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REPORTS

Energetic Return Rates from Limber Pine Seeds

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Limber pine seeds were potentially a valuable food resource for native occupants of the high mountains of the intermountain west. The seeds are rich in fats and proteins, with a greater caloric content by weight than pinyon pine seeds. The seeds are available in late summer, and collecting them is fairly easy, yielding large returns per time spent collecting. If the seeds are eaten whole or ground into meal without hand-hulling, return rates are very high, similar to rates for large and small game animals. The kernels are difficult to remove from their hulls, however, resulting in very low return rates if hand-hulled. Energetic considerations indicate that whole or ground limber pine seeds could have served as an important storable late summer food for prehistoric high-altitude occupants.

Figure 1. Limber pine (*Pinus flexilis* James).

Limber pine (*Pinus flexilis* James) is a prominent conifer in the subalpine zone of mountain ranges throughout the intermountain west (Fig. 1), stretching from its main distribution along the spine of the southern and middle Rocky Mountains westward across the Great Basin to southern California's higher peaks (Fig. 2; Little 1971; Steele 1990). In the Great Basin, limber pine grows above an altitude of 2,000 meters on more than fifty mountain ranges (Charlet 1996). Every two to four years in late summer, mature trees bear dozens of tapered cones, each cone containing several score of seeds (Fig. 3). Limber pine seeds were a potentially important food source for people living in the Great Basin's high mountains, and their remains have been found in archaeological contexts in high-altitude residential camp sites (Bettinger 1991; Rhode 2007, 2015; Scharf 1992, 2009; Thomas 1982, 2014a, 2014b), one lower–altitude archaeological site (Danger Cave, Utah; Rhode and Madsen 1998), and outside the Great Basin as well (e.g., Leigh Cave, Wyoming; Frison 1968). According to Julian Steward (1938), native peoples in the northern Great Basin collected seeds of limber pine and/or the closely related whitebark pine (*Pinus albicaulis* Engelm.), though one of Steward's consultants considered the seeds to be "too small and 'too greasy' and the trees too difficult to climb to make them profitable" (Steward 1938:28). Families living in the Lemhi Valley of Idaho collected "white pine" seeds from nearby mountains in quantities large enough to store over the winter (Steward 1938:190). Various northern Great Basin groups collected whitebark pine seeds "on trips east for buffalo;" they were then "stored in the

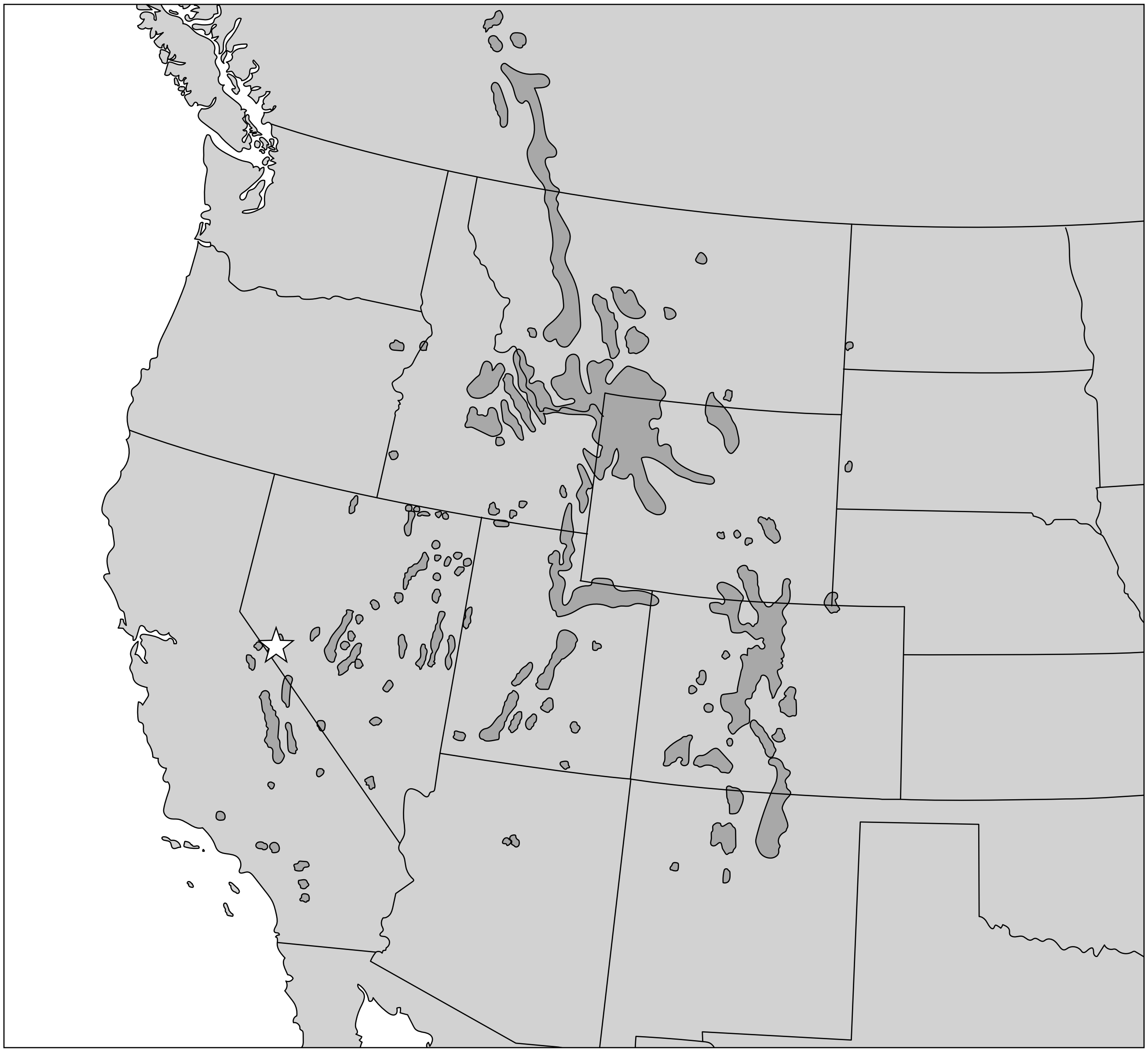

Figure 2. Distribution of limber pine in western North America.
Star indicates collection locality on Corey Peak, Wassuk Range, Nevada (Little 1971).

mountains" in caches or buckskin bags "to be picked up on the trip home" (Steward 1943:362). Kornfeld (2013) noted limber pine's dietary utility in the Middle Park area of Colorado, while in the southern Rocky Mountains the Chiricahua and Mescalero Apache groups apparently collected limber pine seeds wherever they could get them (Castetter and Opler 1936).

Unlike the better-studied singleleaf pinyon pine (*Pinus monophylla* Torr. & Frém.), little is known about the food value of limber pine seed collecting. Here we give the results of experiments to obtain information about the energetic return rates of limber pine collection and processing. The results suggest that limber pine seeds can be either exceptionally rich or poor in the rate of energy return, depending on how much effort is expended to remove the small kernels from their hulls.

LIMBER PINE SEED FOOD VALUE

Seeds of limber pine are moderately large for pines generally, but significantly smaller than those of the pinyon pine (Fig. 4; Krugman and Jenkinson 1974).

Figure 3. Limber pine cones in open stage.

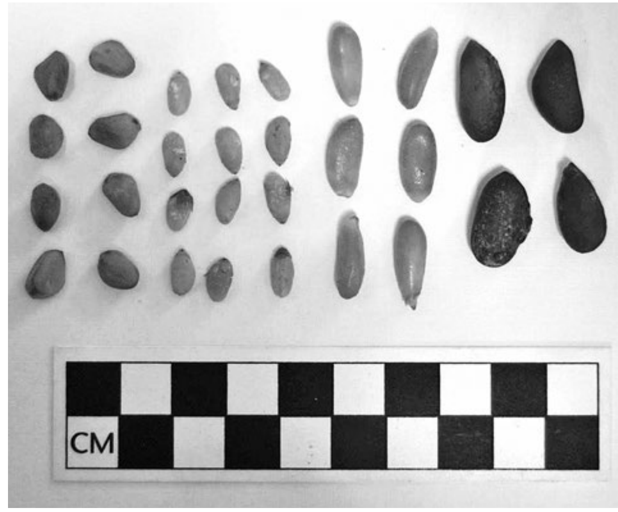

Figure 4. Limber pine whole seeds and cleaned kernels (left) and pinyon pine kernels and unhulled seeds (right).

Each limber pine cone contains ~80–110 seeds, yielding an average of ~14 grams of seeds per cone. Each seed weighs ~0.15 gram, with ~38% of that being the kernel and the rest being the hard bony hull and the papery nucellus. By comparison, the smaller pinyon pine cone holds 15–25 seeds weighing on average ~17 grams; each seed weighs ~0.75 grams, and the kernels account for ~65–78% of total seed weight (Farris 1980, 1982; Lanner 1981; Simms 1984).

Limber pine seeds are fat- and protein-rich, having proportionately much less carbohydrate per unit weight compared to singleleaf pinyon pine seeds. They are more energy-rich than pinyon pine seeds owing to their greater fat content. The kernels yield ~7,600 kcal/kg. in measured gross energy (Table 1), with a calculated energy value based on the proportion of edible fat, protein, and carbohydrate of ~6,300 kcal/kg. (using the USDA National Nutrient Database's Atwater specific energy conversion factors for nuts of 8.37 kcal per gram of fat, 3.47 kcal per gram of protein, and 4.07 kcal per gram carbohydrate [Merrill and Watt 1955; USDA 2014]). The measured gross energy values of the whole

Table 1

NUTRITIONAL CONTENT OF LIMBER PINE AND PINYON PINE SEED COMPONENTS (DRY WEIGHT BASIS)

Sample	% Fat	% Protein	% Ash	% Carbohydrate	% Moisture	% Total Digestible Fiber	Gross Energy (kcal/kg.)	Calc Energy USDA
8/25/09 kernel	58.92	20.01	3.47	17.60[a]	1.75	42.8	7,583	6,342
9/05/09 kernel	56.35	21.43	3.50	18.72[a]	2.36	42.6	7,442	6,222
9/05/09 kernel (year-old)	59.51	21.03	3.74	15.72[a]	5.64	39.94	7,602	6,351
9/05/09 whole seed (year-old)	29.57	11.93	2.59	55.89[a]	7.70	82.96	6,290	5,164
9/18/09 kernel	58.38	24.11	4.10	13.41[a]	5.42	51.2	7,622	6,269
9/18/09 hull	3.01	6.47	1.11	89.41[a]	11.80	98.8	4,931	4,115
Pinyon pine kernel	20.76	10.26	2.44	66.54	12.85		4,305	4,802

[a]calculated by difference

Table 2

NUMBER OF SEEDS PER LIMBER PINE CONE COLLECTED AT FOUR DIFFERENT DATES IN AUGUST/SEPTEMBER, 2009

Date	Average # seeds/cone	Average % seeds filled	Average meat weight/cone (g.)
8/10/09	78.0	18.3	0.6
8/25/09	104.0	98.1	4.9
9/5/09	94.8	88.6	5.4
9/18/09	36.6	84.0	1.5 – 2.3

Table 3

SHAKING SEEDS FROM CONES

Number of cones	Number of seeds removed	Time spent shaking (seconds)	Cones per hour	Seeds per hour
14	1,270	95	531	48,126
124 1st shake	~ 6,240	600	744	37,440
124 2nd shake	464	420	902	3,977
80 1st shake	~ 2,765	300	880	33,180
80 2nd shake	165	180	1,600	3,300

seeds (meat and hull together) are 6,290 kcal/kg., with a calculated energy value of 5,164 kcal/kg. (Tomback [1982] and Hutchins and Lanner [1982] obtained essentially identical nutritional values and ripening schedules for whitebark pine seeds). By comparison, singleleaf pinyon kernels with their greater proportion of carbohydrates yield ~3,800 – 4,800 kcal/kg. energy (Farris 1982; Simms 1985). If stored in the hull, limber pine seeds can retain their nutritional value in storage for years.

LIMBER PINE SEED COLLECTION

Collection experiments were conducted in 2009 in a limber pine grove on Corey Peak, Wassuk Range, Nevada (38.45 °N lat., 118.78 ° W long., 2,978 m. altitude). In early August 2009 when we began our investigations, the proportion of filled seeds we counted in the tightly closed green cones we collected amounted to less than 20%, but by the end of the month nearly all the seeds filled out, though the cones were still closed and green (Table 2). Peak numbers of seeds were available in late August and the first two weeks of September, after which time the cones opened up and the seeds quickly dispersed or were eaten by nutcrackers and jays.

We collected cones from trees in 15 minute bouts, using a 1.5-meter-long shepherd's crook to pull down a tree's branches, twisting off the cones, and collecting them in a burlap sack. One collecting episode, on September 5, yielded 62 cones (= 248 cones per hour); another, on September 18, resulted in 128 cones (= 512 cones per hour), about double the rate. With a little practice, our collecting skills improved significantly. For the purposes of this exercise, we assume a collection rate of 500 cones per hour, well within an experienced collector's capability.

LIMBER PINE SEED PROCESSING

When collected, the cones were in a closed 'green' state. Processing the collected cones involved a three-part process: (1) heating or sun-drying the cones to allow them to open; (2) pulling or shaking the seeds from the cones; and (3) cracking open the small seeds to remove the kernels from their enclosing hulls.

Drying Cones and Removing Seeds

Laying the cones out in the warm September sun for a day or two was sufficient to open them, without additional heating or roasting. This 'sun-drying' requires minimal effort, and the time needed to open the cones is therefore considered negligible. Some ethnographic accounts suggest that 'white pine' cones were opened by roasting over hot ashes (Steward 1943:362), as was routinely done for pinyon pine cones (Chamberlin 1911; Dutcher 1893; Eerkens et al. 2004; Madsen 1986:29 – 31; Muir 1918; Steward 1933:241 – 242; Stewart 1943). Roasting would increase processing costs somewhat, but presumably it was completed incidental to other domestic hearth-related tasks and social activities (Muir 1918; Rhode 1988).

Once the cones are opened, limber pine seeds shake out very easily (pinyon pine seeds, in our experience, require more tenacious manual extrication of the seeds from the cone). We conducted several experimental runs. In the first experiment, 14 sun-dried cones yielded 1,270 seeds with just 95 seconds of shaking, less than seven seconds per cone (Table 3). At that rate, an avid shaker could in an hour remove seeds from approximately 530 cones, about the same number of cones collected in an hour's time. In two other experimental runs shown in Table 3, cones were shaken out once to get most seeds (first shake), then again to get any remainders (second shake). The second shake resulted in little additional yield and a steep decline in overall seed yield per unit time. As with many processing activities, the return rate declines rapidly with too much effort spent trying to get every last edible morsel. These latter two large experimental runs resulted in lower seed yields per unit time than the first example with a smaller number of cones, but they show the general pattern that an hour's worth of collected cones can be easily processed to remove the majority of seeds in about an hour's shaking.

One experiment was also undertaken to remove seeds manually from cones partly opened by oven-drying (modern kitchen oven, ~125°C, two hours). This effort involved tearing the cones apart and digging out the seeds, an enterprise that proved painful to the fingers, time-consuming, and extremely sticky. In one experiment with five closed cones, each cone required an average of 202.4 seconds to remove the seeds, a 30-fold increase in the time expended compared with shaking sun-opened cones. Clearly, passive solar drying and shaking is more energy-efficient. According to Castetter and Opler (1936), the Chiricahua and Mescalero Apache collected limber pine cones before they were fully ripened, then removed the seeds by shaking, as described here.

Processing Limber Pine Seeds

Removing the kernel from its hull involves cracking the seed with a muller or mano and prying out the kernel. Hulling limber pine seeds is much more time-consuming than hulling the larger, thin-hulled singleleaf pinyon pine seeds because the limber pine seeds are smaller and their hulls are thicker. In one experiment, removing the limber pine kernels from 474 seeds (5 cones' worth, 71 grams) took 47 minutes: ~5.9 seconds per seed, 605 seeds per hour, for a yield of 25.4 grams of clean kernels (Table 4). Subsequent runs resulted in even lower returns, possibly because fewer of the seeds were filled or because the seeds were a year old or more.

Putting it all together, even a novice collector can collect ~500 cones in one hour. After letting them passively sun-dry for a couple of days (or roasting over ashes), that collector can spend a leisurely hour or so shaking the seeds out, yielding about five kilograms (10 liters) of unhulled seeds. If we use the fastest hulling rate we accomplished (90.7 grams hulled per hour, yielding 32.4 grams of kernel), those five kilograms of whole seeds will take ~55.1 finger-cracking hours to discard the hulls. Overall, a total of ~57 hours of collecting and processing yields ~1.79 kilograms of kernels. Assuming an energetic value for kernels of ~6,300 kcal/kg., and a dry weight value of 90% of fresh clean kernels, the total caloric return amounts to ~10,149 kcal. However, the long time spent hand-hulling the seeds means that the caloric return rate from collecting and processing limber pine kernels comes to *178 kcal/hour*.

Table 4

HAND-HULLING KERNELS FROM SEEDS

Sample Run	1. 8/25, 3 cones	2. 9/5, 5 cones	3. 9/18, mixed	4. 9/18, mixed	5. 9/18, roasted
Number of seeds	301	474	500	400	1,000
Weight of seeds (grams)	51.2	71	36.6	30.1	80.2
Time spent hulling (seconds)	2,438	2,817	5,190	3,850	10,100
Weight of kernels (grams)	13.8	25.4	14.5	12.2	32.2
Estimated kcal kernels @6,800 kcal/kg.	93.9	172.7	98.6	82.9	219.0
Weight of kernels (grams/hour)	20.4	32.5	10.1	11.4	11.5
Estimated kcal/hour	139.7	220.8	68.7	77.6	78.1

This return rate lies near the low end of return rates reported for Great Basin native plant foods (Table 5). If limber pine seeds are processed all the way down to clean kernels, their low caloric ranking would tend to minimize their utility in a prudent forager's diet unless that diet was very broad or unless return rates were unimportant in allocating time and energy expended on food collection.

But why bother cleaning the kernels from their hulls? Eating the seeds whole or grinding them into meal saves a huge amount of processing time and return rates rise dramatically. The amount of unhulled seeds obtained by collecting and shaking is ~2.5 kg./hour (2.3 kg. dry weight). Using the caloric value of 5,164 kcal/kg. calculated by the USDA energy conversion factors, the return rate is *11,877 kcal/hour*. However, this value assumes that the hull provides significant digestible energy return, which it likely does not (e.g., Kendall 1983; Mealey 1975). The most relevant comparison is made if the hull is considered indigestible and only the 38% of the seed that is kernel is assimilated. If so, the caloric yield of eating unhulled seeds is *5,387 kcal/hour*, an increase of

Table 5

RETURN RATE ESTIMATES (KCAL/HR.) FOR SELECTED GREAT BASIN RESOURCES. ESTIMATES REPORTED IN THIS STUDY ARE HIGHLIGHTED IN BOLD.

Food Source	Mean Value (Range)	Reference
Grasshopper (*Melanoplus sanguinipes*), windrow encounter, unprocessed	272,649 (41,598–714,409)	Madsen and Kirkman 1988
Grasshopper (*Melanoplus sanguinipes*), windrow encounter, minimal processing	~27,265–68,000	Madsen and Kirkman 1988, Jones and Madsen 1991, Ugan 2005
Mormon cricket (*Anabrus simplex*), driving into pit or stream, unprocessed	(73,437–146,875)	Jones and Madsen 1991, Ugan 2005
Cutthroat trout (*Oncorhynchus clarki henshawi*), basket trap	(36,000–80,690)	Lindström 1996, in Ugan 2005
Cutthroat trout (*Oncorhynchus clarki henshawi*), gill net	(33,621–69,643)	Lindström 1996, in Ugan 2005
Deer (*Odocoileus hemionus*), encounter hunt	(17,971–31,450)	Simms 1987
Bighorn sheep (*Ovis canadensis*), encounter	(17,971-31,450)	Simms 1987
Cutthroat trout (*Oncorhynchus clarki henshawi*), spear/harpoon	(17,727–24,375)	Lindström 1996, in Ugan 2005
Pronghorn (*Antilocapra americana*), encounter hunt	(15,725–31,450)	Simms 1987
Tui chub (*Gila bicolor*), basket scoop, unprocessed	(5,243–241,200); (920–~42,300)	Lindström 1996; Ugan 2005
Mormon cricket (*Anabrus simplex*), hand-collected in water	20,869 (10,475-33,156)	Jones and Madsen 1991
Jackrabbit (*Lepus* sp.), encounter hunt	(13,475–15,400)	Simms 1987
Limber pine (*Pinus flexilis*), seeds unhulled	**11,877**	**This study**
Cottontail rabbit (*Sylvilagus* sp.), encounter	(8,983–9,800)	Simms 1987
Ground Squirrel (*Urocitellus* sp.), encounter	(5,390–6,341)	Simms 1987
Cattail (*Typha latifolia*) pollen	5,739 (2,750–9,360)	Simms 1984
Sucker (*Catostomus commersoni*)	5,689	Evans 1990
Tui chub (*Gila bicolor*), basket scoop, processed	5,243	Lindström 1996, in Ugan 2005
Biscuitroot (*Lomatium hendersonii*) root	3,831	Couture et al. 1986
Singleleaf pinyon (*Pinus monophylla*), raw unhulled	**3,710 (2,759–4,662)**; (2416–9,631)	**This study**; Simms 1984
Tui chub (*Gila bicolor*), basket trap, unprocessed	(4,706–38,592); (~825–6,768)	Lindström 1996; Ugan 2005
Cattail (*Typha latifolia*) rhizome, mashed and boiled into soup	3,299 (2,929–3,966)	Madsen et al. 1997
13-lined ground squirrel, encounter hunt (*Ictidomys tridecemlineatus*)	(2,837–3,593)	Simms 1987
Pandora Moth (*Coloradia pandora*) larvae	2,407 (1,840–2,753)	Fowler and Walter 1985
Duck (*Anas* sp.), encounter	(1,975–2,709)	Simms 1987
Maize (*Zea mays*) flour (harvest and process); Planting and harvesting return	2,341; 1,300–1,700	Diehl and Waters 2006; Barlow 2002
Cactus (*Opuntia* sp.) seed	2,253	Diehl and Waters 2006
Jackrabbit (*Lepus californicus*), drive	(628–4,243); 3,563; (415–806)	Simms 1987; M. Zedeño, in Ugan 2005; Palmer 1896, Lowie 1924, Lowie 1936
Mormon cricket (*Anabrus simplex*), hand-collected on land	2,245 (618–4,875)	Jones and Madsen 1991
Gambel oak (*Quercus gambelii*) acorn	2,232	Simms 1987
Mesquite (*Prosopis juliflora*) pod flour	1,998	Diehl and Waters 2006
Tui chub (*Gila bicolor*) net-caught	1,927 (750–7,514); (4,232–20,100)	Raymond and Sobel 1990; Lindström 1996, in Ugan 2005
Black-tailed Jackrabbit (*Lepus californicus*), trap	(1,495–2,656)	Ugan 2005
Pocket Gopher (*Thomomys* sp.), trap	1,718	Simms 1987
Rodent (various), trap	(468–2,340)	Ugan 2005
Bulrush (*Schoenoplectus acutus*) seed	1,699	Simms 1987
Pronghorn (*Antilocapra americana*), drive	(1,161–1,887)	Simms 1987
Prickly pear (*Opuntia* sp.) fruit	1,553	Diehl and Waters 2006
Bitter root (*Lewisia rediviva*) rhizome	1,374; 1,237	Couture et al. 1986; Simms 1987
Cous (*Lomatium cous*) root	1,219	Couture et al. 1986
Tansymustard (*Descurainia pinnata*) seed	1,307; 367	Simms 1987; Diehl and Waters 2006
Shadscale (*Atriplex confertifolia*) seed	1,200	Simms 1987
Saline wild rye (*Leymus salinus*) seed	1,080 (921–1,238)	Simms 1987
Nuttall shadscale (*Atriplex nuttallii*) seed	1,033	Simms 1987
Singleleaf pinyon (*Pinus monophylla*) seed, hulled	**905 (765–1,045)**; 941 (841–1,408)	**This study**; Simms 1987

Table 5 (*Continued*)

RETURN RATE ESTIMATES (KCAL/HR.) FOR SELECTED GREAT BASIN RESOURCES. ESTIMATES REPORTED IN THIS STUDY ARE HIGHLIGHTED IN BOLD.

Food Source	Mean Value (Range)	Reference
Limber pine (*Pinus flexilis*) whole seeds, ground	888	**This study**
Duck (Family Anatidae), drive	(561–1,317)	Simms 1987
Black oak (*Quercus kelloggii*) acorn mush	786	Bettinger and Wohlgemuth 2011
Barnyardgrass (*Echinochloa crus-galli*) seed	702	Simms 1987
Peppergrass (*Lepidium* sp.) seed	684	Simms 1987
Bluegrass (*Poa compressa*) seed	491	Simms 1987
Sunflower (*Helianthus annuus*) seed	486 (467–504)	Simms 1987
Bulrush (*Schoenoplectus maritimus*) seed	470	Simms 1987
Bluegrass (*Poa bulbosa*) seed	418	Simms 1987
Goosefoot (*Chenopodium* sp.) seed	383	Diehl and Waters 2006
Great Basin wild rye (*Leymus cinereus*) seed	370 (266–473)	Simms 1987
Indian ricegrass (*Achnatherum hymenoides*) seed	345 (301–392); 333–336	Simms 1987; Jones and Madsen 1991
Bulrush (*Scirpus microcarpus*) seed	302	Simms 1987
Reed canarygrass (*Phalaris arundinacea*) seed	291 (261–321)	Simms 1987
Scratchgrass (*Muhlenbergia asperifolia*) seed	249 (162–294)	Simms 1987
Cattail (*Typha latifolia*) seed	260 (227–357)	D. Rhode, unpublished
Sego lily (*Calochortus nuttallii*) raw	215.7	Smith et al. 2001
Sego lily (*Calochortus nuttallii*) baked	207	Smith et al. 2001
Foxtail barley (*Hordeum jubatum*) seed	206 (138–273)	Simms 1987
Sedge (*Carex* sp.) seed	202	Simms 1987
Bulrush (*Schoenoplectus* sp.) root	200 (160–257)	Simms 1987
Princes plume (*Stanleya pinnata*) greens	178 (57–353)	Hooper and Rhode 1995
Limber pine (*Pinus flexilis*) seeds hulled	**178**	**This study**
Yampa (*Perideridia gairdneri*) bulb	172	Couture et al. 1986
Cattail (*Typha latifolia*) rhizome, cleaned	197 (128–267); 157 (42–260)	Simms 1987; Jones and Madsen 1991
Saltgrass (*Distichlis stricta*) seed	153 (146–160)	Simms 1987
Biscuitroot (*Lomatium canbyi*) root	143	Couture et al. 1986
Iodinebush (*Allenrolfea occidentalis*) seed	111 (90–150)	Simms 1987
Squirreltail grass (*Elymus elymoides*) seed	91	Simms 1987

30-fold over hand-hulling. This return rate compares well with those estimated for rabbits and other small game, and is several times greater than that for clean pinyon pine kernels (Simms 1987). Seen in this light, the prudent forager would very likely eat limber pine seeds unhulled, either out of hand, roasted, or ground into meal. The ethnographic report of Castetter and Opler (1936:43) for the Apache is of interest in this respect; they note that after the limber pine seeds were collected, “they were then roasted and hulled, or sometimes the seeds ground, shell and all, and eaten.”

If limber pine seeds are eaten whole, no further processing costs are imposed (save possibly roasting). Eating the sharp hull fragments can be disagreeable, however (see the discussion below); to avoid doing so, grinding the seeds to a meal is a likely processing step that would incur extra costs. To gauge this extra cost, we ground two batches of whole seeds using (1) a mano and milling slab and (2) a shallow mortar and pestle, each involving 500 seeds (~40 grams) and each grinding session lasting 300 seconds. This amount of time was sufficient to produce a medium-coarse fatty meal with all the seeds cracked and the kernels released. By extrapolation, the entire 2.3 kg. dry weight of seeds obtained in an hour’s worth of collecting could be ground in about 5.2 hours. If the time spent grinding is added to the energetic calculations given above, and if only the kernel in the meal is edible, the return rate would be *888 kcal/hour*, about the same as pinyon pine kernels and about five times the return rate of hand-hulling limber pine kernels.

The first batch that we ground consisted of raw whole limber pine seeds. The resulting meal, to be honest, tasted awful: it was acrid and pitchy, full of annoying hull bits that caught in one's gums and teeth, and eating it was an unpleasant experience altogether. In the case of the second batch, we briefly oven-roasted the whole seeds before grinding them, which removed some of the nasty pine-pitch flavor and gave them that 'pine-nut' savor. Adding hot water to the roasted-seed meal to make a broth solved the problem of the hull fragments, which promptly dropped to the bottom of the broth out of harm's way, taking with them the overwhelming pitchiness. This nutritious broth tasted delicately nutty with a subtle piney finish, making it a delightful warm drink or soup base.

If ground meal or the broth made from it was the end product sought by native foragers, then evidence of milling and grinding equipment ought to be common at processing sites, as indeed it is at residential occupation sites in the White Mountains of eastern California, Alta Toquima in central Nevada, High Rise Village in Wyoming, and other sites in the high western cordillera (Adams 2010; Bettinger 1991, 1999, 2008; Morgan, Adams, and Losey 2012; Morgan, Fisher, and Pomerleau 2012; Thomas 2014a). Ceramics from the sites might be expected to show residues such as fatty acids, resins, or microfossils attributable to pine, as are occasionally found elsewhere in the Great Basin (Eerkens 2002, 2005; Tuohy 1990).

COMPARING PINYON PINE SEED PROCESSING

Return rates on pinyon pine seeds also increase significantly if they are eaten without being hand-hulled first. In one experiment, we manually extricated seeds from 36 pinyon pine cones, yielding 572 seeds in nine minutes (collecting this number of cones required four minutes). An additional 45 minutes were required to remove the hulls, yielding 210.3 grams of clean kernels (dry weight), a caloric value of 1,010 kcal (USDA energy values). Overall, the return rate of these clean kernels was *1,045 kcal/hour*, similar to previous return rate estimates (e.g., Simms 1987; Table 5). But if those same kernels were consumed in the hull (assuming the hull itself is indigestible), the same caloric energy would have been retrieved in only thirteen minutes of collecting and extricating, for a return rate of *4,662 kcal/hour*. In a second example, 20 minutes of shaking and prying out the seeds from 68 pinyon cones yielded 1,029 seeds. Hulling these seeds took 73 more minutes, resulting in 268.1 grams dry weight of clean kernels. The clean kernels gave a return rate of *765 kcal/hour*, but the unhulled seeds would have resulted in a return rate of *2,759 kcal/hour*. Consuming unhulled pinyon pine seeds raises return rates ~3.6–4.5 times more than the rate obtained by hulling them first. The rate increase is not as great as for limber pine, because the latter seeds are so much more difficult to hull, but it is evident that unhulled pinyon pine seeds rank highly in caloric return rate among plant foods, though less than unhulled limber pine seeds.

DISCUSSION

Return Rates

In a recent paper, Hildebrandt (2013:24) opined that our experimental results drastically overestimated the processing costs associated with hulling limber pine seeds, and that "it is likely that the two nuts [limber pine and pinyon pine] are comparable" in terms of return rates of hand-hulled seeds. We admit that we have only moderate experience in hulling pine seeds, so he could be right about some inadvertent overestimation of processing costs on our part. Our experiments convince us, though, that hulling limber pine seeds is much more difficult and time-consuming than the comparatively easy-hulling of pinyon pine seeds, and we very much doubt that hand-hulled limber pine and hand-hulled pinyon kernels will be found to have similar energetic return rates. Nor are pinyon seeds and limber pine seeds nutritionally comparable in their proportions of fats, proteins, and carbohydrates. As Farris (1982) observed long ago for different pine species generally, pinyon and limber pine seeds really are different foods, and they should not simply be lumped together as equivalents (see also Botkin and Shires 1948).

Resource return rates are intimately tied to the treatments and tactics involved, so much so that the same potential food type (e.g., pine seeds) can and probably should be considered to be distinctively different kinds of food resources from a return-rate standpoint, depending on the methods used to harvest, process, and transport the food (Madsen and Schmitt 1998; Metcalfe and Barlow 1992). Our understanding of the variability in caloric return rates under different conditions and using different methods is limited, because few return-rate experiments (especially repeat experiments) have been published (cf. Broughton et al. 2011; Madsen et al. 2000; Morgan 2014). We strongly encourage others to try their hand at their own experiments to add to the data provided here and to better understand the costs involved.

Potential Health Dangers of Unhulled Seeds

One may wonder whether eating pine seed hulls (either from whole seeds or in ground meal) involves ingesting an extreme form of roughage that could be unhealthy. Personal experience shows that eating whole limber pine seeds does not necessarily cause ill effects, though it is not nearly as enjoyable as gulping down a handful of cleaned kernels or sipping a warm cup of pine-nut broth. The presence of pine seed hulls in coprolites from Great Basin archaeological sites demonstrates that eating unhulled seeds was practiced at least occasionally (e.g., Fry 1976; Rhode 2003; Wilke 1978). One coprolite from Bonneville Estates Rockshelter is composed entirely of large pinyon pine hull fragments–a clear case of whole-seed consumption (Fig. 5). However, eating whole pine seeds in bulk may be similar to consuming large quantities of sunflower seeds, prickly pear, melons, sesame seeds, or other seeds in that the practice can at times lead to the development of seed bezoars in the stomach, intestine, or rectum, potentially resulting in painful "proctological crunch," intestinal blockage, fecal impaction, and even rectal perforation (e.g., Eitan et al. 2006; Eitan et al. 2007; Mirza et al. 2009; Purcell and Gremse 1995; Sawnani and McFarlane-Ferriera 2002; Shaw et al. 2007; Steinberg and Eitan 2003; Tsou et al. 1997). Seed bezoars are formed when large quantities of unprocessed seeds are eaten whole; small seeds as well as large ones are known to cause bezoars, so small seeds of plants such as ricegrass (*Achnatherum hymenoides*) may also create bezoars if consumed in quantity. Grinding unhulled pine seeds into a meal, just as ricegrass and other small seeds are processed by grinding, would reduce or eliminate this potential problem.

Front- and Back-Loaded Resources

Hand-hulled limber pine seeds fit the description of a 'back-loaded' food resource: it is relatively easy and inexpensive to collect and store, but is very costly to process further for consumption (Bettinger 1999:73, 2009). Such easily storable resources have advantages in that they reduce the risk of future food scarcity and extend the time window available for further processing (thereby reducing opportunity costs). If hand-hulling is required to eat the seeds, a heavy post-storage processing burden is imposed (the 'back-loaded' costs) that would make them relatively unattractive to potential freeloaders. In a strictly energetic sense, stores of limber pine seeds are an inexpensive and reliable insurance policy against food shortfall, but are still a low-ranked food resource. Accordingly, we would expect limber pine seeds to be commonly collected and cached for future use (as the ethnographic literature confirms [Steward 1943]), but not necessarily to be used unless other higher-ranked resources are unavailable.

Figure 5. Human coprolite fragment from Bonneville Estates Rockshelter, eastern Nevada, containing abundant pinyon pine seed hull fragments.

If hand-hulling is not needed to consume or further process the seeds, then the back-loaded character diminishes considerably. Stores of limber pine seeds would retain all their advantages (low collecting costs, reducing food-shortage uncertainty, extending the time available to process the seeds), but they would be more attractive to freeloaders who would not be deterred by subsequent high processing costs. In such circumstances we would expect the seeds to be commonly collected as a high-return resource, and subject to storage, though not in dispersed and unprotected caches (cf. Morgan 2012); they more likely would be stored in closely guarded facilities such as within private households, and the stores would actually be used more often than back-loaded 'insurance' caches (cf. Tushingham and Bettinger 2013). The additional processing step of grinding roasted seeds to a meal falls between these two extremes, giving a significant post-storage 'back-load' to limber pine seed stores but also yielding a relatively high overall energetic return. In this scenario, we would expect to find milling equipment associated with storage features (pits or other constructions) to facilitate post-storage processing, and to find ground limber pine hull fragments as residue.

The front-back loaded model applies to resources that are compared with one another (Bettinger 2009:49–50). In this respect, hulled limber pine kernels can be characterized as back-loaded relative to hulled pinyon pine kernels, first because limber pine seeds are much more expensive to hull than the pinyon pine seeds, and secondly because pinyon pine seeds are more costly to collect and prepare for storage (~0.20 hours of storage preparation time per 1,000 kcal for pinyon pine seeds, vs. ~0.12 hours per 1,000 kcal for limber pine seeds). Unhulled limber pine seeds, by contrast, appear to be a more energy-rich resource on both the front and back end, so this comparison may not apply if the seeds are consumed unhulled.

How do these seeds compare with other high-altitude resources, such as bighorn sheep or marmot? To be made storable, meat from these game animals requires proper dressing and drying. Zeanah (2000) estimated that processing and drying a bighorn sheep carcass required ~14.5 hours to obtain 13.6 kg. of dried meat with a caloric yield of 27,377 kcal, or 1,888 kcal/hour in preparation for storage (i.e., 0.53 hours of storage time per 1,000 kcal). Compare this return with that for unhulled limber pine seeds (8,568 kcal/hour of storage time) or pinyon pine (4,946 kcal/hour of storage time), and it is evident that meat is highly front-loaded for storage, relative to both kinds of pine seeds.

Tushingham and Bettinger (2013) make the argument that mobile foragers will preferentially use back-loaded resource stores rather than front-loaded resource stores, even though back-loaded resources may be less energetically valuable overall. This is because the risk of energetic loss involved in back-loaded stores is less than for front-loaded stores, if the stores are subsequently not used. Mobile foragers typically use a caching strategy, placing small stores of food dispersed around their foraging range (Morgan 2012). This practice affords mobile foragers flexibility in their pursuits, but it heightens the risk that they will not return to use their stores or that their stores will be taken by others. If the risk of unused caches is fairly high, back-loaded resources are a better bet because the storage cost and therefore the loss is low. Only when front-loaded resources are very likely to be actually used will foragers spend the significant time needed to prepare those resources for storage. Tushingham and Bettinger (2013) use this rationale to explain why the intensive use and storage of acorns (a back-loaded resource) preceded use of the more energetically-valuable salmon (a front-loaded resource) in prehistoric California.

Pine Nut Use and High-Altitude Occupations

If the same logic holds for high-altitude Great Basin habitats, we would expect to find the use and storage of pine seeds to precede the hunting and drying of sheep or marmots. However, the opposite pattern appears to be the case: mountain sheep and marmot hunting have a long history in locales such as the White Mountains and Toquima Range (Grayson 1991), and indeed throughout the Great Basin high country (Canaday 1997), whereas limber pine seed collection and use seems more likely to have been a focus of late prehistoric high-altitude residential occupations (Bettinger 2008). Use of limber pine seeds may have more to do with the establishment of a high-altitude residential strategy in which whole families spent significant time foraging for a range of high-altitude resources, rather than the short-term narrow-focus small-group logistical character of high-altitude hunting. The seasonal timing of high-altitude foraging may also play a role, as the window of opportunity for limber pine seed collecting is tightly restricted to late summer.

SUMMARY

Our experimental investigations into the energetic value of limber pine seeds leads us to the following conclusions.

1. Limber pine seeds are a potentially valuable food resource available in subalpine habitats across the Great Basin during a narrow time window in late summer.

2. The seeds are rich in fats and protein and are highly energetic compared with other plant foods, including pinyon pine seeds.
3. Collection and seed removal is easy, quick, and yields abundant seeds that are storable long term.
4. Consuming unhulled limber pine seeds can yield very high caloric return rates, comparable to those for rabbits and even large game. Extraction of clean kernels is extremely time-consuming, turning a high-value resource into a very low-value one. Roasting and grinding whole seeds to a meal for broth or mixing with other ingredients yields moderately high caloric returns.
5. Based on these energetic observations, we would expect to see limber pine seeds collected when available, stored for food insurance or as a high-value foodstuff. We may find minor evidence of hand-hulling of limber pine seeds, but we would expect much greater evidence of milling equipment and processing waste associated with storage features at likely limber pine seed-processing sites, such as the late prehistoric high-altitude residential occupations at Alta Toquima and the White Mountains.
6. Additional return rate studies are needed to compare with our results, and to provide a better basis for gauging the potential economic place of limber pine nuts in the foodways of intermountain peoples.

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