magnitude of diminution of haypiles after winter should be an indicator of whether the haypile serves as a short-term food resource or the mainstay of diet in winter. Alternatively, if the primary utility of haypiles is a non-food one, any changes in initial size of haypile over winter should be reflective of its decay.

I took several approaches to test the above predictions. I excavated haypiles prior to and after winter. In separate experiments, I determined the rate of decay during winter. Additionally, using behavioral data from the literature (Smith and Ivins, 1984), combined with my own data, I estimated the sizes of haypiles of pikas at another study site. The use of Smith and Ivins' (1984) behavioral data eliminated difficulties associated with estimating the sizes of haypiles from excavations and also provided sizes of haypiles from another popula-

tion. Here I present data that suggest the primary function of haypiles is to provide the mainstay of the diet in winter.

MATERIALS AND METHODS

Pikas were studied July 1990–August 1994 on the West Knoll of Niwot Ridge, Boulder Co., Colorado, (40°03'N, 105°36'W). Elevation of the study site ranged from 3,475 to 3,550 m. The two major plant communities, snowbed and moist meadow, within the study area are free of snow by 14 June and 5 July, respectively (Walker et al., 1994). Vegetation begins to senesce in the 2nd week of August. Thus, green vegetation is available on West Knoll for ca. 10 weeks.

Twenty-nine pikas were marked with colored ear tags to facilitate recognition of individuals as part of a larger project on selection of diet by pikas. Pikas are territorial, and each animal constructs and defends its own complex of haypiles, which consists of several small piles within its territory (Millar and Zwickel, 1972; Smith and Ivins, 1984). The boundaries of each animal's complex of haypiles were recorded during behavioral observations of foraging activities June–August 1992. On 22 and 23 September 1992, I excavated, weighed, and replaced the haypiles of 10 pikas. Only vegetation that had been collected by pikas during the summer of 1992 was included in the estimate of size of haypiles. Brown, decomposing vegetation was considered as remains of haypiles from the previous years and was not included. A 150-g sample was collected from each haypile and dried at 40°C to estimate dry weight. In late July 1993, immediately following snowmelt, leftovers of haypiles of the same 10 pikas were excavated, weighed, and a sample was taken to estimate dry weight. Data on leftovers were used only for pikas that were seen again during summer 1993, i.e., those that survived winter.

To estimate wet weight of biomass of plants collected per haying trip, I recorded the species of plant and type of tissue (flowers, leaves), as well as the number of items collected per trip for 16 animals. The amount of vegetation collected per foraging trip was estimated by multiplying wet weights of each type (flowers, leaves) by the number of items collected at one time.

To estimate proportion of the haypile lost to decomposition, I conducted a decomposition experiment during July 1991–June 1992. I con-

TABLE 1.—Calculations of the total number of haying trips per pika during one haying season at Copper Creek, Colorado. Monthly proportions of observations of haying, total number of all behavioral observations (haying plus five other behaviors) and observation hours were taken from table 3 in Smith and Ivins (1984). Total number of all behavioral observations, including nonhaying ones, are given in parentheses.

	May	June	July	August	September	October
Proportion of time spent haying						
Males (1,937)	0.031	0.163	0.195	0.303	0.232	0.076
Females (1,463)	0.007	0.139	0.162	0.279	0.378	0.036
Total number of observations of haying						
Males	60.1	315.7	377.7	586.9	449.4	147.2
Females	10.2	203.4	237.0	408.2	553.0	52.7
Total (males and females)	70.3	519.1	614.7	995.1	1,002.4	199.9
Hours of observation	35	250	650	490	137	19
Haying trips/hr	2.01	2.09	0.95	2.03	7.32	10.52
Haying trips/mo	872	872	410	881	3,073	4,566
Total haying trips	10,674					

structed eight artificial haypiles that each contained five 30-g (wet weight) subsamples of diet in winter. Composition of diet in winter was estimated from ca. 300 observations of seven pikas collecting vegetation during June and July 1991 (Dearing, 1995). The subsamples were contained individually in nylon-mesh bags (1-mm² mesh) and stored together in a fiberglass screen bag (1-mm² mesh). Artificial haypiles were constructed and placed on the talus in July 1991, near the observation site. One subsample was drawn randomly from each artificial haypile in July 1991, September 1991, December 1991, March 1992, and June 1992. Subsamples were dried at 40°C before weighing. Changes in biomass over time were assessed using repeated-measures analysis of variance and Tukey's HSD.

I estimated the quantity of vegetation stored in haypiles of a population of pikas at Copper Creek, Gunnison Co., Colorado (elevation, 3,200 m) by combining data from the literature with my own. Using data from an extensive analysis of time-budgets of pikas (Smith and Ivins, 1984), I estimated the average number of haying trips made per pika per season (Table 1). Smith and Ivins (1984) reported monthly proportions of observations of haying and total number of observations of haying for males and females separately. To generate the number of haying trips for sexes combined, per monthly hours of observation, I summed the products of the proportion of time spent haying and the total number of observations of haying for each sex.

This total, representing the total number of observations of haying per month for both males and females, was divided by the number of hours of observation per month. Because pikas are diurnally active (Smith and Ivins, 1984), I multiplied the number of observations per hour by 14 h by the number of days per month. To estimate total size of haypiles the total number of haying trips was multiplied by my own data on the average amount of hay carried per trip.

To estimate the length of time (in days) that a pika could feed from its haypile during winter, I divided dry weight of haypiles by the amount of food (dry weight) consumed by pikas, 22 g per day. This amount was determined from pikas kept in captivity at a constant 10°C in another experiment (Dearing, 1997a).

RESULTS

In an average haying trip, pikas collected 1.96 ± 1.8 g of fresh vegetation. This load represents ca. 1.18% of their body weight. Estimates of the amount of vegetation carried per haying trip were based on 716 observations of 16 pikas, with an average of 42.1 ± 6.5 trips per pika.

Haypiles excavated on West Knoll are larger than any previously reported (Table 2). Not accounting for future decay, haypiles constructed by adult pikas contained 350 days of food. Estimates of size of hay-

TABLE 2.—Mean dry weight (kg) (± 1 SE) of all excavated haypiles on West Knoll, Colorado. Sample sizes (*n*) are the number of pikas (West Knoll) or number of hours of observation (Copper Creek). Calculations of haypiles from Copper Creek, Colorado precluded estimations of standard errors and necessitated that sample size be given in hours of observation. Days of food in the haypile were calculated based on a consumption rate of 22 g dry weight/day (Dearing, 1997a). Length of winter is based on data in Walker et al. (1994) for West Knoll and Smith and Ivins (1984) for Copper Creek.

	<i>n</i>	Dry weight (kg)	Wet weight (kg)	Days of food	Length of winter (days)
West Knoll					
All pikas	10	6.858 \pm 0.98	25.2 \pm 3.6	311	295
Adult pikas	8	7.700 \pm 0.95	28.3 \pm 3.5	350	295
Copper Creek					
Adult pikas	1,581	5.691	20.9	258.7	180

piles based on time-budget data taken at Copper Creek by Smith and Ivins (1984) concur with the large haypiles found on West Knoll (Table 2). Not accounting for decay, pikas at Copper Creek stored 259 days of food.

Given the amount of vegetation carried per haying trip, individual pikas on West Knoll made ca. 12,747 trips during summer 1992 to construct a haypile of average size.

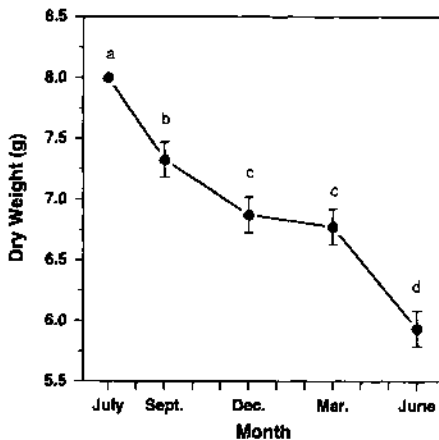


FIG. 1.—Changes in biomass of vegetation stored in haypiles on the West Knoll, Colorado. Sample size is eight for each time period. Error bars are least significant differences. Vegetation stored in haypiles decreased over time (ANOVA, $P < 0.001$, $F = 36.9$, $d.f. = 4,35$). Means with different letters are significantly different.

As summer on West Knoll is ca. 10 weeks long, pikas have ca. 70 days to collect vegetation. To cache a haypile of average size in this period of time, pikas would have to average 13 haying trips/h.

Vegetation stored in artificial haypiles on West Knoll decayed significantly and at a fairly steady rate over winter (Fig. 1). At the end of winter, ca. 25% of the initial dry weight of the haypile was lost to decomposers. Therefore, if a maximum of 25% of the initial haypile was lost to decomposition, haypiles built by adult pikas on West Knoll contained 263 days of available food.

Of the 10 pikas whose haypiles were weighed in summer 1992, seven were seen again in August 1993. Two of these pikas were juveniles during the previous summer, i.e., born in May or June 1992. About $26.1 \pm 7.1\%$ of the dry weight of haypiles constructed by these seven pikas in summer 1992 remained after 10 months of storage. The dry weight of leftovers was 1.571 ± 0.309 kg ($n = 7$). Given that $\leq 25\%$ of the haypile may have been lost to decomposers, combined with the quantity remaining, it appears that pikas on West Knoll consumed a minimum of 175 days of vegetation in haypiles during winter 1992–1993.

DISCUSSION

Ecologists have puzzled over the haying behavior of pikas because, as conspicuous

and frequent as haying is, excavations of their haypiles have suggested that haypiles are insufficient for exclusive feeding in winter (Conner, 1983; Millar and Zwickel, 1972). Moreover, an erroneous interpretation (Conner, 1983; Smith and Weston, 1990) of Millar and Zwickel's (1972) paper on haypiles has propagated the perception that removal of haypiles of pikas in autumn has no effect on overwinter survival. However, Millar and Zwickel (1972) neither removed haypiles nor did they refer to any previous experiments where they had been removed. The data presented here demonstrate that pikas store ample amounts of vegetation for winter. Haypiles of both populations of pikas initially contained ≥ 8 months worth of food. The extensive quantities of vegetation stored in these haypiles suggest that haypiles represent more than simply short-term, emergency sources of food.

The initial magnitude of the haypile, together with the proportion of leftovers, suggests that pikas are profligate hayers, gathering far more than they are able to consume during most years. However, the effective size of haypiles is much reduced when compared to the initial size. Pikas are selective in what they consume from their haypile (Dearing, 1995), in part because efficient transport of vegetation to haypiles in summer requires collection of non-preferred food types. For example, when grazing in meadows during summer, pikas typically eat only heads and not stems of flowers of the same species. In contrast, when haying, pikas clip flowers such that long stems remain attached and carry the clipped vegetation crosswise with the stems in their mouths. This practice enables them to carry several items per trip by using stems as handles. As a result, ca. 10% of the initial haypile is comprised of flower stems. Many of these stems are most likely not consumed, as corroborated by the relative increase in abundance of stems of flower in leftovers of haypiles (Dearing, 1995).

In addition to effective size of haypiles

being discounted by the inclusion of non-edible food items, mass of haypiles is further diminished by consumption by microorganisms and microarthropods during storage (Lear and Seastedt, 1994). At the end of winter, $\leq 25\%$ of the initially stored biomass may be lost to decomposition (Fig. 1). Therefore, pikas must initially store large amounts of vegetation to compensate for that which will be lost to decay.

The amount of the haypile lost to decomposition (25%) combined with the quantity of leftovers (25% of the original) indicate that pikas on West Knoll consumed a minimum of 175 days of vegetation from haypiles during winter 1992–1993. The emergence of green vegetation in summer 1993 was delayed 2–3 weeks longer than average due to a 4 July 1993 snowstorm (Walker et al., 1994). In an average winter, reliance on the haypile may be ca. 150 days. Nonetheless, even in average winters, the contribution of the haypile to diet in winter is still substantial and represents the majority of food consumed during winter.

This estimation of the contribution of haypiles to diet of pikas in winter was biased conservatively. Because pikas store vegetation deep among the rocks, it was impossible to assess the quantity of vegetation stored and consumed by pikas that was not found during excavations of haypiles. Additionally, the daily rate of consumption (22 g) used in this study is higher than that measured by other researchers (Johnson and Maxell, 1966). If pikas consumed vegetation from deeply stored caches not included in the excavation of haypiles or if they consumed < 22 g/day, the length of time pikas fed from their haypiles would be considerably > 175 days.

Conner (1983) proposed that pikas are bet-hedgers, haying for once-in-a-lifetime events of scarcity of food. Yet, pikas inhabit alpine environments (Broadbrooks, 1965; Hafner and Sullivan, 1995) with annual, prolonged intervals of shortages of food. For example, on West Knoll, although there are annual deviations in severity of winter

(Greenland, 1989; Walker et al., 1994), vegetation invariably is absent during winter for ≥ 6 months. Essentially, no evergreen plants occur in this area of West Knoll (W. D. Bowman, pers. comm.; Walker et al., 1994). Hence, pikas on West Knoll annually experience a vegetationless period of ≥ 6 months. Reduction of availability of plants during winter is true of most habitats in which pikas reside (Broadbrooks, 1965; Hafner and Sullivan 1995; Millar and Zwickel, 1972). Therefore, if pikas bet-hedge, I suggest that it is in the collection of vegetation in excess of that actually required for an average winter, as insurance for occasional, annual variation in length of winter or decomposition of haypiles. This idea is supported by the fact that leftovers in haypiles were found in spring.

Haypiles of pikas have been proposed to serve other non-food functions such as nesting sites (Ivins, 1984; Krear, 1965). Pikas do appear to reside in their haypiles as evidenced from the presence of feces in spring, as well as direct observations of pikas sitting within their haypiles. However, nesting does not appear to be the primary function of haypiles because pikas on West Knoll consumed nearly one-half of their haypile.

Pikas have been observed foraging outside of their haypiles during autumn and early winter (Conner, 1983). The contribution of these foraging activities to diet in winter is unknown. On West Knoll, crustose lichens (Conner, 1983) are the only possible supplements to the haypile because essentially no evergreen species of plants occur there (W. D. Bowman, pers. comm.; Walker et al., 1994). The frequency of foraging excursions outside the haypile decreases from October through January (Conner, 1983). This reduction coincides with increasing palatability of haypiles as toxins of plants in the haypile decay. The vegetation stored in haypiles contains levels of phenolic compounds that are three to six times higher than that consumed in summer (Dearing, 1996). Thus, during autumn, pikas may

augment their diet, in part, by foraging outside of the haypile. By January, concentrations of secondary compounds of plants have decayed to levels that approximate those consumed in summer vegetation (Dearing, 1997b). Perhaps not coincidentally, pikas were never seen foraging outside their haypile during February–June (Conner, 1983).

The difference in sizes of haypiles at West Knoll compared to Copper Creek may reflect differences at these two sites in severity of winter and availability of evergreen vegetation. The study site at West Knoll is an alpine setting several meters above treeline. Virtually no evergreen vegetation is present either above or below the snow (W. D. Bowman, pers. comm.; Walker et al., 1994). Photosynthesizing vegetation can be absent there for ≤ 295 days (Walker et al., 1994). In comparison, the Copper Creek site is in the subalpine zone, below treeline with evergreen trees and forbs present during winter (Huntly et al., 1986; Smith and Ivins, 1984). Winter at the Copper Creek site is ca. 180 days, considerably shorter than winter on the West Knoll site (Smith and Ivins, 1984). The combination of a shorter winter and more available vegetation in winter at the Copper Creek site may result in pikas requiring less stored vegetation for winter, and, therefore, caching less vegetation in haypiles.

Previous studies of size of haypiles (Millar, 1974; Millar and Zwickel, 1972) have relied on estimating size of haypiles by excavation only. Both studies reported complete excavation of haypiles sampled. However, other researchers investigating this phenomenon have remarked on the uncertainty in assessing whether the entire haypile had been excavated (Ivins, 1984; A. T. Smith, pers. comm.). This difficulty in accurately quantifying size of haypiles is due to storage practices of pikas and landscape. Individuals store vegetation several meters deep under an area of talus that can comprise several square meters. Hence, it is easy to overlook substantial

pockets of an animal's cache. Moreover, some of the rocks within the complex of haypiles are too large to move without the aid of earthmoving equipment. Thus, it is probable that previous appraisals of sizes of haypiles (Millar, 1974; Millar and Zwickel, 1972) were underestimates. Future studies of sizes of haypiles should incorporate both observational data and excavational approaches.

Pikas have been classified by Vander Wall (1990) as food-hoarders that store for intermittent periods of shortages of food. Other animals included in this category are northern pocket gophers, *Thomomys talpoides*, and acorn woodpeckers, *Melanerpes formicivorus*. Caches of pocket gophers and woodpeckers contain food for ≤ 2 weeks (Vander Wall, 1990). Data presented here demonstrate that pikas collect for and consume from their caches much > 2 weeks worth of food. Including pikas in the category of animals that store for intermittent scarcity of food diminishes the overall importance of the haypile to survival of pikas in winter and may have consequences for future behavioral studies. Thus, I propose that pikas be reclassified in the category with animals (e.g., honey bees) that store to survive prolonged shortages of food.

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