# DEFINING THE CENTRAL MOUNTAINS ARCHAIC: GREAT BASIN NATURAL AND CULTURAL BIOGRAPHIES

## The Archaeology of Monitor Valley, Contribution 5

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CHAPTER 12

# TESTING THE PIÑON ECOTONE HYPOTHESES

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John C. Frémont became "almost obsessed" with piñon pine during his wintertime traverse of the Sierra Nevada in January of 1844. Purchasing a skin bag with a few pounds of pine nuts from local Indians, he found that "when roasted, their pleasant flavor made them an agreeable addition to our now scanty store of provisions" (Frémont et al., 1845, quoted in Lanner, 1981: 95, 107). Although the existence of junipers was well known at the time, Frémont soon would bring piñon pine to the attention of the scientific community, formally recording the name *Pinus monophylla* in his journal (Cronquist et al., 1972: 47).[1]

## DISTINGUISHING PIÑON ECOTONE HYPOTHESES

Multiple 19th-century accounts recorded piñon procurement practices among Native American communities in the Intermountain West (e.g., Hoffman, 1878; Coville, 1892: 353; Dutcher, 1893; Muir, 1894) and Julian Steward concluded that pine nuts were "the most important single food species wherever it occurs" (1938: 27). Commenting on the close correlation between the archaeology and the ethnography in the central Great Basin, I proposed the piñon ecotone hypothesis, initially framed as a direct result of our archaeological surveys of the Reese River Valley (Thomas, 1971a, 1973).[2]

### Testing Steward's Ethnohistoric Model

Beyond the riverine settlements in the Reese River bottomlands, Steward's ethnographic accounts emphasized the dense concentration of winter villages located in the piñon-juniper woodland, typically positioned along long, low ridges fingering onto the valley floor, with several families living on each ridgetop and sometimes several such ridgetop villages within a 1 mi radius. My subsequent archaeological fieldwork attempted to test Steward's ethnographic model by raising questions such as:

- Where exactly are the villages in relation to the lower piñon treeline?
- Could these locations be classified relative to key environmental criteria (espe-

[1] This chapter builds upon and expands hypotheses in Thomas and Millar (2023). I gratefully acknowledge the advice and assistance of Constance Millar, Lorann Pendleton, and David Rhode in preparing this chapter.

[2] The multiple hypotheses involved were introduced in chapter 6, then revised and revisited in chapter 7.

cially water, fuel, aspect, slope, forest vs. shrubland, food resources)?
- Is it possible to model strategic variables (e.g., proximity to water, flat ridgetops, proximity to piñon forest) to predict locations of unknown winter village sites?
- What is the material nature of these villages (especially house foundations, piñon caches, and pine nut processing) (Thomas, 1972: 137)?

Chapters 6 and 7 summarized the three years of archaeological survey in the Reese River Valley that tested Steward's model with a 100% survey along a 12 mi long stretch of the western Toiyabe Range (Thomas and Bettinger, 1976: figs. 2, 3; table 6).

At this stage, the process of testing the piñon ecotone hypothesis involved quantifying Steward's ethnographic observations using a seven-factor polythetic model, then exploring whether the winter villages were indeed located in repeatable and predictable locations within the lower piñon zone (and not other places). All but two of the 65 archaeological sites detected were situated on the predicted loci and only 11 of the potential loci contained no archaeological evidence. That is, more than 95% of the sample sites were situated on potential loci, and 85% of the loci contained sites, a highly significant statistical relationship. We concluded that the polythetic criteria successfully predicted past human behavior based on Steward's ethnographic model (Thomas, 1972, 1973; Williams et al., 1973: 232–234; Thomas et al., 1976).

## Clarifying Ecotone

Chapter 7 touched on my use of the terms *ecotone* and *edge effect* (Thomas, 1971a: 173), both concepts taken from Odum (1959: 278–281; 1971: 157–159, 417). The edge was taken to be the line demarcating two adjacent ecosystems and ecotone defines the two- or three-dimensional zone of transition between those ecosystems. Following Billings (1951), I stressed the importance of thermal belts in conditioning the dynamics and distribution of the piñon-juniper belt (Thomas, 1971a: 64; 1983a). This suggested to me that Western Shoshone communities surely recognized how these ecotone localities provided small-scale wintertime refugia that decoupled sufficient climate processes to create moderated microclimates to persist despite unfavorable changes in surrounding landscapes (Millar et al., 2018).

## Explaining the What, When, Where, and Why of Ancient Piñon Procurement

With the archaeological evidence pointing to the systematic village occupations concentrated in the lower piñon forest, the focus shifted to why this might be so, and two competing hypotheses emerged from follow-up research. In the last third of this chapter, Constance Millar and I propose a new, forest ecology-based hypothesis for piñon procurement.

Hypothesis of Early Intensive Piñon Use: The Reese River and Monitor Valley evidence suggested that people began living in the lower piñon woodland shortly after *P. monophylla* arrived in the central Great Basin (roughly 5000–6000 years ago). These foragers quickly learned the various ways of procuring and processing pine nuts and relied on piñon nuts as their primary food source (Thomas, 1971a, 1973, 1981). I believe that this multimillennial reliance and intensive procurement of piñon nuts explains what, why, when, and where of the piñon village sites. Others have also proposed the similar early and significant exploitation of piñon elsewhere in the Great Basin (McGuire and Garfinkel, 1976; Madsen, 1981; Rhode, 1987: 218–219; Basgall and McGuire, 1988; Reynolds, 1996, 1997; Hildebrandt and Ruby, 1999; Basgall and Delacorte, 2012; Cunnar et al., 2019; see relevant unpublished paper by Lechner et al.[3]).

[3] The 2009 paper, by T.M. Lechner, M.A. Giambastiani, J.P. Barker, and A. Berg, was titled "The archaeology of a pinyon zone in the Desatoya, Mountains, Lander County, Nevada." It was presented at the 38th annual meeting of the Nevada Archaeological Association in Lovelock, NV.

Hypothesis of Late Intensive Piñon Use: Others have proposed a different scenario for the Owens Valley corridor in the southwestern Great Basin, hypothesizing that whereas people lived in the lower piñon woodland for millennia, pine nuts remained only a secondary resource because they relied more heavily on other food sources. These foragers opportunistically took piñon seeds using a simpler, less costly brown-cone strategy to supplement their diet. Dependence on piñon nuts increased significantly ~cal A.D. 1300 when people switched to a labor-intensive green-cone procurement strategy, giving these Numic-speaking processors a means of outcompeting pre-Numic populations across the Great Basin (Bettinger, 1975, 1976a, 1977, 1989, 1994, 1999; McGuire and Garfinkel, 1976; Bettinger and Baumhoff, 1982, 1983; Delacorte 1990; Giambastiani, 2007).

These conflicting piñon ecotone hypotheses can now be explicitly tested against the available archaeological record from the Intermountain West.

## ANTIQUITY OF PIÑON PROCESSING

Despite the serious theoretical and operational difficulties that still cloud our understanding of piñon procurement, a considerable body of archaeological evidence from the Great Basin is available today to test the conflicting piñon ecotone hypotheses.

### Early and Middle Holocene Piñon Procurement

After retreating southward during the Younger Dryas cold snap, piñon pine migrated northward during the Early Holocene. Even cooler and wetter temperatures likely limited the northern boundary of *P. monophylla* south of the Humboldt River (defining the so-called piñon curtain).[4] Table 12.1 charts the progressive northward movement of piñon in the western Great Basin. Piñon pine had been in the region of Owens Lake since the Late Pleistocene, and the Inyo Mountains contained the northernmost populations of piñon during the Early Holocene (Cole et al., 2013; Miller et al., 2019: fig. 3-5e;). Piñon entered the Inyo Mountains by 9500 cal B.C. but remained a minor component of the tree canopy dominated by Utah juniper (Jennings, 1988, 1995).[5]

Piñon nuts first appeared archaeologically at Danger Cave by 5580 cal B.C. (Rhode and Madsen, 1998). This correlates with the disappearance of limber pine nuts in the local ethnobotanical record and reflects the rapid transition in distribution and migration of both species in the Bonneville Basin. Noting that the nearest known occurrence of limber and piñon pine is 25 km away, Rhode and Madsen (1998) concluded that humans transported the nuts to Danger Cave and suggested that their presence signals that piñon became a valued resource post-5000 cal B.C. (see also Louderback and Rhode, 2009).

The drier, warmer Middle Holocene triggered an upward movement of piñon-juniper woodlands in the Great Basin and Colorado Plateau (Wigand and Nowak, 1992; Jennings and Elliott-Fisk, 1993; Wigand et al., 1995; Cook et al., 2004). Piñon migrated rapidly northward during the Early to Middle Holocene transition into the central Great Basin along the Nevada and Utah border (Cole, 1985; Nowak et al., 1994a; Cole et al., 2013; Miller et al., 2019: fig. 3-F), moving into the Schell Creek and Pequop Mountains by 4800 cal B.C. (perhaps due to milder winter temperatures, but remaining absent 30 mi west in the Ruby Mountains). Arid conditions of the Middle Holocene may have fostered some migration toward higher elevations; colder winter conditions likely limited movement of piñon further north (Nowak et al., 1994a; Grayson, 2011). Northward migration of piñon along the east slopes of the Sierra remained quite limited, stopping and starting in response to the variable climate (Wigand, 2017; Miller et al., 2019: fig. 3-10).

[4] Detailed in chapters 5 and 6 (Mehringer, 1977; Spaulding, 1985, 1990; Thompson, 1992; Nowak et al., 1994a; Rhode and Madsen, 1995; Wigand et al., 1995; Quade et al., 1998).

[5] Piñon is today the dominant woodland tree in this area.

Evolving Middle Holocene subsistence patterns increasingly relied on lower ranking plant foods including small, hard-coated seeds, bulrush rhizomes, cactus pads, and fruits (Rhode, 1990). There was a corresponding decrease in abundance of high-ranked artiodactyls, but not lower-ranked fauna (such as leporids). This likely reflected gender-specific foraging strategies (Louderback, 2022) including, to a lesser degree, a few upland plant foods at Bonneville Estates Rockshelter (located several hundred meters higher than Danger Cave and closer to upland piñon pine; Madsen and Rhode, 1990; Thompson, 1992; Rhode and Madsen, 1998).

## Late Holocene Piñon Procurement

Generally cooler and wetter than the Middle Holocene, the Late Holocene fluctuated significantly between cool-moist and warm-dry conditions (Nowak et al., 1994b; Grayson, 2011: 242–253; Cole et al., 2013).[6] The piñon woodlands reached their (precontact) maximum in expanse and abundance with the cool-wet Neoglacial that favored tree growth, cone production, and seedling establishment (Wigand and Nowak, 1992; Wigand et al., 1995). The Late Holocene Dry Period and Three Drought Interval (ending cal A.D. 1350) resulted in a significant decline in piñon from Neoglacial times (Wigand, 1987; Stine, 1990; Wigand and Nowak, 1992; Cook et al., 2004).[7] Piñon pine also increased markedly with respect to juniper during the post-Neoglacial (Wigand and Rhode, 2002).

*P. monophylla* continued moving northward during the Late Holocene, approaching modern northward limits within a few centuries (table 12.1). Piñon in the central Great Basin approached its northern extent along the Nevada-Utah border shortly after 4300 cal B.C.

## Piñon Procurement in the Central Mountains Archaic

Late Holocene piñon procurement in the Central Mountains Archaic is beyond dispute, but the exact nature of pine nut harvesting is subject to multiple interpretations.

- *Macroevolutionary perspectives*: "The weight of evidence currently suggests that intensive piñon exploitation—the kind described by Steward and attested archaeologically in eastern California—was not routinely practiced in central Nevada until after 650 B.P. Further, I suspect that this intensive pattern will turn out to be younger still as one proceeds from central to eastern Nevada, and across Utah, which is what the record at present suggests" (Bettinger, 1999: 65).
- *Resilience perspectives:* I suspect that full-scale piñon exploitation—the kind described by Steward and the kind attested to archaeologically throughout the Great Basin—was routinely practiced in central Nevada and everywhere across the Intermountain West soon after piñon arrived there.

Chapters 6–10 detailed the archaeological evidence of piñon procurement across the Intermountain West, and this section relies on these data to compare the contrasting perspectives relevant to the piñon ecotone hypotheses.

[6] Chapters 7 and 8 detailed and confirmed this sequence. More mesic conditions triggered an expansion of the woodland and montane forests (Grayson, 2011: 253–259), with the piñon pine-juniper woodland appearing in the middle elevations of the central and western Great Basin (Wigand, 2010). Gatecliff Shelter was surrounded by piñon-juniper woodland 3780–1500 cal B.C., with perhaps a higher proportion of juniper (Thompson and Hattori, 1983; Thompson and Kautz, 1983; Thompson, 1992: 13).

[7] During the Neoglacial, desert shrub vegetation was replaced by expanding grass and sagebrush communities, as trees grew in lower, mid-level elevations (Wigand, 1987; Mehringer and Wigand, 1990; Wigand et al., 1995; Chambers et al., 1998: 103; Wigand and Rhode, 2002). The elevations of the upper tree lines diminished in the White Mountains (LaMarche, 1973) and the Sierra Nevada (Scuderi, 1987). Millar et al. (2018) speculate that limber pine was rare to absent in the Wassuk Range during the Middle Holocene, but limber pine expanded across the Wassuk Range during the colder, wetter Neoglacial. The piñon-juniper woodland expanded to reach its maximum at mid and low elevations by the terminal Neoglacial (Madsen, 1985; Wigand, 1987; Mehringer and Wigand, 1990; Miller and Wigand, 1994; Wigand et al., 1995; Wigand and Rhode, 2002).

TABLE 12.1

**Northern Movement of *P. monophylla* along the Eastern Slope of the Sierra Nevada Range**
After Miller et al., 2019: fig. 3-10, with some data derived from Wigand, 2017.

| Location | Piñon Arrival (Estimated) |
|---|---|
| Hidden Valley | cal A.D. 1550 |
| Geiger Grade | cal A.D. 550 |
| Pinenut Range | cal A.D. 550 |
| Stillwater Range | cal A.D. 500 |
| Painted Hills (near Pyramid Lake) | cal A.D. 300 |
| Slinkard Valley | cal A.D. 460 |
| Deep Springs Overlook | 1300 cal B.C. |
| Wyman Canyon | 2500 cal B.C. |
| Bodie Hills (near Mono Lake) | 3000 cal B.C. |
| Silver Canyon | 3600 cal B.C. |
| Gatecliff Shelter (Toquima Range) | 3800 cal B.C. |
| Schell Creek (Pequop Range) | 4800 cal B.C. |
| Danger Cave (Leppy Hills) | 5580 cal B.C. |
| Papoose Flats (Inyo Mountains) | 5900 cal B.C. |
| Pellisier Flats | 6800 cal B.C. |
| Volcanic Tablelands | 7800 cal B.C. |
| Alabama Hills | 9300 cal B.C. |
| Inyo Mountains (low elevation) | 9500 cal B.C. |
| Owens Lake | 15,000–20,000 cal B.C. |

The Piñon Ecotone Hypothesis: My hypothesis initially held that *P. monophylla* nuts became a Central Mountains Archaic staple coincident with its arrival—unless other options (especially large-game hunting and/or wetland-tethered plant resources) offered higher return rates than piñon. Steward (1938: 232) emphasized the importance of ethnographic piñon ecotone encampments that provided ready access to stored seeds (especially pine nuts), water, sufficient wood for housing and fuel, and avoiding extremely low winter temperatures (see also Thomas, 1988: 562–563). These conditions were most often satisfied near canyon mouths along the piñon ecotone and winter encampments clustered near the mountain masses rather than valleys. These camps were scattered at intervals of several hundred yards to a mile along mountainside streams, often clustered in dense colonies depending upon which food resources could be stored within convenient distance of each camp.

Edge Effects in the Reese River and Monitor Valleys: The Reese River Valley is relatively well watered today and there is every reason to suspect this area was more mesic than most midbasin valley systems during the Holocene. Most water is concentrated in flowing channels, largely montane feeder streams that ultimately drain into the north-flowing Reese River itself, and this hydrological regimen is clearly related to the distribution of ecotone sites mapped there. Archaeological data from Reese River strongly support a lower foothill positioning strategy; the 65 recorded sites clustered an average of about 500 m from the lower foothill

margin, just as Steward's ethnographic model suggested they would.

In nearby Monitor Valley, Gatecliff Shelter was surrounded by piñon-juniper woodland by at least 3800 cal B.C., with perhaps a higher proportion of juniper (Thompson and Hattori, 1983; Thompson and Kautz, 1983; Thompson, 1992: 13). Starch analysis on millingstones from Gatecliff Shelter demonstrates that pine nuts and grasses were being processed during the occupations of Horizon 9 (1910–1710 cal B.C.) and Horizon 8 (1640–1615 cal B.C.; Rhode and Richey, 2020), findings corroborated by the plant macrofossil assemblages in contemporaneous firehearths (Rhode and Thomas, 1983). Diagnostic projectile points from multiple piñon ecotone sites further suggest that piñon processing in the central Great Basin was firmly established during the Post-Middle Holocene Transition (Devils Gate phase; Hatoff and Thomas, 1976; Thomas et al., 1976).

Systematic regional survey shows that Monitor Valley conformed to some degree to the early, intensive piñon ecotone hypothesis, but the woodland was significantly less occupied than equivalent areas in the Reese River Valley.[8] But because the Monitor Valley woodland lacks a sharply defined lower margin, different edge effects apparently operated here. East-facing Toquima sites (fronting Monitor Valley) were deliberately selected to minimize distance to the ecotone, suggesting that (as at Reese River), edge effects operate here (Thomas, 1988: fig. 204). Sites on the western Toquima flank (fronting Big Smoky Valley) show an opposite selectivity, distanced an average of 150 m farther away from the lower foothill margin. This may be due to the patchy distribution of woodland trees across the west-facing flank and because the piñon-juniper zone in Monitor Valley is not directly subjected to moisture-laden Pacific frontal systems as is the Reese River, meaning that temperature inversions created broader, less circumscribed stands of woodland vegetation, especially along the west-facing flank.[9] These results largely conform to earlier thoughts regarding multiple piñon procurement strategies along the logistical and residential continuum (Thomas, 1981, 1983a).

Piñon Procurement Elsewhere in the Central Mountains Archaic: Giambastiani et al. (2012) identified 32 piñon-related features in the northern Monitor Range, with two dozen likely piñon caches and half that many house ring foundations. Residential use of the piñon zone began during the Elko interval and continued with an intensity less than the Reese River Valley but higher than the rest of Monitor Valley to the south.

Systematic archaeological survey in Grass Valley documented a long-term occupation of the piñon-juniper woodland beginning during the Devils Gate phase (Gatecliff series points) and lasting through Euro-American contact (Wells, 1983: vi). Wells believes that piñon procurement in Grass Valley involved stays of just a few weeks, with communities likely wintering to the north, closer to the Humboldt River (1983: 106); this contrasts with the Reese River pattern, where many piñon ecotone settlements seem likely occupied through the winter. Just to the

[8] Nearly 85% of the available Reese River piñon ecotone loci were occupied, but less than one-quarter of comparable loci in Monitor Valley showed signs of occupation. Absolute site density is significantly higher at Reese River than in Monitor Valley. Absolute density of aboriginal houses is more than four times higher in Reese River Valley than in Monitor Valley. Reese River sites contain between 1.5 and 3 times the number of time-sensitive artifacts than equivalent sites in Monitor Valley (Thomas, 1988: 613).

[9] David Rhode (personal commun., 2021) suggests an intriguing way to test the edge-effect hypothesis by comparing the north-south distribution of Great Basin winter villages relative to the northernmost piñon distribution. If winter temperatures were a major driver of winter village location, then winter villages both north and south of the piñon line would be situated in the cold pogonip-filled valleys and at the warm inversion threshold on the slopes. Steward's (1938) map of winter villages below the "piñon line" seem to map right along the lower mountain edges, presumably at the piñon ecotone and the point of warmer winter temperatures, as anticipated in the piñon ecotone hypothesis. To the north of the piñon line, winter villages are located along rivers and streams in valley bottoms. These northerly locales must be subject to inversions as well, so wintering along the rivers would be much colder than inhabiting the canyon mouths along the mountain front. If winter villages were positioned in those cold valleys to be closer to stored food resources, then maybe the distribution of winter stores (including pine nuts) was a more important variable than winter temperature after all.

north at Cortez (near the modern limit of the piñon woodland), Delacorte et al. (1992: 116–117, map 1) found that piñon camps were lacking entirely—in contrast to patterns in southern Grass, Pine, Reese River, and Monitor valleys—suggesting that the surveyed area represented only part of the complete settlement subsistence system.

In the Desatoya Range (west of Reese River), Lechner and colleagues (see fn. 3) documented multiple piñon settlements with Elko series accounting for half the points associated with rock rings (where Gatecliff points were common as well). Rosegate points are more abundant at settlements without rock rings. Lechner et al. (fn. 3) interpreted the Desatoya Range survey as reflecting piñon ecotone use over the last 4000 years but differing from elsewhere in the Central Mountains Archaic because of the relative abundance of ground stone tools and scarcity of rock ring features.[10] They further suggested that these sites were stopovers where hunting groups geared up before working the Desatoya Mountains or Smith Creek Valley. The high frequency of millingstones may indicate these sites were short-term camps, where other family members stayed while logistical hunters were away.

Toward the eastern margin of the Central Mountains Archaic, the piñon-juniper woodland appeared along the flanks of the Pequop Range and Goshute Valley at least 4800 years ago (12.1). Juniper dominates the modern piñon-juniper woodland of the Bonneville Basin, and if similar densities held in the past, then pine nut harvests in this area were likely less promising than in the west, where more piñon trees grew (West et al., 1998). Not until the Neoglacial (~1000 cal B.C.) did James Creek phase piñon camps appear in the Goshute Range (positioned below present-day piñon groves at 5800 ft), near where Cunnar et al. (2019) believes that green cones were cached.[11]

Upland sites occupied during the subsequent Late Holocene Dry period in the Pequop range were only infrequently recorded between ~5800–5900 ft (Cunnar et al., 2019), suggesting that because lowland water was limited at the time, winter base camps were set up at higher elevations. If so, then this reflects patterns seen in Monitor Valley and elsewhere in the Central Mountains Archaic, with a shift away from logistical, male-based hunting toward family-based gathering coeval with the occupation of higher-altitude sites (such as Alta Toquima). This transformation took place about cal A.D. 1 in the Goshute Valley, with increased site density and likely emphasis on geophytes as well (Cunnar et al., 2019: table 13.14).

## Piñon Procurement in the Stillwater Range

Several independent factors limited potential piñon harvests in the Stillwater Range. For one thing, piñon trees did not arrive in the Stillwaters until around cal A.D. 500 or a bit later[12] and juniper still dominates the modern piñon-juniper woodland. If similar densities held in the past, then piñon harvests were likely far less productive than in the Sierra Nevada or to the south in the Inyo-White and Coso mountains where piñon trees grew in far higher densities (West et al., 1998).

Increased precipitation (primarily in the winter) sparked a rejuvenation of wetlands and, during these mesic times, the overall increase in regional productivity narrowed the differential between wetlands and uplands (reflected in the mix of resources and mobility evident ethnographically). The arrival of piñon opened the options for upland foraging, creating the possibility of settlements tethered to, but not exclusively focused on Stillwater Marsh (Thomas, 1985). Even

[10] This raises the obvious question of whether piñon had actually reached the Desatoya Range by 4000 years ago; while this seems likely, I am not aware of any packrat midden evidence confirming or disproving this suggestion.

[11] Ethnohistoric Shoshone and Goshute communities set up winter base camps downslope from the near piñon groves (Steward 1938, 1941).

[12] Grayson (2011: table 8.4) dates piñon arrival in the Stillwater Range to cal A.D. 700 (citing Wigand and Nowak, 1992, and Wigand, 2002); table 12.1 documents that piñon likely arrived in the Painted Hills (near Pyramid Lake) by ~cal A.D. 300 and the Pinenut Range by ~cal A.D. 500 (Wigand, 2017; Miller et al., 2019: fig. 3-10).

if piñon was present in economically viable densities, resource selection and transport-cost models suggest it might not have been worth transporting pine nuts at all if other resources were more profitable due to the distance from the piñon groves (Raven, 1990; Kelly, 1995, 2001; Zeanah et al., 1995; Zeanah, 2004).[13] Alternatively, the wetlands could have taken on new significance with storable food and the locus of winter foraging even if piñon was available.

Systematic random sampling showed that unlike the floor of the Carson Sink, the Stillwater Mountains had much more evidence of bifacial tools and virtually no bipolar reduction. Although this led Kelly (2001: 293) to conclude that the piñon-juniper belt might have experienced both residential and logistical mobility, the scarcity of upland millingstones suggests piñon and other seed harvesting was rarely undertaken during these forays. Human bone collagen (Schoeninger, 1995: 103) further demonstrates that despite its apparent importance elsewhere in the Great Basin, piñon did not figure prominently in the Stillwater diet.[14]

## Piñon Procurement in the Southwestern Great Basin

Randomized regional sampling of the piñon-juniper zone in northern Owens Valley and the surrounding mountains showed that residential piñon camps in the White Mountains postdate cal A.D. 600 (Bettinger, 1975, 1976a: 86). These sites contained highly diverse assemblages, rock rings (interpreted variously as dwellings and piñon caches), large numbers of basin and slab millingstones, manos, projectile points (mostly Desert series), bifaces (including knives), unifaces (scrapers), cores, and debitage. Although substantially smaller than lowland occupation sites, some piñon camps suggested long-term (winter) occupation, while others seemed to be short-term piñon collecting stations (Bettinger, 1982a).

These data provided a baseline for the macroevolutionary hypothesis and the proposed hypothetical trajectory for piñon exploitation along the southern Sierra (Bettinger, 2015: 64):

> Along with other plant foods, pinyon became more important following the introduction of the bow.… However, the intensive ethnographic pattern of routinely acquiring and storing nuts in bulk on the spot for winter use, and the consequent tethering of the fall-winter settlement to camps near these stores in the pinyon woodlands, did not immediately develop (Bettinger, 1999: 65). In Owens Valley, for example, archaeological *pinyon camp* sites with house rings and storage features located in the pinyon woodlands, midslope between 7000 and 9500 feet in the Inyo and White Mountains (e.g., Bettinger, 1989), constitute about 60% of the sites dating to the Klondike [Marana] phase (A.D. 1300–1850), a figure that probably approximates the quite substantial ethnographic level of intensity.… By contrast, during the preceding Baker [Haiwee] phase (A.D. 600–1300), when the bow was first introduced, only about 40% of sites are pinyon camps and the bulk of them probably postdate A.D. 1000 (Bettinger, 1977).

Regionalized random sampling of nearby Deep Springs Valley supported this hypothesis, recording a dozen piñon-camp components at seven sites (Delacorte, 1990), associated with Rosegate and Desert series points, ceramics, and some postcontact artifacts. The total absence of Elko points left "little doubt that pinyon camps were not in use prior to A.D. 600" (1990: 235). Bettinger

[13] Optimization models require a consideration of foragers' options (Simms, 1987), and it is not economically viable to transport piñon in its cone for more than a few hundred meters (Zeanah, 2004), but field processing to remove pine nuts from the cones shows they can be profitably transported quite far (Jones and Madsen, 1989; Rhode, 1990; Metcalfe and Barlow, 1992; Barlow and Metcalfe, 1996).

[14] "The relatively positive $\delta^{15}N$ values in human bone collagen (9% and higher) suggest that piñon provided little to the diet because the piñon $\delta^{15}N$ value is close to zero. The nuts from species available near the Carson Desert (*Pinus monophylla*) are high in fat (23%) and carbohydrates (54%), but also contain a significant amount of protein (10%) relative to other plants (Lanner, 1981). If piñon had provided a major portion of the diet to prehistoric occupants of the Carson Desert, the human bone collagen nitrogen isotope values should be lower than those measured" (Schoeninger, 1995: 103; 1999).

(1989, 1991) and Delacorte (1990) hypothesized further that pine nuts recovered from lowland residential bases reflected an expedient, brown-cone strategy of procurement by communities hunting artiodactyls, especially bighorn.

Because millingstones and domestic structures were more common in Deep Springs Valley, Delacorte (1990: 268, 283) hypothesized more significant residential occupations of the piñon-juniper zone than in the neighboring White Mountains. Delacorte suggested that Deep Springs Valley communities, with smaller population sizes, frequently established new sites (perhaps reflecting some ownership of piñon stands).

Delacorte (1990: 290) contrasted the Deep Springs Valley evidence with the Reese River Valley pattern, which he felt were often reoccupied by a relatively large population residing in carefully picked localities with ready access to fuel and water. Arguing that piñon camps and cache sites in Deep Springs Valley were generally confined to higher elevations and rarely occupied for more than a few weeks. Deep Springs Valley communities wintered on the valley floor, occasionally returning to retrieve cached nuts (Delacorte, 1990: 296). Delacorte believed this explained why millingstones were more abundant and widely distributed in Deep Springs Valley—communities continually moved between several long- and short-term encampments. Delacorte thought that millingstones were curated in the Reese River piñon-juniper woodland due to the more frequent and longer residential occupation of winter camps, suggesting that "the community played a more central role in the development of the Reese River Valley than in Deep Springs Valley."[15]

The combined Inyo-Mono evidence showed that most excavated sites date to the late prehistoric interval, although some pre-cal A.D. 700 radiocarbon (and other) ages are reported (Bettinger, 1989; Eerkens et al., 2004). Regional survey data largely point to a post-cal A.D. 700 age for piñon camps (Bettinger, 1975, 1976a; 1977; Delacorte, 1990).

McGuire and Garfinkel (1976) took exception to Bettinger's (1976a) conclusion that rock rings and millingstones represented the initial introduction of piñon nuts into the Owens Valley/Deep Springs diet after cal A.D. 600, arguing instead that the White Mountains reflect a shift in existing piñon procurement strategies. McGuire and Garfinkel hypothesized that pre-cal A.D. 600, pine nuts were obtained less intensively in the brown-cone stage, but when increasing population pressure required "a whole new regime of pinyon harvesting" (1976: 84), foragers switched to a green-cone strategy. This observation spurred development of the macroevolutionary argument of green-cone intensification during the Late Prehistoric period (Bettinger and Baumhoff, 1983; Bettinger 1994, 1999).[16]

Others have hypothesized that piñon was exploited earlier than the Bettinger-Delacorte estimate, becoming increasingly intensive through time (McGuire et al., 1980; Madsen, 1981). Basgall and McGuire (1988) saw CA-INY-30 as demonstrating that piñon was consumed on a regular basis during Newberry times, well before the cal A.D. 700 age suggested by the macroevolutionary hypothesis. The Ed Powers project turned up piñon in small quantities, particularly in residential structures (Basgall et al., 2003: 359), adding to the growing number of places where piñon use predated the appearance of piñon camps by many centuries (Scharf, 1992; Zeanah and Leigh, 2002).

Because the pre-Haiwee piñon hulls recovered from Owens Valley came mostly from outside the modern piñon-juniper zone, Basgall and Delacorte (2003) suggested that these easily transported resources were taken in relatively small-

[15] Piñon camps at nearby Fish Lake Valley also differed from Deep Springs Valley, because they were larger and frequently located along drainages near the piñon-juniper ecotones (Delacorte, 1990: 313), with abundant lithics and bedrock milling facilities suggesting a lengthier occupation, likely throughout the winter.

[16] Several burn features at Sherwin Summit in northern Owens Valley are consistent with ethnographic accounts of green-cone roasting pits that contained burnt piñon remains. Radiocarbon dates on green-cone processing refuse collected from the rock circle features and burn features dated to the last 300 years and implied use of intensive green-cone processing and storage (Eerkens et al., 2004: 23).

scale piñon procurement sessions embedded within upland hunting trips. If so, such coincidental collection events perhaps also explained the transport of piñon and other lowland resources to Midway, an alpine hunting camp in the White Mountains (Scharf, 1992). Alpine residential use of the White Mountains during this interval is confirmed by radiocarbon dates (from Short Stop and Rancho Deluxe) of cal A.D. 260–650. Evidence of uphill piñon transport to Midway is bolstered by the presence of goosefoot and tansy mustard seeds in the same contexts. These could have been casually collected by hunters on their way to the mountains, with piñon nuts and seeds serving as trail food for long-distance residential and logistical moves (Basgall et al., 2003: 360).

The Birch Creek houses (near Bishop) document more significant Newberry piñon exploitation. Although pine nut shells were ubiquitous in the Newberry-age house flotation samples, pine nut frequencies at Birch Creek are "much lower than found in the average late prehistoric flotation sample" when piñon nuts constituted a "veritable staple resource" (Basgall and Delacorte, 2012: 10–11). Basgall and Delacorte hypothesized that the Newberry houses at both Birch Creek and CA-INY-30 were consistent with a "brown cone" strategy, thought to presage a more intensive "green cone" strategy reflected in the large quantities of piñon in lowland late prehistoric contexts of Owens Valley. This intensification was thought to follow the introduction of bow technology, with specialized piñon camps in the uplands including storage cairns and roasting features reflecting intensive exploitation (Bettinger, 1975, 1977, 1982b).

Contrasting patterns emerged at Papoose Flats (central White-Inyo Mountain Range), where archaeological sites of all time periods cluster near the fluctuating Middle and Late Holocene piñon ecotone (Reynolds, 1996, 1997).[17] The surprisingly large number of Little Lake and later points associated with rock ring sites and milling equipment suggested to Reynolds that intensive, green-cone piñon procurement started in the Newberry period (if not earlier). Subsequent archaeological survey in the Coso Range (Hildebrandt and Ruby, 1999) also documented significantly higher point frequencies and obsidian hydration rim readings from 2000 cal B.C. to cal A.D. 1350. They attributed this pattern to intensified use of upland resources (particularly piñon) and argued for green-cone processing during the Elko interval.

Intensified piñon processing at both Papoose Flats and the Coso Range is two millennia earlier than originally hypothesized for northern Owens Valley (Bettinger, 1976a, 1989) and Deep Springs Valley (Delacorte, 1990). Reynolds based her intensification model on the large number of Elko points (dating 1500 cal B.C.–cal A.D. 600) reflecting an 88% association with domestic facilities (including rock rings and millingstones) suggesting "use of the more intensive...green cone method during this time" (Reynolds, 1996: 155).[18] Such early green-cone processing contrasts with macroevolutionary arguments linking resource intensification, rising human population densities, and the alleged expansion of Numic-speaking peoples across the Great Basin (Bettinger, 1994; Bettinger and Baumhoff, 1982).

Hildebrandt and Ruby (2006) questioned this linkage and emphasized that Coso Range sites with rock rings (identified as piñon caches and piñon camps) tended to date much later than sites lacking rock rings.[19] Statistically significant associations with rock rings contrasted with the pattern for millingstones, which were strongly

[17] Reynolds (1996: 155; 1997) found piñon macrofossils in packrat middens dating 7030–6600 rcybp, placing piñon locally at the beginning of human occupation there (see also Jennings and Elliot-Fisk, 1993).

[18] Hildebrandt and Ruby (2006: 14) elaborated the point: "It follows that green-cone processing would be part of the logistically organized system; that is, task-specific groups focused on green-cone procurement, and transported the processed nuts down to lowland residential bases for later consumption." If so, the allegedly high costs associated with green-cone harvesting would make it unlikely that this activity could have occurred during short-term logistical forays to the uplands.

[19] Specifically, Hildebrandt and Ruby (2006: table 9) found that Middle Holocene projectile points (23.3%) were associated with sites having rock rings, and this was also true for Elko interval sites in which 28% were associated with rock rings. For subsequent Rosegate and Desert series points, associations with rock rings jumped to 38% and 40% respectively.

associated with all time periods. Hildebrandt and Ruby (2006: 26, 29) reasoned that

> if green-cone processing is directly linked to the use of rock rings, but rock rings and milling gear are not obviously always linked to one another, it follows that milling gear was probably also used for resources other than green cone pinyon nuts—most importantly the highly ranked brown cone pinyon nuts

and concluding that

> these findings suggest that while the original green-cone hypothesis stands, Bettinger (1976a, 1989) and Delacorte (1990) may have underestimated the importance of pinyon use during earlier time periods.…. The high return rate of pinyon nuts, combined with the fact that they are abundantly present in Newberry period residential bases on the valley floor (e.g., Basgall and McGuire, 1988), surely indicates that they were more than a casual resource prior to 1,350 B.P.

## Piñon Procurement Elsewhere in the Western Great Basin

Piñon entered the far western Great Basin by 3000 cal B.C. in the Bodie Hills. Piñon progression stalled at Mono Lake until ~1500 years ago (Nowak et al., 1994b), reaching the present-day northwestern boundary near the southwest shores of Pyramid Lake (Painted Hills) about 300 years ago (Cole et al., 2013; Miller et al., 2019: table 12.1).

The Oxbow survey between Owens Valley and the Walker Basin documented piñon procurement at two sites in Adobe Valley (northern Benton Range), both with abundant millingstones and multiple basalt rock rings clustered in the piñon-juniper belt (Hall, 1990: 155). The modern Owens, Mono, and Walker basins host the purest (most dense) stands of piñon trees in the Intermountain West—a major contributing factor to the annual megafires of today. Hall (1990: 192, 734) saw the Adobe Valley complex as centered on piñon harvesting that have spanned the last two or three millennia with multiple residential or task-oriented occupations of the surrounding forested ridges, slopes, and benches.

In his Walker River and Pine Grove Hills archaeological survey, Rhode (1987: 218–219) recorded numerous stone circles and millingstones in the piñon woodland, which he saw as consistent with piñon procurement beginning in Gatecliff times (earlier than reported for Borealis and Owens Valley). This was followed by a late prehistoric intensification characterized by Desert series points and/or historic materials (consistent with Bettinger, 1977). Piñon in the Wassuk Range grew close enough to lacustrine resources that pine nuts collected and cached could be easily transported to lacustrine residential base camps at Walker River. Rhode (1987: 410) felt that in years when piñon nuts were abundant, longer-term residential occupation of the piñon woodland was likely reflecting a settlement pattern similar to that recorded ethnographically in Owens Valley (Steward, 1933; Bettinger, 1983). Because distances were too great for transporting piñon harvests to resource bases near Walker Lake, winter residences were set up in the Pine Grove Hills (parallel to ethnohistoric accounts of Northern Paiute settlements).

Giambastiani's (2007) Slinkard Valley (CA) survey focused on the archaeology of piñon procurement and found the vast majority of sites clustered within the piñon-juniper. Giambastiani recorded 30 piñon camps, primarily associated with Late Archaic and ethnohistoric artifacts (Rosegate and Desert series points, glass beads, and other diagnostic Euro-American debris), plus several associated rock circle features assumed to be piñon related. Although others have argued that such stone circles may represent houses or perhaps hunting blinds, Giambastiani attributed the vast majority in Slinkard Valley to intensification of piñon harvesting in the green-cone stage (after Bettinger, 1976a, 1982a; Delacorte, 1990).

Data supporting Middle Archaic piñon camps in Slinkard Valley are slim and parallel the Coso Range survey (Hildebrandt and Ruby, 2006) where earlier piñon camp assemblages (represented by Elko series and other dart points) con-

tained mostly milling gear and flaked stone debris. Giambastiani concluded that the earlier site assemblages with millingstones involved brown-cone procurement and the regular use of rock circles associated with a subsequent green-cone strategy.[20] We now know that piñon pine did not arrive in Slinkard Valley until ~cal A.D. 460 (Miller et al., 2019) undermining any sequence of brown-cone/green-cone distinctions before that date.

## Piñon Procurement in the Southern Great Basin?

The early intensive piñon ecotone hypothesis holds that pine nuts became a staple as soon as they were present someplace (assuming they were highly ranked among local foods). If so, maybe one should expect to find significant pine nut use in the southern Basin, where piñon pine has grown since the Late Pleistocene. Would this mean that pine nuts were commonly used by Paleoindian communities?

No hard evidence suggests early piñon procurement in the southern Great Basin (and pine nuts were certainly not the staple they became later). So perhaps Early Holocene food sources in the southern basin (such as marshland resources) ranked higher than pine nuts, or maybe high Paleoindian mobility was inconsistent with piñon procurement. The existing archaeological record remains silent on these possibilities.

## Little Ice Age

Piñon-juniper woodlands reexpanded in selected places during the Little Ice Age (Wigand and Nowak, 1992; Gray et al., 2006) and the proportion of piñon relative to juniper has increased notably within the past few centuries (Wigand et al., 1995; Biondi and Bradley, 2013). The megadrought in the second half of the 1500s that impacted much of western North America prompted a decline in piñon-juniper woodlands (Swetnam and Betancourt, 1998). Expansion and infill (increasing tree density within woodlands of previously lower density) then resumed and continued during the 1600s through the mid-1800s (Miller et al., 2008; Floyd et al., 2017). The current northern geographic boundary of *P. monophylla* is probably governed by late winter and early spring temperatures, when rapid temperature fluctuations can cause dormancy to break early, making piñon pine susceptible to frost damage (Nowak et al., 1994a).

Changes in Piñon Pine Distribution within the Last Two Centuries: Packrat middens, pollen proportions, and tree-ring chronologies document unprecedented expansion and infilling of the piñon-juniper woodlands since the late 1800s (Mehringer and Wigand, 1990; Wigand et al., 1995; Burwell, 1998; Swetnam et al., 2016; Miller et al., 2019: table 3-4). While some attribute this primarily to natural climate phenomena (Floyd et al., 2004; Barger et al., 2009), others see the woodland expansion as recovery from extensive tree harvests during the Comstock period involving (but not limited to) fuel wood, mine timbers, building construction, charcoal production for smelting, and railroad timbers (Young and Budy, 1979). Still others think that increased grazing combined with climate change of the late 1800s to early 1900s triggered woodland reduction due to increased fire frequencies (Touchan et al., 1995; Boyden, 2004; Bradley and Fleischman, 2008; Swetnam et al., 2016). Potential triggers include fire suppression in the 20th century, considered by some to be a major cause of expansion (Miller and Tausch, 2001) and increasing atmospheric $CO^2$ (Bazzaz, 1990; Archer, 1995).

Piñon and juniper woodlands expanded up and down slope within the last two centuries

[20] Giambastiani (2007) thought Slinkard Valley evidence revealed an error in my interpretation of piñon harvesting in the Reese River Valley (Bettinger, 1976b; Hatoff and Thomas, 1976; Thomas et al., 1976). She particularly took exception to the conclusion that most rock circle features in the piñon ecotone were house foundations. Giambastiani (2007) proposed instead that the Reese River rock circles were late prehistoric green-cone storage features, as interpreted for Slinkard Valley and the Coso Range (Hildebrandt and Ruby, 2006). She had a good point that underscored both the ambiguities of assigning function to simple rock circles without excavation and the green-cone/brown-cone distinction in general.

(Cottam and Stewart, 1940; Hattori and Thompson, 1987a, 1987b; Bradley and Fleischman, 2008), with tree densities >600% of previous historic estimates in sagebrush ecosystems and desert grasslands by the end of the 20th century (Margolis, 2014). The woodlands differentially infilled, expanded, and/or contracted (Chambers, 2001; Weisberg et al., 2007). Although rates of tree establishment declined after the 1920s, expansion infill still occurs in the generally warming and more arid climate. The proportion of young versus precontact woodlands strongly supports the argument that the most significant piñon-juniper expansion and infill took place in the early 20th century, although some believe that expansion is still increasing (Miller and Wigand, 1994; Miller and Tausch, 2001). A survey of the Shoshone Mountains (Reese River Valley) showed young trees accounting for 57%, mixed age stands 33%, and old-growth woodland only 10% (Weisberg et al., 2008).

In short, documenting the expansion and contraction of piñon pine into the 21st century is an ongoing, moving target. Over the most recent decades, the net effects of mortality vis-à-vis expansion swings toward the declining side of the equation (Shriver et al., 2022).

The Comstock Hypothesis: Precise charting of piñon-juniper expansions into formerly nonwoodland communities in Nevada and Utah is difficult due to the reestablishment of woodlands harvested during the Comstock Mining era (between 1863 and 1908, peaking between 1884 and 1891). Many believe that mining impacts were widespread and, while the piñon-juniper forest was not wiped out, the range was seriously diminished (Charlet, 2008; Lanner and Frazier, 2011). Hattori and Thompson (1987a, 1987b) and Strachan et al. (2013)[21] argue instead that piñon and juniper were harvested mostly near the mining districts, the impacts decreasing quickly with distance. Steep terrain may also have limited cutting, with tree harvesting the greatest on slopes <15%, rapidly declining on slopes >25%. Hattori and Thompson (1987b) conclude that the most severe historic deforestation depicted in historic accounts and photographs (including Thomas, 1971b) are likely exaggerated due to their proximity to mining settlements (see also Ko et al., 2011).

Wage labor and economic dependence nucleated and tethered 19th-century indigenous settlements around white-owned ranches, which further decreased the pursuit of traditional native economic activities. When piñon pine nuts became a cash crop in the mid-19th-century Great Basin, Western Shoshone families sometimes camped in Grass Valley for several days to obtain piñon nuts, some consumed locally and others sold and/or traded to Anglo-Americans (Wells, 1983: 165–166). Coville (1892: 353) commented that "pine nuts [among the Panamint Paiute] are often sold in markets in California and other Western States, being disposed of precisely as peanuts are in the East" (see also Chamberlin, 1911: 34, for the Goshute).

By the time early 20th-century ethnographers began reconstructing precontact economies, many indigenous subsistence activities were no longer practiced, but piñon exploitation was remembered vividly since it was, and still is, being practiced in many areas (Wells, 1983: 172–174). The Comstock hypothesis[22] holds that 19th-century Euro-American disruptions differentially altered the Great Basin landscape to the extent that Julian Steward and his generation of ethnographers likely overstated the importance of piñon in indigenous economies—specifically among the Western Shoshone. Although accepting the overall importance of piñon procurement in the precontact Great Basin, Wells questioned the

[21] Estimates of the quantity of piñon and juniper cut for charcoal fuel in the Great Basin during this Comstock era range from 600,000–750,000 acres (Young and Budy, 1979; Lanner, 1981), representing 3.4–4.25% of the total acreage of woodlands in Utah and Nevada (Miller et al., 2019: fig. 3-25).

[22] The rich silver deposits of silver in Virginia City, Washoe, and other mining boomtowns including Austin, Belmont, and Cortez are collectively named "the Comstock Lode" after Henry Comstock, part owner of that property discovered in June 1859. The remarkable output of silver in such mining districts over the next decade justified the establishment of a U.S. branch mint (closed in 1893) in Carson City, Nevada.

degree of persistence of piñon harvesting during the historic period (1983: 168) and argued that Comstock impacts were less severe on upland piñon stands than on valley-bottom resources (especially geophytes and grass seeds). When discussing most subsistence practices, Shoshonean consultants usually described events only remotely within their personal experience—perhaps done by parents and grandparents before contact, but rarely did they see such activities as children. The piñon harvest was an exception because most Western Shoshone people living in the 1920s and 1930s had done this since childhood. Wells laments the lack of ethnography for the early historic period, separate and distinct from that of the prehistoric past and adds that "what Steward's informants have given us probably contains elements of both, a fact that was surely recognized by Steward himself, but that is ignored by many who use his data" (Wells, 1983: 175–176).

## A COLD-AIR DRAINAGE HYPOTHESIS

The hypothesis of early and intensive piñon ecotone procurement originally considered the role of thermal belts as reflecting both the distribution of the piñon-juniper ecotone and also ancient settlement patterns, but it wasn't until the follow-up Monitor Valley surveys that I began to appreciate how heavily cold air drainage and thermal inversion conditioned the specific locations of the piñon ecotone village sites (Thomas, 1988: 538). Archaeological evidence (summarized above) demonstrates that rather than relating to the specifics of piñon procurement, known winter village locations tended to cluster near the ecotone only in the very highest valleys of the Great Basin—those with valley floors exceeding 6000 ft. That's why I now propose a new hypothesis to address this distribution.

The cold-air drainage (CAD) hypothesis suggests that across the Intermountain West—a landscape defined by sequences of steep mountain ridges, lower-elevation meadows, and river valleys—foragers deliberately sited settlements to avoid low-lying topographic features where cold, dense air collected during still (that is, windless) nighttime hours to produce colder temperatures than surrounding higher elevations. These cold-air pockets offered vulnerable species and ecosystems a sort of refuge that allowed more time to adapt to new conditions. The negative impacts of cold-air drainage on hunter-gatherer lifeways are noteworthy, with significant implications on elevational foraging-pattern adaptations and drought sequencing through time. The CAD hypothesis transcends generic edge effects by focusing directly on specific microtopographic patterns that directly conditioned the positioning of both winter piñon villages and alpine residences. For now, I concentrate on the piñon ecotone settlements.

Origins of the cold-air drainage hypothesis lie in a seminal article by W.D. Billings (1954). In the Virginia Mountains (western NV), Billings found that throughout the year, the minimum temperatures in the piñon-juniper zone were 10°–15° warmer than in the neighboring sagebrush covered bottoms (400–1300 ft lower elevation). Noting that resultant thermal belt above the layer of cold night air coincided with the distributional limits of woodland, Billings saw the downhill drainage of cold air into the valleys impacted the lower margin of the piñon-juniper zone, and "it would not be surprising if such thermal belts exist on most of the mountain ranges of the central and western Great Basin" (1954: 117).

It turns out that Billings was correct and subsequent research has significantly expanded understanding of cold-air drainage in landscapes of the Intermountain West. Trapped by surrounding high terrain, topographically defined cold-air pools contain a layer of stagnant air much colder than the air above, sometimes resulting in long periods of poor air quality and fog (Glickman and American Meteorological Society, 1999). The associated icing or freezing precipitation can delay the melting of snow and ice and have impacts on hydrology (Whiteman et al., 2001). The fog also associated with CAD near lakes or

wetlands in the basins is a nocturnal atmospheric process that helps sustain cooler air temperatures in cool-air pools because on calm clear nights, air in contact with the ground surface cools more rapidly due to radiative energy loss. This colder-denser air decouples from the free atmosphere at the same elevation and sinks into topographic depressions. Such cold-air pools generally occur in concavities and places cut off from the free atmosphere, typically along flat valley bottoms in mountainous terrain with valley constrictions and even in relatively small swales and minibasins at higher elevations. These cold-air drainage processes may increase during climatic warming conditions (Daly et al., 2010).

I believe that because nearby exposed ridges and topographic convexities are not prone to the decoupling and sinking of colder denser air, Western Shoshone communities deliberately located their piñon villages in such places. Although the other locational factors spelled out in the previous piñon ecotone hypothesis remain in play—especially ready access to water, ample firewood, and minimizing transport costs of piñon procurement—I now think that Central Mountains Archaic foragers thoroughly understood the realities of cold-air drainage and applied those ecological principles to their advantage.[23]

[23] The cold-air drainage hypothesis has far-reaching implications for the specific siting of alpine residential villages at Alta Toquima and elsewhere; I am extremely grateful to Constance Millar for meaningful advice on this point. Cold-air pooling in topographic depressions increases the likelihood of the late spring snowpack persisting at elevations above 9000 ft, creating potential climate refugia sites for snow-dependent species at mid elevations, where significant topographic shading and cold-air pooling potential exist (Curtis et al., 2014; Cayan et al., 2021). Cold-air drainage is associated with regions of permafrost and provided unique microclimates that influenced species distributions and diversity. Because of decoupling from the free atmosphere, these cold pool areas may respond differently to climate change than surrounding regions. Both CAD hypotheses could be tested by pairing the distributions of known piñon-winter villages and alpine residences with automated algorithms now available for mapping regions of cold-air pooling in complex terrains (e.g., Lundquist et al., 2008; Daly et al., 2010; McEvoy et al., 2014; Millar et al., 2014, 2021; Millar and Westfall, 2019; Cayan et al., 2021; see 2009 unpublished paper by C. van de Ven, and S.B. Weiss, titled "Downscaling to the climate near the ground: measurements and modeling along the macro-, meso-, topo-, and microclimate hierarchy" presented at the American Geophysical Union, San Francisco, CA.

## BROWN CONES, GREEN CONES, AND RED HERRINGS

The piñon procurement strategies discussed so far invite a closer look at exactly how Great Basin communities gathered and processed pine nuts (Hoffman, 1878: 473; Dutcher, 1893; Muir, 1894; Lowie, 1909, 1924; Chamberlin, 1911; Egan, 1917: 241; Kelly, 1932, 1964; Steward, 1933, 1938, 1941, 1943; Stewart, 1941; Downs, 1966; Wheat, 1967; Lanner, 1981: 102; Fowler, 1982, 1989: 49–53; Bettinger and Baumhoff, 1983; Simms, 1985a, 1985b, 1987: 121–124; Madsen, 1986: 29; Bettinger, 1999). Beginning with McGuire and Garfinkel (1976), most Great Basin archaeologists have generically compressed these various practices into dichotomous categories termed the *brown-cone* and *green-cone* procurement strategies.

### Brown-Cone Strategy

The so-called brown-cone strategy describes the piñon nut harvesting that begins when the cones are fully mature, brown, and very brittle, depending on region and elevation but usually in mid to late September (Hoffman, 1878: 473). Nuts already fallen from the trees are picked up and pine cones are pulled from trees with poles, sometimes struck with a stick to free the loosely enclosed nuts. This technology is simple and the caloric return rates are relatively high, something on the order of 850 to 1500 cals/hr (Simms, 1985a: table 3; 1985b). If mats are placed under cone-bearing trees (Steward, 1933: 241; Lanner, 1981: 102), that rate can rise to more than 4000 cals/hr. Only a handful of wetland plant taxa generated return rates comparable to brown-cone procurement of piñon nuts (Zeanah, 2002: 237).

### Green-Cone Strategy

The contrasting green-cone strategy harvests begin when the mature cones are still green,

pitch-covered, and tightly closed, commonly 2–4 weeks before maturity (Dutcher, 1893; Steward, 1933: 241–242; 1938: 28). Piñon cones remain green during much of the summer, but by mid-August or so, their caloric content and weight are quite low and would not reward the effort necessary to process them. John Muir well summarized this strategy in the late 19th century:

> The cones, which are a bright grass-green in color and about two inches long by one and a half in diameter, are beaten off with poles just before the scales open, gathered in heaps of several bushels, and lightly scorched by burning a thin covering of brushwood over them. The resin, with which the cones are bedraggled, is thus burned off, the nuts slightly roasted, and the scales made to open. Then they are allowed to dry in the sun, after which the nuts are easily thrashed out and are ready to be stored away (Muir, 1894; see also Rhode, 1988).

So-called green-cone procurement begins when the few loose nuts are individually gathered, with a hooked pole helping shake cones from limbs or to bring them within reach. These unripe cones are then roasted and stored for later processing.

Caloric return rates from green-cone procurement remain uncertain. Bettinger and Baumhoff (1983: 832) argue that "because green cone procurement begins well in advance of full cone ripening, competition with animals is virtually eliminated, and the period of harvest—and thus the overall take of nuts—is much greater than with brown cone procurement. Because green cone procurement entails more elaborate processing, the yields per unit of time are lower than in brown cone procurement."[24] Simms admitted that whereas there are "no experiments that specifically address mass green cone procurement… it would probably be similar to or more efficient than the return rate given…for brown cone procurement" (1987: 124).[25]

## Macroevolutionary Implications of Piñon Procurement

McGuire and Garfinkel (1976: 84) were the first archaeologists to rank-order the brown-cone and green-cone procurement strategies into an evolutionary sequence, arguing that a significant intensification took place ~A.D. 600, featuring "a whole new regimen of pinyon harvesting, including the roasting of green cones." Bettinger and Baumhoff (1983: 832–833) elaborated this point to argue that brown- and green-cone procurement "are so different, particularly in terms of their return rates per unit of time invested, that they should occur under different circumstances and should be treated as different activities in any microeconomic model, including that variety termed optimal foraging" (see also Bettinger, 1989: 109; 1999; 2009).[26]

Despite minimal comparative evidence, diet breadth and transport models suggest that brown-cone piñon should be included in the diet early in prehistory, the nuts harvested and moved to lowland residential sites. Some have argued that the presumed higher costs of green-cone harvesting were delayed until subsequent intensification triggered more residential activity within the piñon-juniper uplands (Jones and Madsen, 1989; Rhode, 1990; Barlow and Met-

[24] Bettinger (2009: 26–31) used hypothetical estimates to demonstrate optimal foraging constraints. I am not aware of follow-up experiments designed to determine specific caloric return rates for green-cone harvesting and processing.

[25] Simms (1987: 120–124) noted the weeks-long seasonal sequence of pine nut collection, starting with full-on green-cone processing, then as the cones are beginning to open and seeds are getting exposed, then through the rest of the season when the cones empty out and seeds are (briefly) available on the ground. He reported two experiments, one by Kevin Jones when the seeds were still in the cones (green cone verging on brown cone), and one where the seeds had just begun to fall and lay in quantities on the ground (helped considerably by windstorm the previous night—very early brown-cone stage). The return rates were quite similar, perhaps slightly greater in the green-cone experiment.

[26] "The non-intensive brown cone procurement is cheap but offers low potential yields; its exclusive use makes sense where the contribution of pine nuts to the diet is limited because demand is low with respect to preferred resources, and therefore overall subsistence costs are low. The more intensive green-cone procurement is relatively expensive, but the maximum yield—especially when used in combination with brown cone procurement is relatively high; its use makes sense only where pine nuts must constitute a larger fraction of the diet because demand is high with respect to preferred resources, and therefore overall subsistence costs are higher" (Bettinger and Baumhoff, 1983: 832).

calfe, 1996; Zeanah and Simms, 1999; Hildebrandt and Ruby, 2006).

## Some Corvid Perspectives on Piñon Procurement

I think that the presumed brown-cone to green-cone evolutionary progression is a caricature that distorts the complexities of piñon procurement and has provided a misleading baseline from which to view the deep history of the Great Basin. Let us view the dynamics of piñon procurement from some other perspectives. This section sketches out the piñon harvesting strategies of Clark's Nutcrackers[27] and a subsequent section explores forestry nursery practices for doing the same.

Let's begin with the birds. Nutcrackers (*Nucifraga columbiana*) are morphologically and behaviorally adapted to collecting, transporting, and consuming the seeds of singleleaf piñon pine.[28] Piñon seeds change dramatically in both size and composition as they ripen and Vander Wall (1988) details the evolutionary processes that have conditioned nutcrackers to respond quickly to these changes to exploit temporarily abundant seed sources most effectively.[29] These corvids vary rates of foraging intensities by switching from closed to open cones during a three- to four-week interval when both cone types are available. During the 50- to 75-day harvesting interval, nutcrackers have the ability to store enough piñon seeds to provide twice the energy needed not only to survive the winter at subalpine elevations, but also into coming spring and summertime (table 12.2).

Here's how they do it.

Early Seed Harvest: Beginning in July—more than a month before the piñon seeds ripen—nutcrackers spend part of their time and energy extracting unripe seeds from tightly closed green cones.

Although nutcrackers handle seeds for shorter times than later in the harvest, energetic rewards during this interval do not equal energetic expenditure because the unripe seeds are small, with little caloric value. That nutcrackers forage at all during the early season is mostly to gain information about the quantity and quality of the pending seed crop yield,[30] enabling them to adjust strategies for potential seed shortages before they occur (Vander Wall et al., 1981; Vander Wall, 1988: 629).

Harvesting Ripe Cones: Nutcrackers continue harvesting pine nuts throughout the rest of the fall, depending on the cone crop abundance and competition from other animals removing the seeds. Piñon pine seeds change rapidly during late summer and fall, increasing exponentially in both size (dry mass) and caloric content, in late August/early September reaching a maximum stable value averaging 23 kJ/g. Pine nuts also increase in digestible carbohydrates, proteins, and lipids as they mature.

Early in the harvest, nutcrackers move detached cones to feeding perches, where they can remove seeds significantly faster than from those still attached to the tree. After transporting the cones to the firm, interior branches, they wedge the unripe cones in tree crotches and remove the seeds by hammering with their beaks

[27] This account draws upon Vander Wall's (1988) study of piñon pine procurement in the Raft River Mountains of northwestern Utah.

[28] Nutcrackers store more piñon seeds than any of their competitors, except for red squirrels (*Tamiasciurus hudsonicus*), which store whole cones (Hutchins and Lanner, 1982).

[29] Vander Wall (1988) also documents the foraging relationships between piñon seeds and those of limber pine (*P. flexilis*). Because the opening of cones greatly increases seed extraction rates and because limber pine cones ripen and begin opening about seven to 10 days earlier than piñon pine, this means that early in the fall, nutcrackers forage more frequently on the medium-sized limber pine seeds and largely ignore the larger piñon pine seeds. Because limber pines grow much closer to desirable subalpine caching areas, loads of seeds can be quickly transported to storage areas. Although smaller, limber pine seeds contain more energy per unit dry mass than piñon pine seeds, apparently due to their higher concentration of lipids. The switch of nutcrackers from limber pine to piñon in late September coincided with seed depletion from limber pine cones. In this way, nutcracker behaviors also carry important implications for the vertical subsistence strategies involving alpine residential settlements (Rhode and Richey, 2020: 358–362).

[30] During this brief period, nutcrackers bill-click seeds rapidly, moving the seed to the back of their mouth and into the sublingual pouch. Not only does this practice check the quality, it helps maneuver the seed into the pouch as it fills.

TABLE 12.2

**Sequence of Collecting, Transporting, and Consuming the Seeds of Singleleaf Piñon Pine by Clark's Nutcrackers (*Nucifraga columbiana*) in the Raft River Mountains, Utah**
Data from Vander Wall, 1988.

| | Foraging Intensity (no. of birds on cones) | Seed Extraction Time (sec/seed) | Handling Time (sec/seed) | Seeds Detached and Transported (%) | Cone Size (dry mass, mg) | Energy Content (kJ/seed) |
|---|---|---|---|---|---|---|
| Late July | – | – | – | 0–20 | – | 0 |
| Early August | – | 70 | – | 20–80 | 40 | 0 |
| | Cones first open ---------- | | | | | |
| Late August | 3–5 | 60–70 | 10–17 | 80–100 | 100–200 | 0–1 |
| Early September | 7–10 | 20–60 | 14–20 | 20–100 | 250–350 | 1–3.5 |
| Late September | 7–14 | 6–10 | 20 | 0–20 | 250–350 | 3.5–8 |
| Early October | 14–17 | 3–5 | 15 | 0–20 | 340–350 | 7.5–9 |
| Late October | 7–18 | 7–8 | 10–15 | 0–10 | 325 | – |

between cone scales. Nearly all piñon pine seeds extracted by nutcrackers in August were removed from the cone in pieces because the seed coats had not yet fully hardened.

By mid-September, nutcrackers switch over and forage almost exclusively on attached cones where they can remove seeds significantly faster from the mature still-attached cones. After the cones ripen and open up in place (mid-to-late September), foraging intensifies as nutcrackers shift from feeding on detached cones to the open cones in the tree canopy, significantly increasing seed extraction rates. During this prime time, nutcrackers further intensify foraging efficiency by concentrating on the most productive trees within a stand, selecting cones with the greater number of edible seeds, and sorting edible from inedible seeds as they extract them from cones (Vander Wall and Balda, 1977). Rather than working intensively on single cones, nutcrackers hop through the crowns of cone-bearing trees, peering into the cones and extracting from one to 20 seeds from the selected cones.

Table 12.2 shows that the mean seed-extraction times for nutcrackers (measured as seconds/seed) decreased steadily from early August through mid-September, maxing out during the last week of September (Vander Wall, 1988: fig. 9). The reason is that the woody tissues of the cone bracts are deteriorating, permitting nutcrackers easier access to the ripening seeds. Seed extraction costs increase steadily during early October until seeds become more difficult to find. Although nutcrackers still forage on pinecones, they no longer collect significant numbers of seeds for storage and the return rates approach zero.

Seed Transport and Caching: Nutcrackers begin to stuff their sublingual pouches with piñon seeds in earliest September and this marks the beginning of transport and storage. Early in the harvesting cycle, nutcrackers usually eat a few seeds, but once they begin filling the pouch with seeds they do not eat again until emptying the pouch. Although increased numbers of seeds are placed in the pouch after that, fewer are eaten due to the increased energy contained in each of the ripening seeds.

Nutcrackers sometimes cache seeds in the piñon-juniper woodland, just a few meters from where they were collected. But the amount rarely exceeds 10%–20% of the seeds stored because they usually transport piñon seeds by nonstop flights from foraging areas at lower elevations to subalpine caching areas. They repeatedly carry

seeds at least 3 km from a harvest locale and maximum flight paths reach 5 km.[31] Their stereotyped behavioral sequence consists of searching for an appropriate cache site, loosening the soil with the bill, burying one or more seeds, then raking soil and litter over the cache site. Under the most favorable conditions, nutcracker caches can store piñon seeds for 50 to 75 days.

If maximizing seed storage is assumed to be the primary objective, these nutcracker seed-harvesting behaviors might seem counterproductive: Why transport seeds to faraway cache areas when they easily could store them closer to harvest trees, saving considerable time and resulting in more nuts being stored? By caching seeds on windswept subalpine ridges and cliff faces, nutcrackers can minimize cache robbing by rodents (including golden-mantled ground squirrels, chipmunks, and deer mice) that frequent the piñon-juniper woodland (Vander Wall, 1988). So, while caching seeds near the harvest trees might temporarily increase the number of seeds stored, this would ultimately diminish the number of seeds actually available in the late winter or spring.

Fitness Benefits: Because nutcrackers are capable of tracking changes in the resource value of pine nuts during the harvest, they increase the number of seeds they store. In so doing, they try to store more food than actually required at the time so they can rely on stored piñon seeds well after the winter is over—effectively financing the energetic costs of early breeding and feeding nestlings and fledglings throughout the summer (Vander Wall and Hutchins, 1983). Seeds sometimes survive in the caches into late August, just as the new piñon crop is ripening in the trees. In this way, successful piñon procurement in the fall significantly affects nutcracker biology throughout the year. And in years of low to moderate piñon production, this may determine whether nutcrackers successfully survive the winter and breed.

[31] This estimate is specific to the Raft River Mountain study area; elsewhere nutcrackers have been known to transport seeds much further (e.g., Vander Wall and Balda, 1977).

## Emerging Resilience Perspectives

The nuanced and shifting piñon procurement strategies[32] of Clark's Nutcracker reveal the brown cone-green cone evolutionary dichotomy to be a red herring—an apparently legitimate set of facts with surface relevance that unintentionally divert attention from the central issue, which is simply: Is Julian Steward correct that piñon pine "is the single most important food species where it occurs" (1938: 27)?

The lessons and practices of modern forest ecologists and the competing avian and mammalian taxa who harvest piñon to survive are vastly more relevant to understanding the Great Basin human past than the overblown green-cone/brown-cone distinction. I have problems framing piñon procurement into such evolutionary, sequential, dichotomous, normative, essentialist, either-or categories[33] and fully agree with Simms that piñon procurement is best seen as a "harvest cycle…with return rates and productivity per unit area [varying] through the cycle…pine nuts are not only highly ranked, but as the cycle unfolds, they can be harvested through a variety of techniques that effectively lengthens the harvest season…and increases the ability to accumulate a large quantity of nuts as well as obtain a high [return] rate" (1987: 124).[34] So viewed, piñon maturation is a process, not an abrupt transition from green to brown and, contrary to the macroevolutionary abstraction, so-called evolution of intensive green-cone harvesting

[32] Chapters 14 and 15 detail the relevance of resilience to the Intermountain West.

[33] Simms et al. (2013: 183) warned of the "remarkably persistent" tendency for archaeologists to cast the past in normative terms: "optimal foraging theory and costly signaling theory are not essentialist categories that characterize even the behavior of a single individual, let alone an entire group, culture, or period. This was a flaw of the traveler-processor model" (Bettinger and Baumhoff, 1982).

[34] David Rhode (personal commun., 2021) adds that "from my own fitful experience, I've always wondered how anyone could get decent returns from brown cone collection at all (apart from using mats as Steward reported, or from extraordinary circumstances like Simms's windstorm). Whenever I've visited pine nut groves in the brown cone stage, I've been late to the party and all the other critters beat me to the buffet. The only decent crops I ever got were in the late green cone stage."

does not necessarily result in a maximum yield relative to the brown-cone strategy.

Despite variable duration, technology, rates of caloric return for the specifics of harvesting pine nuts, I think that practices analogous to corvid piñon procurement have persisted from the arrival of *P. monophylla* in the central Great Basin 6000 years ago. In years of locally abundant piñon crops, why bother piling up green nut caches because "when a good crop occurs, it is far more abundant than the local population can harvest" (Steward, 1938: 27)? And in locally lean years, I suspect that human Great Basin harvesters have always known exactly how to pull out the all the stops, moving to better places and procuring piñon any way they could.

Green-cone procurement was not an esoteric evolutionary breakthrough. Great Basin foragers were ecologists of the highest magnitude, and they knew what the competing corvids know, making it their (survival) business to understand the nuances and variability of their staple resources. Is it conceivable that humans took several millennia to figure out midseason piñon harvesting strategies and remained oblivious to the simple ways of enhancing pine nut harvests during the early and late seasons? I don't think so.

## OPERATIONALLY DEFINING PIÑON ECOTONE VILLAGE ARCHAEOLOGY

Granting the multiple complexities and options involved in smart piñon procurement strategies, how can these be translated in our observations of the archaeological record?

Great Basin archaeologists typically classify habitation sites within the piñon-juniper woodland as piñon settlements, piñon camps and so forth—all characterized by flaked stone tools and debris, milling gear, stone circles, and often pottery (e.g., Bettinger, 1975, 1976b, 1989; Madsen, 1986: 31–32; Simms, 1989: 17–18; Delacorte, 1990; Basgall and Giambastiani, 1995; Reynolds, 1996; Hildebrandt and Ruby, 2006). In general, archaeologists tend to interpret one or more large rock ring features in the piñon-juniper woodland as house foundations for fall and/or winter dwellings. Small circular groupings of stones lacking internal living space are typically thought to be remnants of pinecone-processing features or caches. The presence of millingstones and handstones in the piñon-juniper zone are often seen as representing pine nut processing in which roasted piñon nuts were hulled, ground into flour, and cooked.

Numerous difficulties arise from the vague arguments and assumptions linking the behavioral and archaeological correlates of piñon procurement. The following sections explore these issues, from the functions of rock rings to the geographic distribution of millingstones, and detail the implications of the false evolutionary sequence from brown-cone to green-cone strategies.

### What's Up with Rock Rings?

Although most archaeologists agree that the presence of stone circles within the piñon-juniper woodland is somehow related to piñon procurement, we have long struggled with operationally distinguishing between domestic house foundations and rock-encircled storage features (e.g., Bettinger, 1975; Thomas and Bettinger, 1976; Thomas, 1988, 2020: 411–415, 820–830). These simple stone circles define a functional continuum from rough-and-ready features intended for hunting disguise to well-constructed house foundations, often with doorways, designed to hold a nonstone superstructure in place.

Hunting blinds tend to be relatively crude constructions made with raw materials close at hand, often defining the "nest like stone enclosures" observed by John Muir (1894: 320–322). These blinds were designed for temporary concealment of hunters and often show a distinctive outward orientation. Although many such blinds are circular, they lack well-defined doorways and were intended to blend imperceptibly into the natural setting, with little attention paid to the interior of these features. Rock blinds tend to be

smaller in diameter and relatively taller than typical house foundations.

House foundations reflect an inherently inward-looking orientation because their primary function is to improve local living space, especially with respect to storage, warmth, and shelter. Summertime houses at Alta Toquima usually have east-facing doorways toward the summer solstice sunrise and houses in the piñon-juniper woodland of Monitor Valley usually have entryways facing further south, toward the wintertime solstice (Thomas, 1988: fig. 214; 2020: fig. 28.13).

Rock rings built for processing piñon nuts sometimes resemble house foundations, but smaller. Pine nut storage features are usually positioned within the modern mature piñon forest, often situated near bedrock to discourage rodent incursions. Various methods of storing pine nuts have been documented in which the nuts or cones are piled within a circle of stones, then covered with branches and earth (Coville, 1892: 353; Steward, 1933, 1941: 209–259; Shutler, 1956; Davis, 1965: 12; Lanner, 1981; Madsen, 1986: 31–32; Simms, 1989: 17–18). Hoffman (1878: 473) recorded the pine nut caches between Eureka and Belmont (NV) as stone circles 2–4 ft in diameter and felt that "birds and animals got into caches more often than did their owners."[35]

We found 11 stone rings during the randomized Reese River survey, each made of small boulders with the circles ranging from 2 to 4 m in diameter (Thomas, 1971a: 149–150). In the follow-up piñon ecotone survey in the lower Toiyabe Range, we mapped 32 more stone rings that ranged from 2.0 to 6.0 m in diameter (Williams et al., 1973; Hatoff and Thomas, 1976; Thomas et al., 1976). Bettinger (1976b) excavated one of these, a Western Shoshone house with a terminal occupation dating A.D. 1880–1890. I think that nearly all the Reese River rock rings were domestic house foundations, but Wells (1983) and Giambastiani (2007) suggest instead that most were more likely built for piñon cone storage.

Bettinger's randomized Owens Valley survey recorded 128 circular floors, most of them stone encircled, ranging 1–12 m in diameter (1975: 145–147). He interpreted some as summer dwellings and others as winter houses, with the smaller stone rings likely functioning as piñon nut caches—but he did not attempt to distinguish them because of the obvious ambiguities (1975: 145–146).

Delacorte (1990: 85–89) grappled with the same issue for the 37 rock rings recorded in his Deep Springs Valley survey, where maximum diameter averaged ~4 m and ranged from 1.1 to 9.0 m (1990: 85, table 4.3). Delacorte concluded that they served a variety of functions, some as foundations for wood or brush domestic structures (after Steward, 1933: 263–266; 1941: 209–259), others as caches (Steward, 1933: 242; 1941: 209–259) or features for processing pinecones (Bettinger, 1989). Delacorte emphasized that some of the rock-ringed features probably served multiple functions through time, constructed initially as domestic structures, then later reused as roasting facilities. Whereas a feature's size or location might preclude some functions—extremely small rings could not possibly have served as a house foundation (Bettinger, 1975: 145–146; Delacorte, 1990: 85)—Delacorte suggested that excavation was required to define specific function(s).

Difficulties like these led Vierra (1986: 118) to create an index to separate domestic from storage features based on the configuration of the encircling stone circle. In ethnographic examples, the stored nuts and cones were retrieved first by removing the rocks piled on top of the cache, throwing or rolling them outward, then taking away the branches and piled up earth to reach the stored nuts. Vierra reasoned that piñon storage features should have a definable archaeological signature based on a relatively sharply defined inner ring surrounded by a more random scattering of rocks around the perimeter and he postulated that the ratio of inner-to-outer

[35] As argued above, I see Great Basin foragers as having been excellent ecologists, and it seems likely that they found a better way of storing pine nuts (as for instance the cache in a cliff wall on the west side of Monitor Valley, capable of holding eight bushels and still sealed with pine pitch; Shutler, 1956).

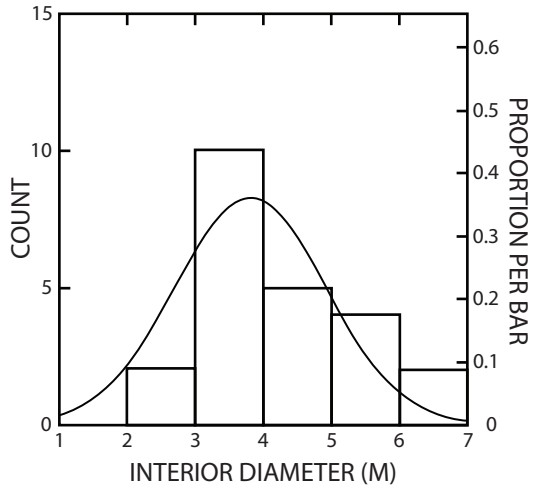


FIG. 12.1. Inside diameters for 23 of the stone rings recorded in the piñon ecotone survey of the Toiyabe Range (Thomas and Bettinger, 1976).

stone ring diameters could help define stone ring function (1986; see also Simms, 1989: 17–18).

As a test case, Vierra began by intuitively classified 130 stone rings from Pahute and Rainier mesas (Nevada Test Site) as piñon caches, roasting ovens, hunting blinds, or rocks surrounding habitation structures. He thought these stone circles defined a bimodal distribution, with domestic structures built with narrow rock rings and storage facilities exhibiting a more diffuse circular rock scatter (1986: 118).[36] Comparing interior-exterior diameters in this sample, Vierra proposed a 0.5 ratio cut-off point to distinguish the thicker walls of piñon nut storage facilities from the more tightly engineered stone circles anchoring domestic residential structures. When Simms (1989: 18) applied this distinction to stone rings within the catchment of the Bustos site, he concluded that seven (with interior diameters ranging from 2.1 to 3.4 m) were pine nut storage caches and suggested that Vierra's dichotomy of interior-exterior ratios "may serve as a rule of thumb in archaeological reconnaissance, useful for differentiating between pine nut storage rings and houses rings" (1986: 18).

While applauding any operational criterion capable of separating domestic houses from cache features, I am skeptical of Vierra's results and did a small test of my own. Table 12.3 compares the interior diameters of 78 stone circles from the Reese River, Monitor, and Owens Valley surveys. 1t plots the interior diameter for the stone circles recorded in the piñon ecotone survey (mean interior diameter of 3.81 m). These hardly define a bimodal distribution and applying Vierra's criteria to this sample, table 12.3 compares the interior ratios.[37] After detailed excavations at Alta Toquima, Pinyon Houses, Two Eagles, and Crater Middens, Bettinger and I unequivocally concluded that these stone circles—excavated or not—represent deliberate and intact structural features engineered as part of domestic house construction (Bettinger, 1989: 42, 114, 178, tables 2.1, 5.2; Thomas, 2020: 69–142).

These results fail to support Vierra's hypothesis. The interior-exterior ratios of these known domestic dwellings range from 0.204 to 0.791 m and do not distribute in bimodal fashion (fig. 12.2). At each site, the mean interior-exterior ratio exceeded the 0.5 cut off point and led to the false conclusion that many of these known domestic houses served instead as rock-lined storage features.[38]

[36] Noting Vierra sampled only a portion of Pahute and Rainier mesas rock rings, Pippin (1998: 84) was skeptical: "Although his distinction between roasting ovens and pinyon caches may be valid, the hunting blind and habitational structure categories are questionable. Most, if not all, of the features in these classifications are probably rock caches in various states of decay." Pippin based this conclusion on three factors: (1) earlier features would have provided a low-cost supply of rocks for building later ones, (2) more than 75% of the features were built on bedrock exposures or substrates with only a thin mantel of sediment and (3) "their almost perfect (>99%) association with pinyon trees."

[37] Exterior stone ring measurements were not taken during the piñon ecotone survey (Thomas et al., 1976).

[38] These findings call into question Simms' (1989: 18) conclusion regarding the seven rock rings in the Bustos catchment facilities in the White Pine Range. Simms excavated half of one ring (26WP1745, fig. 6) exposing a lining of closely spaced angular stones across the ring, with macrofossil samples containing some immature pine nut hulls and a cone fragment from within the ring showing some signs of heating, leading him to conclude this was a piñon storage feature. While this

TABLE 12.3

**Comparison of House Sizes from Reese River, Monitor Valley, and Owens Valley**

| Site | Interior Diameter | | | | Reference |
|---|---|---|---|---|---|
| | Range | Mean | Standard Deviation | Sample Size | |
| Reese River Piñon Ecotone Survey | 2.0–6.0 | 3.81 | 1.108 | 23 | Thomas and Bettinger, 1976 |
| Alta Toquima | 2.2–3.8 | 3.105 | 0.478 | 27 | Thomas, 2020: 91–137, table 3.3 |
| Pinyon House | 2.1–3.7 | 2.760 | 0.416 | 5 | Bettinger, 1989: 28–47 |
| Two Eagles | 1.0–3.9 | 2.490 | 0.635 | 10 | Bettinger, 1989: 115–126 |
| Crater Middens | 2.0–3.0 | 2.677 | 0.533 | 13 | Bettinger, 1989: 178–196 |

Sometime back, Bettinger (1975: 145–146) optimistically projected that "future investigations of [rock ring] features will probably disclose characteristics by which each structure could be distinguished" and he wisely concluded that "clear-cut differences were not observed in the field [so] a detailed analysis was not attempted." Nearly a half-century later, Great Basin archaeologists are no closer to defining these baseline distinctions without detailed excavations.

## Absence of Grinding Stones: An Absence of Grinding?

Archaeologists generally regard millingstones and handstones recorded in the piñon-juniper woodland as likely related to pine nut processing of some kind, but readily acknowledge that they could have been used for many other functions as well, and their curious distribution across the Great Basin clouds their value as piñon-processing diagnostics.[39]

A Millingstone Enigma: I was puzzled by the results emerging from my randomized regional sampling of the Reese River Valley, where only a handful of millingstones could be documented among the 2500 finished artifacts we encountered: "Considering that grinding stones have been considered as one the 'twin hallmarks' of the Desert Culture (Jennings, 1957: 7), relatively few (34) such specimens were recovered in the Reese River fieldwork; the Danger Cave excavation yielded more than 1000 grinding stones" (Thomas, 1971a: 146). The puzzle became complicated when McGuire and Garfinkel (1976: table 1) noted that although grinding stones seem pretty scarce at Reese River, they are ubiquitous in Owens Valley (Bettinger, 1975, 1976a) and elsewhere in the piñon-juniper woodlands—hardly in keeping with the piñon ecotone hypothesis promoting piñon as the staple Great Basin resource whenever and wherever it occurs (Williams et al., 1973; Thomas, 1973; Thomas et al., 1976).

A Rock Ring Enigma: Bettinger (1999) and Zeanah (2002) compounded the millingstone enigma when they compared regional distributions and frequencies of grinding stones and rock ring features:

- If the foraging communities of the Reese River and Owens valleys relied heavily on prehistoric piñon procurement (as Stew-

conclusion seems correct and the results do show it was used for storage, the interior-exterior ratio is 0.6, exceeding the 0.5 cutoff point and clouding the Vierra criteria as applied to the other unexcavated stone rings at Bustos and elsewhere (Simms, 1989: table 3).

[39] Current efforts toward analyzing starch from piñon and other plants hold great promise for assigning specific functions to individual ground stone artifacts (Rhode and Richey, 2020; see relevant unpublished paper by Louderback et al., 2021), but the problems are far from resolved. The 2021 paper, presented by L.A. Louderback, T. Townsend, and D.T. Giambastiani, was titled "Bedrock milling features and ground stone artifacts yield pinyon starch in west-central Lincoln County, Nevada, USA." It was presented at the Great Basin Anthropological Conference in Las Vegas, Nevada.

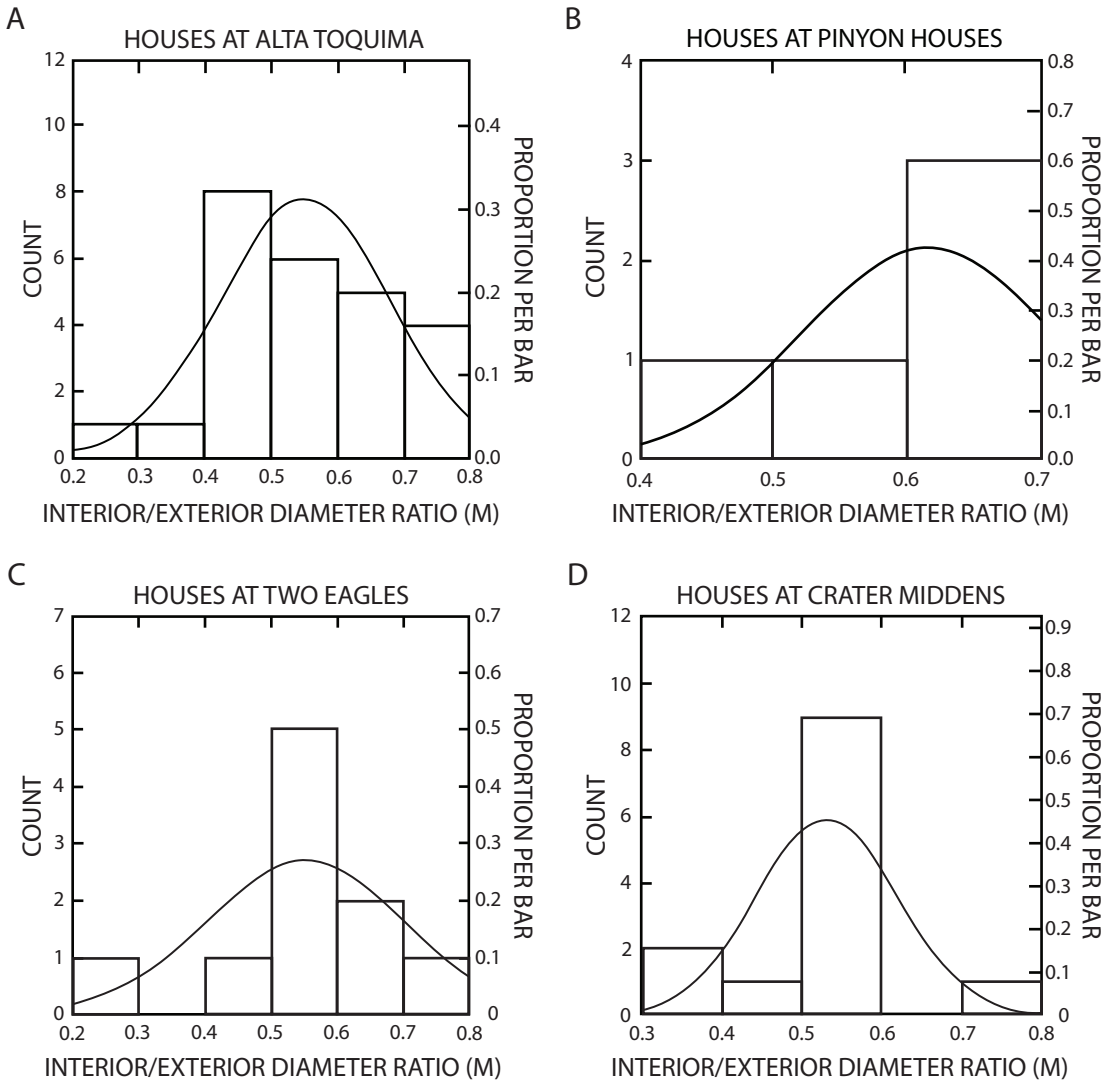


FIG. 12.2. Ratio of interior to exterior house diameters from: **A.** Alta Toquima (mean = 0.128), **B.** Pinyon House (mean = 0.617), **C.** Two Eagles (mean = 0.552), and **D.** Crater Middens (mean = 0.531). Dimensions extracted from Thomas et al., 1976, and Bettinger, 1989; see also table 12.4.

ard had documented for the ethnohistoric period), and

- if millingstones and rock rings are diagnostic of piñon procurement, then
- why does the central Great Basin have "an order of magnitude" fewer rock rings than in Owens Valley, with differences in millingstone frequencies "nearly as large?" (Bettinger, 1999: 65).

Several others have noted the same disparity (including Simms, 1985b: 169; Madsen, 1986; Delacorte, 1990; Delacorte et al., 1992; Bettinger, 1999: 64–65; Kelly, 2001; Giambastiani et al., 2012; see relevant unpublished paper by Lechner et al. [fn. 3]).

I have variously tried to rationalize these disparities by exploring a few obvious practices that seemed relevant, including the historic-

TABLE 12.4

**Comparison of Interior-Exterior Ratio of Houses Excavated in Monitor Valley and Owens Valley**

| Site | Interior-Exterior Ratio | | | | Reference |
|---|---|---|---|---|---|
| | Range | Mean | Standard Deviation | Sample Size | |
| Alta Toquima | 0.250–0.791 | 0.551 | 0.128 | 25 | Thomas, 2020: 91–137, table 3.3 |
| Pinyon House | 0.476–0.696 | 0.617 | 0.094 | 5 | Bettinger, 1989: 28–47 |
| Two Eagles | 0.204–0.773 | 0.552 | 0.147 | 10 | Bettinger, 1989: 115–126 |
| Crater Middens | 0.385–0.70 | 0.531 | 0.087 | 13 | Bettinger, 1989: 178–196 |

period rock robbing at Mateo's Ridge (Hatoff and Thomas, 1976) and avocational artifact collecting. Simms (1983) discussed significant ancient scavenging and reuse of milling equipment across the Intermountain West and argued that it contributed to the relative abundance of grinding stones in Late Prehistoric sites of the eastern Great Basin (see also Thomas, 1971a: 175).

I thought perhaps this disparity arose from a recovery bias because relatively few millingstones are preserved on surface sites in the central Great Basin. After all, we excavated more than 100 grinding stones at Gatecliff Shelter (Kramer and Thomas, 1983) and another 100 from Alta Toquima (Thomas, 2020: 323–233). So millingstones are certainly not rare everywhere in the central Great Basin, they just seem to be conspicuously rare at the surface sites we surveyed. And while I thought the numbers of excavated millingstones at Gatecliff and Alta Toquima were impressive, I also remembered that Bettinger's excavation of three residential sites in Owens Valley (at Pinyon House, Two Eagles, and Crater Middens) produced more than three times the Monitor Valley number.

Gatecliff Shelter frequencies might be inflated because ground stone fabrication became a significant onsite activity on Horizon 9 (1910–1710 cal B.C.) where multiple millingstones were fashioned onsite from locally available welded tuff, limestone, and quartzite. Although some millingstones were heavily worn, others showed only minimal surface preparation (Kramer and Thomas, 1983: table 58). It looked like many more millingstones were manufactured at Gatecliff and not necessarily employed in onsite food processing. Many were made of nonlocal sandstone and, in one case, a millingstone blank weighing more than 75 pounds was carried to Gatecliff from 10 mi away (Thomas, 1983b: 476)—suggesting considerable investment and curation of nonlocal toolstone.

Central-place foraging theory suggests that the scarcity of milling equipment in many parts of the piñon-juniper woodlands may reflect decisions about whether to reside near the piñon harvest or transport piñon and live elsewhere. If so, this might help explain the differential distribution of milling equipment and rock rings across a landscape but would not explain their regional absence or abundance. And if tool curation, scavenging, and site looting variously depressed millingstone and rock ring abundance in the piñon-juniper woodland of central Nevada, why wouldn't similar processes impact comparable abundances elsewhere in the Intermountain West?

There is no question that millingstones and stone rings are vastly more abundant in Owens Valley and elsewhere in the western Great Basin than the Central Mountains Archaic—and this disparity remains difficult to explain.

## Differential Piñon Woodland Density

Zeanah (2002: 242–247) attacked the millingstone and rock ring enigmas from another

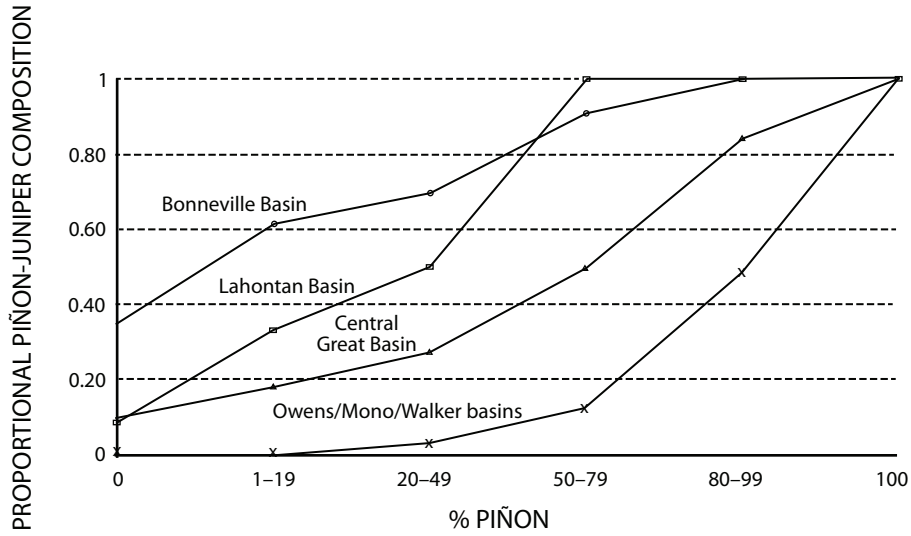


FIG. 12.3. Percent piñon in the woodlands of four Great Basin regions (after West et al., 1998, and Zeanah, 2002: fig. 8.6).

angle by wondering whether perhaps the regional-level disparities might be reflecting variable piñon productivity. West et al. (1998) found that piñon pine densities across 66 randomly selected Great Basin mountain ranges varied considerably with respect to aspect, elevation, and especially an east-west gradient—with richer piñon stands in the western and central Great Basin than elsewhere (see also Beeson, 1972; Koniak, 1986; Zeanah, 2002: 243–247). Addressing the obvious relevance to the piñon ecotone hypotheses and regional strategies of piñon procurement, Zeanah hypothesized that the proportion of modern piñon trees is highly correlated to the productivity of the associated piñon harvests (2002: 244–246, fig. 8.8).

Figure 12.3 plots modern piñon tree densities within the four most relevant segments of the Great Basin (after West et al., 1998; Zeanah, 2002: table 8.3), ranking piñon pine proportions on a scale from 1 (100% piñon density) to the lowest piñon density scaled at 8 (100% juniper density). The far western segment (including the Owens, Mono, and Walker basins) host the purest (most dense) stands of modern piñon trees in the Intermountain West. Piñon tree density in the central Great Basin drops off considerably and juniper trees dominate the piñon-juniper woodlands of the Lahontan and Bonneville basins.

Millingstone Densities: Figures 12.4 and table 12.5 expand Zeanah's previous analyses (2002: table 8.2) to provide a yardstick for comparing absolute densities of archaeological ground stone distributions recorded in a dozen archaeological surveys across the Great Basin. The highest densities of archaeological millingstones cluster in places with the highest piñon densities, particularly the Coso Range (Hildebrandt and Ruby, 1999, 2006), Slinkard Valley (Sierra Nevada Range to the southwest of Topaz Lake; Giambastiani, 2007), Owens Valley (Bettinger, 1976a, 1977), Deep Springs Valley (Delacorte, 1990), and the Wassuk-Pine Grove catchments near Walker Lake (Rhode, 1987).

Figure 12.5 also documents the correlated drop-off between piñon density and archaeological millingstones in the central Great Basin uplands of the Reese River Valley (Thomas, 1971a; Thomas and Bettinger, 1976), Grass Val-

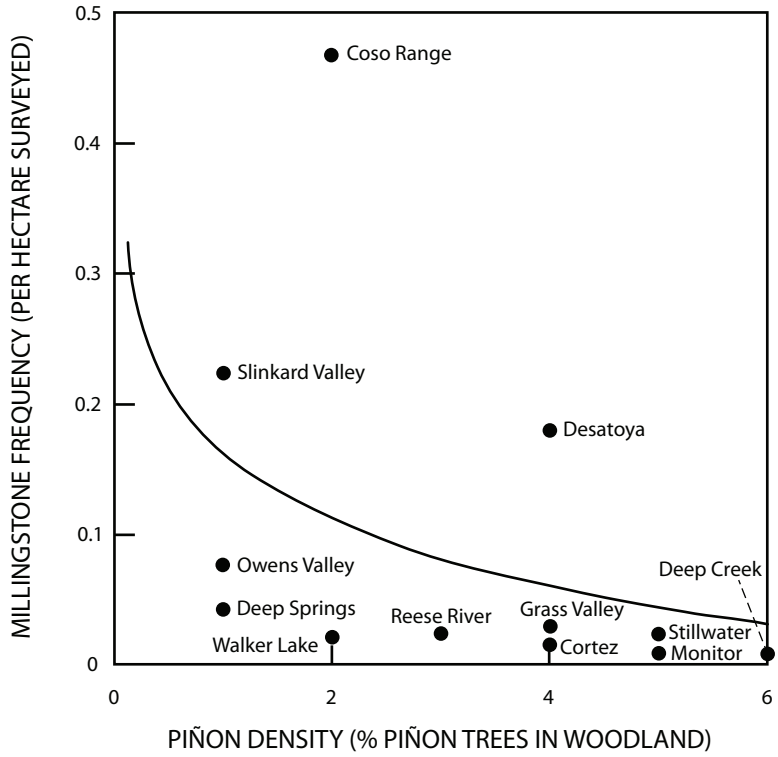


FIG. 12.4. Frequency of ground stones (per hectare surveyed) plotted against piñon density rankings, with 1 equal to 100% piñon and 6 equal to 100% juniper (modified from Zeanah, 2002, table 8.2).

ley (Wells, 1983), Cortez (Delacorte et al., 1992) and Monitor Valley (Thomas, 1988).[40] The Desatoya Range (Dalton Canyon) generated an anomalously high density of millingstones, many associated with Elko points (unpublished paper by Lechner et al., 2009: 183–187 [fn. 3]).[41] The lowest-ranking peripheral zones of piñon density in the Stillwater Range (Kelly, 2001) have correspondingly low millingstone densities.

[40] Giambastiani et al. recorded 450 millingstones in their archaeological survey of the northern Monitor Range. They note the ad hoc quality of these millingstones that, "for the most part, were derived from local deposits of raw material, were used for short periods of time, and quickly replaced when fractured" (2012: 112–113). This report does not provide sufficient provenience information to assign the proportion of millingstones coming from the piñon-juniper woodland.

[41] Lechner and Giambastiani (2009: 183) recognize the likelihood of brown-cone piñon procurement, but "question the de facto association between campsites and the intensive use of pinyon."

Rock Ring Densities: Figure 12.5 defines a parallel trend by correlating rock ring frequencies with piñon density rankings across the Great Basin. Those mountain ranges with the highest densities of piñon pine also have the highest recorded number of rock rings (especially in the White Mountains, the Coso Range, Slinkard Valley in the Sierra Nevada, and Walker Lake uplands). Intermediate piñon densities in the Toiyabe and Shoshone ranges correlate with rock ring densities in the Reese River Valley, Desatoya Range, Grass Valley, Cortez, Monitor Valley, and the Stillwater Range.

This expanded database strongly supports Zeanah's (2002: 247) previous conclusion:

> Consistent with expectations based on central place foraging models, pinyon productivity accounts for ground stone tool densities in pinyon-juniper wood-

TABLE 12.5

**Comparing Archaeological Survey Results and Piñon Pine Forest Densities with Great Basin Artifacts**
Piñon density rankings after West et al., 1998; see also Zeanah, 2002: fig. 8.6, table 8.3.

| Archaeological Survey | Adjacent Mt. Range | Relative Rank | Area Surveyed (ha) | Rock Ring Features | Rock Rings/ ha | Milling-stones | Milling-stones/ ha | References |
|---|---|---|---|---|---|---|---|---|
| Owens Valley | Inyo-White Mountains | 1 | 775 | 86 | 0.110 | 60 | 0.077 | Bettinger, 1976a, 1977 |
| Deep Springs | White Mountains | 1 | 750 | 36 | 0.048 | 32 | 0.043 | Delacorte, 1990 |
| Slinkard Valley | Sierra Nevada | [1] | 441 | 35 | 0.079 | 99 | 0.224 | D. Giambastiani, 2007 |
| Coso | Coso Range | [2] | 753 | 90 | 0.120 | 347 | 0.467 | Hildebrandt and Ruby, 2006 |
| Walker Lake | Wassuk Range | 2 | 192 | 91 | 0.473 | 4 | 0.021 | Rhode, 1990 |
| Reese River | Pine Grove Hills Toiyabe Range Shoshone Mountains | 3 | 1000 | 31 | 0.031 | 24 | 0.024 | Thomas, 1973; Thomas and Bettinger, 1976 |
| Grass Valley | Toiyabe Range Simpson Park Mountains | 4 | 1000 | 4 | 0.004 | 29 | 0.029 | Wells, 1983 |
| Dalton Canyon | Desatoya Range | [4] | 610 | 8 | 0.013 | 109 | 0.179 | Lechner and Giambastiani[1] |
| Cortez | Cortez Mountains | [4] | 1152 | 2 | 0.002 | 18 [23] | 0.015 [0.020] | Delacorte et al., 1992 |
| Monitor Valley | Toquima Range/ Monitor Range | 5 | 4775 | 7 | 0.002 | 36 | 0.008 | Thomas, 1988 |
| Stillwater | Stillwater Range | [5] | 968 | 0 | 0.0 | 22 | 0.023 | Kelly, 2001 |
| Toana Draw | Toana Range/ Pequot Mountains | 6 | 1984 | – | – | 24 | 0.008 | Zeanah, 2002: table 8.2 |
| Deep Creek | Deep Creek Mountains | 6 | 448 | – | – | 3 | 0.007 | Zeanah, 2002: table 8.2 |

[1] The 2009 paper by T.M. Lechner and M.A. Giambastiani is titled "The archaeology of a pinyon zone in the Desatoya Mountains, Lander County, Nevada." It was presented at the 38th Annual Meeting of the Nevada Archaeological Association in Lovelock, Nevada.

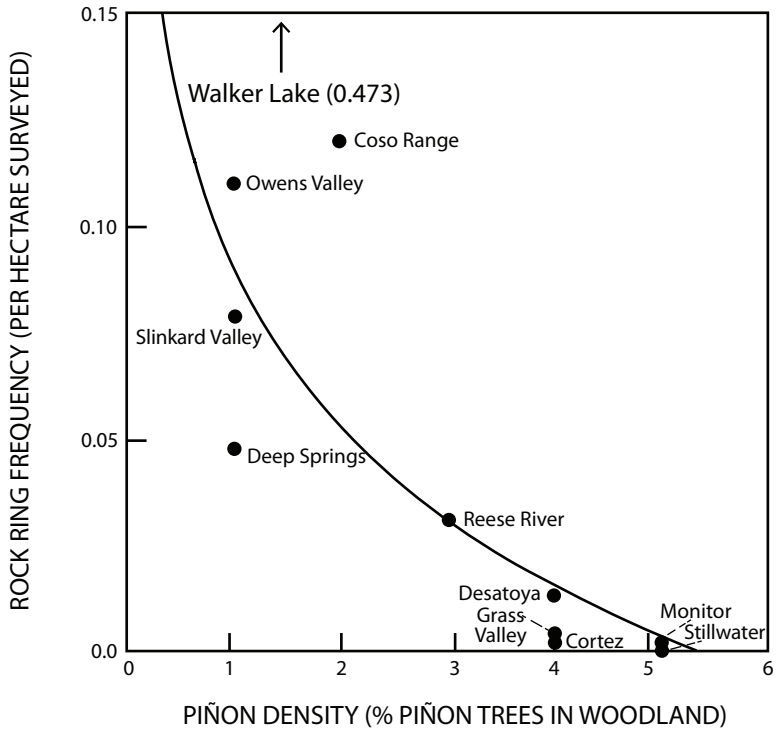


FIG. 12.5. Frequency of stone rings (per hectare surveyed) plotted against piñon density rankings, with 1 equal to 100% piñon and 6 equal to 0% piñon (modified from Zeanah, 2002, table 8.2).

lands better than the span of pinyon availability or the antiquity of pinyon procurement.

Although these updated archaeological results also extend Zeanah's conclusion to include rock ring feature densities, they fail to explain the processes behind the enigmas themselves.

Archaeologists have long taken millingstones and rock rings as a reflection of past piñon procurement, but nobody has satisfactorily explained the radically different frequencies and distributions between the central and western Great Basin—both known to be prime piñon procurement areas in the past.

## Another Red Herring?

I see the brown cone/green cone hypothesis as a bogus issue. The evolutionary progression from brown cone to green cone harvesting simply does not hold up. Like corvids and modern forestry nurseries foragers employed both strategies over the few weeks the ripened seeds were available. And even if accepted, the brown cone/green cone sequence fails to account for the different temporal dynamics of pine nut use in different regions of the basin. And on top of that, we cannot come close to operationally defining the outcomes of brown cone/green cone strategies in the archaeological record. The same is true in trying to distinguish objectively between stone circles built as residential foundations from those constructed as piñon storage or processing facilities.

Granted, distinguishing houses from storage is an important consideration when attempting to identify winter villages, but is it necessary to tell houses from storage rings to identify piñon procurement? Maybe the occurrence of stone rings within the piñon-juniper woodland is

enough of a guide (though their absence certainly would not preclude past piñon use).

So perhaps (like the questionable brown-cone/green-cone evolutionary sequence), the storage-dwelling distinction is another red herring—an abstraction that detracts from more serious, open-minded considerations of piñon procurement through time and space. In the next section, Constance Millar and I frame a forest ecology hypothesis of significant regional differences in piñon cone and seed morphology, competitive seed predation, interannual cone production and masting, fire regimes and climatic factors within the basin—with significant implications for piñon procurement strategies in Owens and Monitor valleys that might explain why piñon cone-processing rings are vastly more common in the western Great Basin.

## A FOREST ECOLOGY-BASED PIÑON PROCUREMENT HYPOTHESIS

### Constance I. Millar and David Hurst Thomas[42]

So far, this chapter has attempted to test conflicting piñon-procurement hypotheses with equivocal results. The piñon ecotone hypothesis holds that piñon pine became a staple resource ~5000 cal B.C., shortly after its arrival in the central and eastern Great Basin. Over the next millennia, piñon procurement spread throughout the expanding range of piñon pine using techniques documented ethnographically (Coville, 1892; Dutcher, 1893; Chamberlin, 1911: 69; Steward, 1933: 241–242).

The alternative hypothesis from the macroevolutionary perspectives sees early piñon procurement as a relatively low-level subsistence activity restricted to ripe (brown) cones. Sometime after ~cal A.D. 600, communities in the Inyo-Mono region first discovered high-cost methods for harvesting, storing, and processing unripe (green) pine nuts. Roughly cal A.D. 1300, these Numic-speaking processors employed their unique, intensified, green-cone piñon procurement to outcompete brown-cone harvesting by pre-Numic travelers and spread throughout the rest of Great Basin (Bettinger, 1999: 65; 2015).

Beyond distractions from the false brown-cone/green-cone evolutionary sequence, testing these competing hypotheses is complicated by multiple midrange theoretical issues, making it difficult to link piñon-procurement behaviors directly to archaeological diagnostics. This is because piñon harvesting has routinely been defined in the archaeological record by the presence of millingstones and rock rings within the contemporary piñon-juniper woodland (Bettinger, 1976a; Delacorte, 1990).[43] Hildebrandt and Ruby (2006) urged archaeologists to drop millingstones as an archaeological signature because these utilitarian artifacts were used for multiple purposes (see also Basgall and Giambastiani, 1995), leaving rock rings as the stand-alone defining criterion. Subsequent attempts to distinguish stone circles used for house foundations from those employed for piñon afterripening or as cone/nut caches have failed (fig. 12.2, table 12.3).

Compounding the problem is the fact that rock ring (and millingstone) frequencies vary significantly across the Intermountain West, with the enigmatic upshot that rock rings are notably underrepresented in the central Great Basin—exactly where the resilience hypothesis projects they should be most abundant. This disparity cannot be explained by tool curation, recovery bias (surface/buried), stone robbing, avocational collecting, or prehistoric recycling.[44]

Because of these uncertainties clouding ancient piñon procurement, we will explore what modern forestry practices can teach us about how piñon

[42] We thank David Charlet, Don Grayson, Dave Rhode, and Robert Westfall for their thoughtful reviews of this section; see also Thomas and Millar (2023, 2024).

[43] Issues also arise when contemporary treelines are projected into to the past; Reynolds (1996, 1997) may have been successful in doing so within the Inyo Range, but few others have made the attempt.

[44] Also curious is that rock ring (and millingstone) densities correlate closely with tree densities in the modern piñon-juniper woodland (fig. 12.3) defining an east-west gradient with far richer piñon stands in the western Great Basin than elsewhere (Zeanah, 2002: 244–246).

nuts are collected and stored. We also consider aspects of piñon woodland ecology to ask whether anthropologists may have overlooked an unsuspected degree of variability that could have significantly impacted human foraging practices.

## Modern Forestry Perspectives on Piñon Harvesting

Professional practices provide insight into the details and challenges of piñon procurement. Both the United States Forest Service (USFS) and the British Columbia Tree Seed Centre (BCTSC), as well as state and local agencies and private forestry companies, need large quantities of conifer seeds from diverse pine species to provide seedlings for reforestation (Hamrick et al., 1979; Edwards, 1980; Kolotelo, 2006; Karrfalt, 2008). These agencies employ a standardized sequence of steps in collecting conifer seeds, practices that require considerable knowledge about cone and seed biology for the species and geographic region of application.

Differences in seed yield result from multiple factors relating to species, cone size, reproductive success of the current cone crop, timing of collection, and postcollection cone handling. Cones obtained from natural stands and seed orchards require monitoring and precollection evaluation of potential crop size, threats from cone and seed predators, and cone-seed maturity. It is necessary to match collection timing with full-seed maturity without losing seed to natural dispersal, predation, or decay. Sampling accelerates as cones and seeds approach full maturity (August to September for most conifer species; Edwards, 1980).

Such seed-collection programs must also consider the well-known, year-to-year variability in cone productivity that characterizes conifer species. Near-ripe cones can be collected in a good cone-crop year without added attention because the seeds can be rapidly dried and simply shaken out. When pressing research or conservation concerns dictate that seeds be obtained regardless of the crop size or condition in a particular year, more labor-intensive methods are required, especially in light-cone years, to collect adequate cones before natural predators consume or remove them. In extreme cases, the ripening cones are bagged midsummer on the tree in wire cages to allow ripening in situ. Alternatively, unripe cones can be collected and afterripened. This procedure requires considerable experience and timing because the cones must be nearly mature (within about three weeks of full maturity, depending on species), then ripened under appropriate species-specific conditions (generally dark and cool, but sometimes moist and warm, followed by drying). If the timing is misjudged, and/or afterripening is done incorrectly, the cones remain closed (case-hardened), and the seeds will never ripen.

A recent example comes from a research project in which one of us (Millar) has been involved that regards sequencing the genome of Great Basin bristlecone pine (https://whitebarkfound.org/our-work/genome-projects/bristlecone-pine-genome-project/). Logistically, only a single year was available to collect cones from a White Mountains (CA) population and to obtain the few seeds needed to sequence the genome. The seed crop that year was meager. Grant-funding obligations required that a very old-aged tree be sequenced; land-managing agency permissions restricted access to certain trees, no protection bags could be installed, and no ladders used. To obtain a few viable seeds from the one tree selected for this high-profile research, Millar surveyed developing conelets in trees early in spring and frequently through summer to find trees with accessible cones and select a specific tree. She monitored seed predators over the course of the season and cautiously harvested young unripe cones in mid to late summer to test maturity (leaving a few accessible cones in case the harvested cones were case hardened). The early cones sampled were, in fact, case hardened and useless; even a few of the more mature-appearing cones did not have ripe seeds. Finally, the last cone collected (before cone predators would have gotten

it and low enough to reach from the ground) was successfully afterripened and produced a few viable seeds that became the DNA material for sequencing. This example illustrates the challenge that can exist to obtain even a few viable seeds using low-technology methods.

Postcollection handling (including temporary storage, monitoring, and transport of cones) also requires serious attention to assure high-quality seeds. Freshly picked cones are quite moist, and this moisture must be removed gradually to mimic the natural maturation process and to prevent the cones from overheating (with ensuing fungal decomposition) and/or case hardening. Collecting immature cones or picking them during wet weather compounds the moisture problems. To promote uniform drying, seed collection facilities usually field-store cones for about one month to reduce moisture content before the seeds are extracted. Air movement is more effective than drying by light or heat, so the cone sacks are typically stacked in shelters and exposed to free-circulating cool air to gradually remove moisture; alternatively, cones are laid in a single layer on screens or wire boxes and free-circulating air dries them (Karrfalt, 2008). These sacks cannot be stored in direct sunlight because overheating can damage cones, but they cannot remain wet for extensive periods because that encourages growth and spread of fungi. For piñon, if mature cones are collected, the air-drying time may be as short as one week or considerably longer, depending on the cone thickness and ripeness (Krugman and Jenkinson, 1974).

An initial random sample of cones is then evaluated for basic morphological features, degree of insect or pest activity, estimates of seed yield through half-cone counts (cones are cut vertically and inspected for the presence of mature seeds), and internal seed condition through cutting tests (seeds are cut in half and inspected for viability; Kolotelo, 2006: fig. 2). Cones are kiln-processed in a controlled, warm, dry environment to flex the cone scales, which allows seeds to be extracted by tumbling. Empty seeds are culled, and seed moisture is further reduced to prepare the seeds for long-term storage. Storage conditions vary by species (the convention is to store seeds cool to frozen and keep them in the dark for the longest storage). Even with optimal preparation and storage conditions, however, viability of stored seeds varies by species, from weeks to decades. Piñon seed viability (potential to germinate and produce a seedling) is low relative to many pine species and declines significantly from more than 90% when fresh to below 10% within 6–12 months (Meeuwig and Basset, 1983). In that pine nuts are used in contemporary cooking, common food-safety storage recommendations are also informative. Piñon seeds are high in oil and fat and become rancid within a few months, even with refrigeration. A typical recommendation is to store unroasted, shelled nuts less than three months in a refrigerator, or up to six months in a freezer; if nuts are roasted, they persist longer. For unshelled nuts, recommendations are to store them in the dark, away from heat up to 12 months. Shelled or unshelled, if nuts turn rancid, they are still edible, although many consider them unpalatable.

Further insight into piñon harvesting and seed preparation/use can be gained from contemporary practices of modern Paiutes in the Great Basin, who harvest piñon nuts for personal and commercial purposes. They follow many traditional methods, which were described by early 20th-century ethnographers (e.g., Kroeber, 1925) and in an informative documentary video (Kroeber and Barrett, 1961). Summarizing from these resources, the process can be described as follows: In late summer, Paiutes assess piñon seed maturity as coinciding with the time when rubber rabbitbrush (*Ericameria nauseosa*), which grows widespread throughout piñon woodlands, flowers and turns bright yellow-orange. At that time, families travel to the woodlands and with wooden poles (some with hooks on the end) knock cones from the trees. Cones are gathered, spread on

tarps on the ground, and allowed to air-dry for up to a week, during which time many cones dry and scales separate, allowing seeds to be shaken out. Cones that remain closed are buried with burning charcoal to steam-heat them in the soil; many more cones open this way.

Seeds in their shells are brought home, and further processed using only as many nuts as will be used directly (others are stored in the shell). Women set a small fire. Using wooden tongs, small pieces of hot charcoal are stirred with a handful of piñon seeds that have been placed on a flat woven tray. Stirring the charcoal pieces with the seeds allows them to be lightly roasted. Then the handful of roasted seeds is placed on a rock millingstone, and lightly ground with a stone mano. Shells (chaff) of roasted piñon nuts are more readily removed following this action than if unroasted. The seeds and chaff are transferred to a flat winnowing tray and when the wind is right, the seeds and chaff are tossed in the air, allowing the shell pieces to be blown off. Remaining in the tray are the shelled nuts, which are transferred to the millingstone and, with small amounts of water added, are ground with a mano to a flat paste. The paste is added gradually to a watertight basket or earthen bowl, more water is added, and it is stirred with a wooden hook. The remaining milky beverage is drunk directly, which was a favored preparation for traditional Paiute use of pine nuts.

We believe these modern forestry and contemporary Paiute practices provide useful insight into past piñon procurement strategies in that they highlight the complexities of combining the science of cone and seed biology with experience and subjective judgment.

## Regional Variability in Piñon Ecology

Steward emphasized that piñon pine was "the most important single food species where it occurs, but harvests are unpredictable" (1938: 27), and he repeatedly lamented the erratic nature of the harvest (1933: 241; 1938: 27, 65, 70, 88): "Had crops been reliable each year. . . the harvest would have supported many times the population" (Steward, 1938: 27). This set the stage for anthropologists to universally assume that *P. monophylla* reproductive ecology is similar across the Great Basin, and that the unpredictable cycling of good and poor seed years rendered piñon a notoriously erratic resource.[45]

This section raises the possibility that this uniformitarian assumption is wrong in important ways: What if the one-size-fits-all, boom-and-bust piñon cycling was not universal across the entire Great Basin and, rather, relevant distinctions have evolved that would affect cone and seed procurement? Below we contrast significant ecological differences between the singleleaf piñon pine woodlands of the western Great Basin with those of the central Great Basin and explore implications for piñon procurement practices by people living there.[46] We highlight the specific ecological factors that could impact piñon cone harvesting and processing practices (including so-called green- vs. brown-cone harvest strategies) and relate these to the startling disparities in the archaeological distribution of piñon-processing facilities across the Great Basin.

## The Piñon Reproductive Cycle

We begin by summarizing the relevant elements of sexual reproduction in piñon pine (Krugman and Jenkinson, 1974; Meeuwig et al., 1990). Piñon trees reach sexual maturity in ~25–35 years, but do not produce large seed crops until trees are ~100 years old. Microstro-

[45] Steward (1938: 27; 1955) rejected the existence of overarching band structures in the Great Basin (per Service, 1962) in large part because unreliable seed yields (especially piñon) did not allow family clusters to participate in true village life; contacts remained largely ad hoc.

[46] By "western Great Basin," we refer to the geographic corridor of valleys and ranges directly east of the Sierra Nevada, extending from the Bodie Mountains to the southern Owens Valley. By "central Great Basin," we refer to the uplands of the Shoshone, Toiyabe, Toquima, and Monitor Ranges, and the valleys/basins around them.

bili, or pollen cones that contain the male gametes (within pollen grains), develop first in young trees, followed in several years by macrostrobili that contain the female gamete and develop into seed cones. Pollen cones, small and flimsy, are usually borne lower in the crown and disintegrate after pollen is dispersed. Seed cones are woody at maturity, borne higher in the crown, and often remain on the tree for months to a year after cone maturity. Like most pine species, piñon is sexually monoecious, meaning that pollen cones and seed cones are borne on the same tree and trees can self-pollinate. More viable seeds, however, result from cross-pollination among trees (Forshell, 1974).

Piñon pines, as do most pine species, require two years to produce a mature seed cone and ripe seeds. Buds destined to become seed cones are initiated in mid spring (~May) approximately 2.25 years (26–27 months) before cones are fully mature and remain within the terminal bud of branches. In spring of the following year, terminal buds expand, conelets mature, and become receptive. Pollination occurs soon thereafter. Pollinated conelets overwinter in dormancy, and the female gametes (ova) are fertilized the following spring, in April or May, approximately four months prior to cone maturation (Lanner, 1970; Owens and Fernando, 2007). Small, green, fleshy conelets, less than half the size of mature cones, are visible in the growing season after pollination. Cones and seeds mature during the next growing season. Second-year cones are much larger than first-year conelets, but remain green throughout summer, becoming brown and woody near maturity. Cones and seeds become ripe in late August to late September of the second year (Vander Wall, 1988). Only at maturity do cone scales separate and both cones and seeds become capable of falling off the tree although many seeds remain in the cone, and the cones on the tree, for months thereafter. Seeds are large and wingless at maturity. The exact timing of this reproductive cycle varies with aspect, elevation, and weather (Lanner and Phillips, 1992).

After maturity, piñon seed cones, whether on the tree or on the ground, remain capable of opening and closing mechanically for several years in response to atmospheric humidity. At the base of pine cone scales are two types of tissues that respond differently (expand or shrink) to atmospheric humidity (the tissues are hygroscopic). When conditions are humid, cones remain tightly closed; as air humidity lowers, cones open again. This cycle occurs frequently as weather conditions and humidity levels change (more detail below).

## Ecological Variability in Piñon Cone and Seed Conditions

We highlight five specific factors that differ significantly between the western and central Great Basin: (1) diversity and abundance of piñon cone and seed predators; (2) interannual variability in cone production (masting); (3) cone morphology, size, seed number, and seedcoat thickness; (4) fire regimes and cone morphology; and (5) climate and weather effects. For each factor, we explore the relevant ecological background and summarize geographic differences in cone and seed conditions. We postulate that these ecological factors, individual and cumulative, point to significantly greater unripe (green) cone harvesting by foragers living in the western Great Basin and far greater reliance on ripe cone (brown, woody) harvesting by people of the Central Mountains Archaic.

Piñon Cone and Seed Predators: Conifer cones and seeds are important sources of nutrition for many native species and piñon is no exception. Nonhuman seed predators damage and remove piñon seeds, with widespread and cumulative impacts that reduce the volume of nuts available for competing human populations. Seed predators range from insects that infest and destroy maturing piñon conelets and seeds (Forcella, 1978, 1980; Jenkins, 1984; Christensen and Whitham, 1993; Negron, 1995: 97) to birds and mammals that consume cones and seeds both on the tree before seed maturity and on the ground


FIG. 12.6. Douglas's tree squirrel (*Tamiasciurus douglasii*), the major pinecone predator in the western Great Basin. **A.** Douglas's tree squirrels spend most of their time in pine tree crowns. **B.** Douglas's tree squirrels harvest unripe pinecones from branches and allow them to drop to the ground. **C.** In the western Great Basin, Douglas's tree squirrels scatter-hoard cut cones into small holes in the ground below trees. **D.** Fresh pine branch tips clipped by Douglas's tree squirrels in late spring to serve as food source (fresh cambium) until cones can be retrieved when snow melts. Here the branch tips remain after the snow has melted.

after seed maturity. These nonhuman predators collectively reduce the number of seeds that mature on the tree (important for human use) and on the ground (important from the tree's perspective). A developing seed crop can be obliterated by insects alone in the first or second year of cone maturation (Negron, 1995). We believe that the number of seed-predator species, their modes of foraging, and local abundances are critical in understanding the strong competition for piñon nuts faced by humans.

The western Great Basin hosts vastly more species of piñon seed predators than the central Basin. Table 12.6 lists the presence/absence of 29

TABLE 12.6

**Predators and Dispersers of Piñon Pine Seed in Western and Central Great Basin**

Nonexhaustive list. WGB = Western Great Basin; CGB = Central Great Basin. +++ is more abundant; + is less abundant. Footnotes: [1]Although seed and cone insects are very important predators on piñon pine, and information exists on some of them, we have no comprehensive understanding of the differences between the WGB and CGB. [2]Alhough bears are absent today from interior Nevada, including the region we identify as the central Great Basin, there is some evidence that bears may have been in the prehistoric Great Basin (Lackey et al., 2013). The evidence is unsupported, however, and for now we exclude them from the CGB.

| **Taxon**<br>**Latin name (Common name)** | **WGB** | **CGB** | **Importance to pinyon seed predation** | **Predation context (Tree [T], Ground [G])** | **References** |
|---|---|---|---|---|---|
| **Insects** | | | | | |
| Diverse species | Unknown[1] | Unknown[1] | High | T, G | Forcella, 1978, 1980; Jenkins, 1984, Christensen and Whitham, 1993; Negron, 1995 |
| **Birds** | | | | | |
| *Nucifraga columbiana* (Clark's Nutcracker) | +++ | ++ | High | T, G | Vander Wall and Balda, 1981; Hutchins and Lanner, 1982; Vander Wall, 1988; Audubon Guide to North American Birds, 2022 |
| *Gymnorhinus cyanocephalus* (Pinyon Jay) | +++ | ++ | High | T, G | Balda and Bateman, 1971; Vander Wall and Balda, 1981; Audubon Guide to North American Birds, 2022 |
| *Aphelocoma californica* (Western Scrub-Jay) | +++ | Absent | HIgh | T, G | Bardwell et al., 2001; Beedy and Pandolfino, 2013; Audubon Guide to North American Birds, 2022 |
| *Aphelocoma woodhouseii* (Woodhouse's Scrub-Jay) | + | Absent | Moderate | T, G | Audubon Guide to North American Birds, 2022 |
| *Cyanocitta stelleri* (Steller's Jay) | +++ | Absent | Moderate | T, G | Beedy and Pandolfino, 2013; Audubon Guide to North American Birds, 2022 |
| *Loxia curvirostra* (Red Crossbill) | +++ | Absent to rare | High | T, G | Benkman, 1999; Siepielski and Benkman, 2007 |
| *Pinicola enucleator* (Pine Grosbeak) | +++ | Absent | Important | T, G | Beedy and Pandolfino, 2013 |
| *Coccothraustes vespertinus* (Evening Grosbeak) | +++ | Absent | Moderate | T, G | Beedy and Pandolfino, 2013 |
| **Mammals** | | | | | |
| *Tamiasciurus douglasii* (Douglas's tree squirrel) | +++ | Absent | High | T, G | Smith, 1970; Steele, 1999; Benkman and Siepielski, 2004 |
| *Callospermophilus lateralis* (Golden-mantled ground squirrel) | +++ | +++ | Moderate | T, G | Hutchins and Lanner, 1982; Bartels and Thompson, 1993 |
| *Peromyscus maniculatus* (Deer mouse) | +++ | +++ | Moderate | G | Hollander and Vander Wall, 2004 |

TABLE 12.6 *continued*

| Taxon<br>Latin name (Common name) | WGB | CGB | Importance to pinyon seed predation | Predation context (Tree [T], Ground [G]) | References |
|---|---|---|---|---|---|
| *Peromyscus sonoriensis* (Pinyon mouse) | +++ | +++ | Moderate | G | Hollander and Vander Wall, 2004 |
| *Neotamias speciosus* (Lodgepole chipmunk) | +++ | Absent | Moderate | T, G | Hall, 1946; Hollander and Vander Wall, 2004; Jameson and Peeters, 2004 |
| *Neotamias dorsalis* (Cliff chipmunk) | Absent | +++ | Moderate | T, G | Hall, 1946; Hollander and Vander Wall, 2004; Jameson and Peeters, 2004 |
| *Ammospermophilus leucurus* (White-tailed antelope ground squirrel) | +++ | ++ | Moderate | G | Hollander and Vander Wall, 2004 |
| *Neotamias umbrinus* (Uinta chipmunk) | ++ | ++ | Moderate | T, G | Hall, 1946; Hollander and Vander Wall, 2004; Jameson and Peeters, 2004 |
| *Neotamias amoenus* (Yellow-pine chipmunk) | +++ | + | Moderate | T, G | Hall, 1946; Hollander and Vander Wall, 2004; Jameson and Peeters, 2004 |
| *Neotamias minimus* (Least chipmunk) | +++ | Absent | Moderate | T, G | Hollander and Vander Wall, 2004 |
| *Perognathus parvus* (GB pocket mouse) | +++ | +++ | Moderate | G | Hollander and Vander Wall, 2004 |
| *Ursus americanus* (Black bear) | +++ | Absent[2] | Moderate | T, G | Goodrich, 1991; Kuhn and Vander Wall, 2007; Lackey et al., 2013 |
| *Dipodomys panamintinus* (Panamint kangaroo rat) | +++ | Absent | Moderate | G | Hollander and Vander Wall, 2004 |
| *Dipodomys ordii* (Ord kangaroo rat) | +++ | +++ | Moderate | G | Hall, 1946; Hollander and Vander Wall, 2004; Jameson and Peeters, 2004 |
| *Neotamias panamintinus* (Panamint chipmunk) | ++ | Absent | Moderate | T, G | Hall, 1946; Hollander and Vander Wall, 2004; Jameson and Peeters, 2004 |
| *Neotamias senex* (Shadow chipmunk) | ++ | Absent | Moderate | T, G | Hall, 1946; Hollander and Vander Wall, 2004; Jameson and Peeters, 2004 |
| *Sciurus griseus* (Western gray squirrel) | ++ | Absent | Low | T, G | Verts and Carraway, 1998; Matson et al., 2010; J. Patton (UCB, personal commun., 2020); CIM unpub. obs. |
| *Otospermophilus beecheyi* (California ground squirrel) | +++ | Absent | Low | G | Smith et al., 2016 |
| *Otospermophilus variegatus* (Rock squirrel) | Absent | + | Low | T, G | Oaks et al., 1987 |
| *Canis latrans* (Coyote) | +++ | +++ | Low | G | Hall, 1946; Jameson and Peeters, 2004; Lendrum, 2017 |
| *Megascops asio* (Screech owl) | ++ | ++ | Low | G | Shuford and Fitton, 1998 |
| **TOTAL (excluding insects) 29** | **26** | **15** | – | – | – |

primary seed predator species, plus a large number of insect predators, their distribution and relative abundances, and their significance as predators. Insects are very important predators of conifer cones and seeds, and piñon pine is no exception. Although studies have been done on piñon insects, no comprehensive evidence exists to indicate differences in their numbers, abundances, or significance between the Great Basin regions. Of 29 seed predators listed, 26 species occur in the western Great Basin and only 15 in the central Great Basin. Only three species (Woodhouse's Scrub Jay, cliff chipmunk, and rock squirrel) are found in the central Great Basin and not in the western Great Basin. One additional species (black bear) may have occurred in the paleohistoric central Great Basin as well as the western Great Basin and was extirpated ~90–140 years ago (Lackey et al., 2013). Documentation of the newspaper and journal references on which these claims are made is not provided, however, making the basis for range extension of black bears across Nevada unsupported.

Tree squirrels (genus *Tamiasciurus*) are the major predator species in this context. Douglas's tree squirrel (*T. douglasii*) is absent from the central Great Basin, but ubiquitous in dense populations throughout the western Great Basin (table 12.6). The only other tree squirrel in the Great Basin (*T. hudsonicus*) does not occur in the central Great Basin; that species is found in eastern Nevada and western Utah. Tree squirrels forage almost exclusively on conifers, preferring pine cones and seeds, including piñon (Steele, 1999). Tree squirrels are excellent climbers, have strong jaws, and spend most of their time in tree crowns (fig. 12.6A, B). Starting in mid to late summer, tree squirrels aggressively cut cones off branches while the cones are unripe and cache them for later use in middens of many cones or small holes in the ground that store up to five cones (fig. 12.6C). A single squirrel can cut up to 80% of the predispersal cones ripening on a tree (Benkman et al., 1984).[47]

Wherever present, tree squirrels outcompete corvids both in early cone harvest and total number of cones harvested in a season (Siepielski and Benkman, 2007). Important corvid piñon predators in the Great Basin include the Piñon Jay (*Gymnorhinus cyanocephalus*) and Clark's Nutcracker (*Nucifraga columbiana*). Like tree squirrels, these birds depend heavily on pine nuts for their sustenance, for direct forage, and for caching (storing underground) for future use. As the name implies, nuts of various piñon pine species, including singleleaf piñon, comprise the primary food of Piñon Jays, who harvest seeds from cones on the trees in late summer and fall as well as eating seeds that fall on the ground. Although Piñon Jays will take seeds from unripe (green cones), they prefer to wait until cones are ripe (Balda and Bateman, 1971; Marzluff and Balda, 2010). Further, although Piñon Jay flocks are very large, they move frequently and do not obliterate single stands. Piñon Jays also consume seeds of Jeffrey pine (*Pinus jeffreyi*), a species restricted to the western Great Basin. While Piñon Jays occasionally consume seeds from limber pine (*P. flexilis*), they rarely stray to high elevations where those pines occur. Endemic to both the western and central Great Basin, available evidence suggests they are most abundant in the west.

Clark's Nutcrackers (detailed earlier) are important piñon seed predators, although their primary nut source is whitebark pine (fig. 12.7A) and secondarily limber pine, with piñon used when other species are less productive and/or later in the season. The birds begin to break open and clip cone-bearing branchlets from pines in midsummer to check for seed condition, at least one month prior to maturity (fig. 12.7B). Collecting large numbers of mature seeds in throat pouches that are adapted for transport, Clark's Nutcrackers can reduce the developing cone crop within a given stand by 57% (fig. 12.7C, D; Christensen et al., 1991). Where whitebark and

[47] In addition to cones and seeds, in autumn and early spring, when cone caches are buried under snow, tree squirrels also clip hundreds of young branch tips to eat fresh cambium (fig. 12.6D) and, in the process, greatly denude the tree of future reproductive buds (seed cones). In addition to reducing future cone crops, these stresses can lead to tree decline and even tree death.

limber pines are present, Clark's Nutcrackers start with those species and move down to woodlands to feed on piñon in late summer. They are more likely to consume piñon seeds in large numbers when the crops of their preferred species are low or seasonally depleted (Vander Wall, 1988). Clark's Nutcrackers also forage on Jeffrey pine, which occurs near piñon woodlands, but only in the western Great Basin. Although flocks of Clark's Nutcrackers are smaller than those of Piñon Jays, they remain faithful to location, meaning that the flocks forage consistently in particular stands (as crops remain), often flying back and forth to high elevations to plant piñon seeds (Vander Wall, 1988). While Clark's Nutcrackers occur in both the western and central Great Basin, they are more prevalent in the western Great Basin, where extensive stands of whitebark pine, Jeffrey pine, and related forage tree species grow. Sparser populations of limber pine in the central Great Basin attract small numbers of predators, and Clark's Nutcracker populations appear to be smaller there, as well.

Three other corvid species (Western Scrub Jay, Woodhouse's Scrub Jay, and Steller's Jay), also forage on piñon seeds. Western Scrub Jays occur in the California and western Great Basin region (Beedy and Pandolfino, 2013). Although acorns are the primary food of Scrub Jays in their central California range, populations in the Inyo-Mono region of eastern California depend heavily on piñon nuts for up to 75% of their diet and are referred to as Pine Scrub Jays (Bardwell et al., 2001). Pine Scrub Jays are genetically adapted to eat piñon nuts with long, shallow bills as compared to the stout, recurved bills of the Acorn Scrub Jay of central California (Bardwell et al., 2001). Bardwell et al. (2001) found in experimental studies that Pine Scrub Jays are efficient and important predators of piñon nuts, consuming piñon nuts 30% faster than do Acorn Scrub Jays. Woodhouse's Scrub Jays, an uncommon species generally, also eat piñon nuts. They occur in central Nevada but are quite rare. Stellar's Jays are more cosmopolitan foragers than Scrub Jays, with a wide elevation range, including piñon woodlands, where they consume piñon nuts.

Another group of birds that is very important in pine nut consumption includes species of crossbills and grosbeaks. Appearing like large finches, these conifer forest-inhabiting birds have bills adapted to pry open pinecone scales and consume their seeds. Red Crossbills (*Loxia curvirostra*) are particularly significant pine nut predators (Benkman et al., 2001). Their large bills have crossed mandibles that enable them to wrench open pinecone scales prior to and at maturity to extract and consume seeds. Crossbills have long been studied for their coevolutionary role in cone-scale thickness of pines and interactions with tree squirrels (Benkman, 1999). Red Crossbills are common in the western Great Basin but absent or rare in the central Great Basin. Pine Grosbeaks (*Pinicola enucleator*; the name indicates its pine-loving nature and ability to extract pine seeds) and Evening Grosbeaks (*Coccothraustes vespertinus*; the name indicates its ability to break open seeds) have massive bills capable of readily cracking or crushing pinecone scales to retrieve nuts. Both species range in the western Great Basin, and, although piñon woodlands are not their primary habitat, these Grosbeaks commonly forage from piñon pines (Beedy and Pandolfino, 2013). Pine Grosbeaks and Evening Grosbeaks are absent from the central Great Basin.

Black bears (*Ursus americanus*) range widely throughout North America and are voracious consumers of pine nuts including piñon. When pine seeds are available, bears eat them almost to the exclusion of other foods (Kendall, 1983). In the modern Great Basin, black bears occur only in the western Great Basin (Goodrich, 1991; Grayson, 2011); as noted above, they might have occurred in the central Great Basin prehistorically, but the evidence is unsupported. Where large cone middens from tree squirrels occur (as in the Rocky Mountains region), bears will forage these cones on the ground. In the western Great Basin, however, tree squirrels generally do not cache large middens in the ground so bears


FIG. 12.7. Clark's Nutcracker. **A.** Nutcracker resting on pine branch. **B.** Unripe cones cut from trees by Clark's Nutcrackers in early August (≥ one month before maturity) to check seed condition. **C.** Nutcracker breaking mature whitebark pine cone open with seed in its beak. **D.** Bird casting seeds into its throat pouch for transport. Photo: James Blanchard.

cannot depend on squirrel-cached cones. Rather, being excellent tree climbers, bears consume large quantities of seed from unripe cones in crowns of Jeffrey pine and whitebark pine trees in summer (Kuhn and Vander Wall, 2007), and they likely do the same with piñon. Bears also consume large quantities of piñon cones that have fallen to the ground in western Great Basin woodlands in late summer and autumn (fig. 12.8; Millar, unpublished obs.).

Other than the Douglas's tree squirrel, the most important seed-predator rodent species are ground feeders who consume piñon seeds fallen from the trees (table 12.6). A few exceptional species forage seeds on the tree, primarily from ripe cones. Golden-mantled ground squirrels

(*Callospermophilus lateralis*) occur in both the western and central Great Basin and, although they are primarily ground-dwellers, they can climb low in trees and will consume piñon seeds. Of the seven chipmunk species listed in table 12.6, four occur only in the western Great Basin. Chipmunks are excellent climbers, with a diverse diet that includes piñon seeds, fruits (berries and others), grasses, fungi, snails, and insects. Compared to squirrels, chipmunk jaws are not strong, and they are incapable of chewing into green or closed cones of the heavier coned pine species such as piñon.

Western gray squirrels (*Sciurus grisius*) are agile tree climbers and range widely along the Pacific Coast region and in the western Great Basin. They have a broad diet and occur primarily in piñon-juniper woodland elevations east of the Sierra Nevada where they consume abundant piñon nuts. Rock squirrels (*Otospermophilus variegatus*), which occur only in the central Great Basin, are ground squirrels; they can climb trees and will take piñon nuts on occasion. Although they occur in piñon-juniper woodlands, rock squirrels are restricted to rocky habitat (talus, boulders) and are not widespread or important piñon predators at the landscape scale. Rock squirrels' range is primarily in the far eastern Great Basin and Southwest. Hall (1946) described one outlier distribution (one location, one specimen) in the northern Toiyabe Range, but in the last five years, Millar has observed an occasional rock squirrel in the lower Pine Creek campground and a single individual in Mill Canyon of the Toquima Range. Overall, while they appear to occur in the central Great Basin, rock squirrels are not significant piñon seed predators.

Implications: Given the vastly higher numbers of piñon seed-predator species in the western Great Basin compared with those in the central Great Basin (26 of 29 species vs. 15 of 29 species) and their relatively greater abundances in the western Great Basin, human foragers were far more vulnerable to competition for piñon seeds than their central Great Basin counterparts. This is why we postulate that, in regard to procurement of adequate piñon nut supplies, Inyo-Mono communities were forced to harvest far more unripe (green) cones before their competition got them. By contrast, Central Mountains Archaic communities could routinely have secured adequate piñon seeds—and especially those with the highest qualities—and they likely would delay harvest until the (brown) cones fully ripened.[48]

Interannual Variability in Cone Production and Masting: Although most pine species including piñon require two years for seed cone development, mature and healthy trees produce at least some cones every year. Variation in the number of cones produced per tree and per stand is common between years, and the pattern of interannual cone production varies by species. Some pines, such as lodgepole pine (*Pinus contorta*), produce moderate crops annually (Lester, 1967), while others, such as western white pine (*Pinus monticola*), produce large crops about every four years (Rehfeldt et al., 1971). These patterns are usually explained by the species-dependent amount of energy (based partly on the seed size) drained by producing a large crop and the time required to restore energy to produce another large crop. In many other species, pines and otherwise, large crops are produced at erratic intervals, with variable size crops intervening.

This boom-and-bust cycle of variable interannual fruit production is called masting, defined as the synchronized production of seed at long intervals by a population of plants (Janzen, 1971). A behavior long recognized in many tree species around the world (first noted in the 14th-century European literature [Koenig, 2021] and in the modern era [Salisbury, 1942]), masting occurs both among plants within a local population and among populations across a large

[48] The corvid study developed above established that piñon pine seeds change rapidly during late summer and fall, increasing exponentially in both dry mass and caloric content and only late August/early September do they reach a maximum stable value (table 12.2). Pine nuts also increase in digestible carbohydrates, proteins, and lipids as they mature (Vander Wall, 1988).


FIG. 12.8. Black bears, which range throughout the western Great Basin mountains but not in the central Great Basin, consume nuts of piñon pines abundantly. **A.** In autumn, bear tracks are evident in the sandy soil of the Bodie Mountains, where their paths form a dense network among piñon pine trees. **B.** Evidence of cone consumption by bears**. C.** Bear scat filled with remains of pine nuts and shells. Photo: Dave Rhode.

regional landscape. Long-lived and wind-pollinated tree species most commonly have masting behaviors; oaks and beech species are among the taxa historically recognized to mast, as are many conifer species (Crone et al., 2011). Piñon pine species of subsection *Cembroides* are known to mast (Forcella, 1981).

The science of masting, including efforts to understand factors that regulate high, low, and erratic annual production of fruits, has exploded in recent years, and many theories have been investigated to explain underlying variables (Buonaccorsi et al., 2003; Kelly et al., 2020; Koenig, 2021). A consensus has emerged involving both ultimate (evolutionary) and proximate (ecological, climatic) factors. At the evolutionary level, economies of scale (EOS) are recognized as pervasive and convergent factors that are the fundamental bases for masting within species (Kelly, 1994). The two primary EOS recognized are predator satiation and pollination efficiency (Pearse et al., 2016; Bogdziewicz et al., 2021). Pollination efficiency refers to an adaptive function of mast production of pollen to ensure widespread fertilization of female strobili and development of abundant viable seeds. Pollination efficiency is considered of little importance in most pine species, which produce vast and adequate quantities of pollen even in nonmast years.

Predator satiation—by far the oldest, continuously accepted factor for the evolution of masting (Salisbury, 1942; Koenig, 2021; Zwolak et al., 2021)—addresses masting as an evolved mechanism for trees to overwhelm fruit and seed predators and ensure tree reproduction (Janzen, 1971). During years of meager fruit production, predator populations decline for lack of food; an unexpected year of heavy fruit production both provides more seeds than existing predators can consume (saturating the predator population) and allows adequate surplus seed for tree reproduction (Buonaccorsi et al., 2003). Predator populations that grow in high-crop years crash in subsequent years of low fruit production. This erratic timing of mast years stymies evolution of predator populations from synchronizing with fruit production (Pearse et al., 2020).

Proximal factors for mast fruit production primarily relate to climate and weather patterns (Ascoli et al., 2021; Hacket-Pain and Bogdziewicz, 2021). Erratic intervals between mast years correlate with large-scale regional climate modes such as ENSO (El Niño–Southern Oscillation), as well as annual weather that favors or inhibits fruit production (Koenig, 2021; Wion et al., 2021). Given an evolutionary capacity for masting, favorable (and unfavorable) sequences of years that are required for a mast crop to develop can be triggered at large landscape scales by these climate modes. Annual and seasonal weather are the most proximate factors determining whether a mast crop is produced or not; bud initiation and fruit development can be cueing up for a large crop only to be vetoed by unfavorable weather conditions during the fruit development season (Ascoli et al., 2021).

Piñon species are variably recognized as masting taxa. Singleleaf piñons produce "good cone crops" every 3–7 years (Meeuwig et al., 1990), "large crops" in 1 to 3 of 10 years (Forcella, 1981), and the "years between cone crops" as 1–2 years (Krugman and Jenkinson, 1974; Bonner and Karrfalt, 2008). This variability relates to growing conditions (forestry plantations vs. wild) and locations (geographic regions) under which cone crops have been measured. Regarding the latter, and as a result of the evolved predator-satiation strategies, considerable evidence documents spatial variation within a species' masting expression, and this is related to the presence of cone predators, especially tree squirrels and seed-consuming birds (Smith, 1970; Siepielski and Benkman, 2007; Crone et al., 2011; Zwolak et al., 2021). In whitebark pine, for instance, geographically separated communities were found to form a continuum of strategies from masting to nonmasting depending on the presence and abundance of cone and seed predators, especially squirrels, birds, and bears (Crone et al., 2011).

We suggest that the significant differences of important piñon cone and seed predators within the Great Basin triggered the evolution of regional differences in piñon masting—with stronger piñon masting in the western Great Basin and weaker to no masting in the central Great Basin. While aware of no published evidence for this hypothesis, unpublished observations confirm strong masting in the western Great Basin (Arnaldo Ferreira [USFS, regional geneticist], personal commun. to Millar, 2022) and Millar's 30 years of unpublished observations in the eastern Sierra Nevada region of the western Great Basin also document very heavy and synchronized cone crops occurring at irregular and long intervals (fig. 12.9A, B). During such mast years, seed is so abundant that viable seeds remain uneaten and cover the ground into late autumn and even into spring (fig. 12.9C). Between mast years small cone crops with variable cone production occur and complete crop failure was never noted except in stressed or dying stands. The strong masting documented in whitebark pine in the western Great Basin further suggests that, with its abundant and aggressive pine seed and cone predators, masting is likely to evolve in other pine species of this region including piñon. We are unaware of studies or published observations regarding piñon cone production in the central Great Basin and the hypothesis of min-

imal or absent masting there remains to be tested.

Implications: We hypothesize that differences in piñon cone and seed predation led to the evolution of pronounced piñon masting within the western Great Basin and that the near-absence of such predation pressures resulted in little to no masting in the central Great Basin. If substantiated, differential piñon pine masting has critical implications for human foragers. Piñon woodlands in the western Great Basin periodically produce heavy piñon seed crops with lean crops in the intervening years. We think that during such sparse-harvesting years, Inyo-Mono foragers were required to harvest unripe (green) cones to outcompete the numerous, abundant, and diverse nonhuman cone predators. Consequently, this early harvest required that foragers resort to costly afterripening and drying techniques to release seeds and assure mature nutritive quality. Because Central Mountains Archaic foragers lived where evolutionary forces minimized such piñon masting, we propose that they could regularly rely on harvesting fully ripened crops. The lack of significant seed-predator competition further ensured that adequate numbers of cones and seeds were available on piñon trees throughout the cone-maturation period to permit mature cone (brown) harvesting. The relative ease of collecting ripe cones (and the higher nutritive value of their mature seeds) typically obviated any need to harvest unripe (green) cones.

Cone Morphology, Cone Size, Seed Numbers, and Seed-Coat Thickness: Morphology is constrained by evolutionary lineage and modified by proximal natural-selection forces. Avian and mammalian predators exert such strong selective pressure on cone morphology that abundant predator populations affect the direction of cone morphology in ways to thwart them.

Tree squirrels are the most widely documented selective force known to affect the evolution of morphology, number of seeds/cone, timing of seed shed, thickness of seed coats, cone attachment to the branch, and fluctuation of seed crops (Smith, 1970; Linhart, 1978; Gurnell, 1983; Siepielski and Benkman, 2007). Studying widely separate regions in the Great Basin with the same pine species (whitebark and limber pines) across locations where tree squirrels were present in some and absent in others, Siepielski and Benkman (2007) demonstrated that convergent evolution in both pine species led to more squirrel-proof cones in regions with squirrels (fig. 12.10). That is, wherever squirrels were abundant, pinecone scales were thicker, had fewer scales and seeds, fewer viable seeds, thicker seed coats (twice as thick), and reflexed cone scales (with sharper tips pointing outward as armor) than did cones in populations where squirrels were absent. Siepielski and Benkman (2007: 213) concluded that "squirrels have an overwhelming influence on cone evolution where they occur." Further, in areas where squirrels are present, and cones have developed thicker scales, squirrels switch to harvesting ever-younger unripe cones, which are easier for them to chew (Smith, 1970).

In addition to tree squirrels, corvids and crossbills have also been documented to influence the direction of cone evolution (Lanner, 1981; Benkman, 1999; Benkman et al., 2001). Where Clark's Nutcrackers and Red Crossbills are abundant, as in the western Great Basin, cone evolution tends toward larger, thicker cones, with tightly sealed scales (fig. 12.10).

Implications: We know of no studies attempting to evaluate geographic variation in piñon cone morphology, either in the Great Basin or beyond. Nonetheless, the widespread evidence for convergent evolution in areas of cone-harvesting squirrels suggests that regional variation in piñon cones could result in heavily armed cones with fewer seeds that are harder to open where tree squirrels and other predator rodents and birds are present. Given the density of these species in the western Great Basin, we postulate that piñon forests in that region evolved adaptive measures to resist squirrel predation and did not in the central Great Basin.


FIG. 12.9. Cone masting in singleleaf piñon pine. **A.** Jeff Wyneken observes a piñon crown with abundant unripe (green) and ripening cones during a mast year, western Great Basin. **B.** Branch with multiple open cones during a mast year, western Great Basin. **C.** Sound piñon seeds remain abundantly on the ground following a mast crop year in the western Great Basin and are not consumed by seed predators throughout the autumn of cone ripening or in the spring after seed fall. **D.** Midsummer (early July) unripe green cone and cone parts on the ground—indication of inspection of seed quantity and quality far before maturity. Such activities reduce the number of mature cones remaining by late summer for harvest.

If so, morphological adaptations of the cones that evolved to thwart squirrels would have impacted human foragers as well. Thicker cone scales that are more tightly closed at maturity and strongly attached to the branch suggest that, like the squirrels, human foragers would opt to harvest unripe (green) cones; and, because tree squirrels are very common in the western Great Basin, this competitive pressure from squirrels would further encourage the people living there to obtain young green cones to assure a decent harvest before the squirrels and birds (also electing to harvest green cones) could get them. Beyond storage costs, those communities harvesting unripe (green) young cones were required to invest in afterripening procedures and protection from mold and fungi. Because tree squirrels and crossbills are absent in the central Great Basin, foragers there could regularly harvest nutritious ripe seeds without the added harvest and processing costs required of unripe cones.

Fire Regimes and Cone Morphology: Not unlike squirrel pressure, fire regimes are a natural-selection force impacting the evolution of and condition of cone morphology (Lamont et al., 2020). Throughout the genus *Pinus*, seroti-

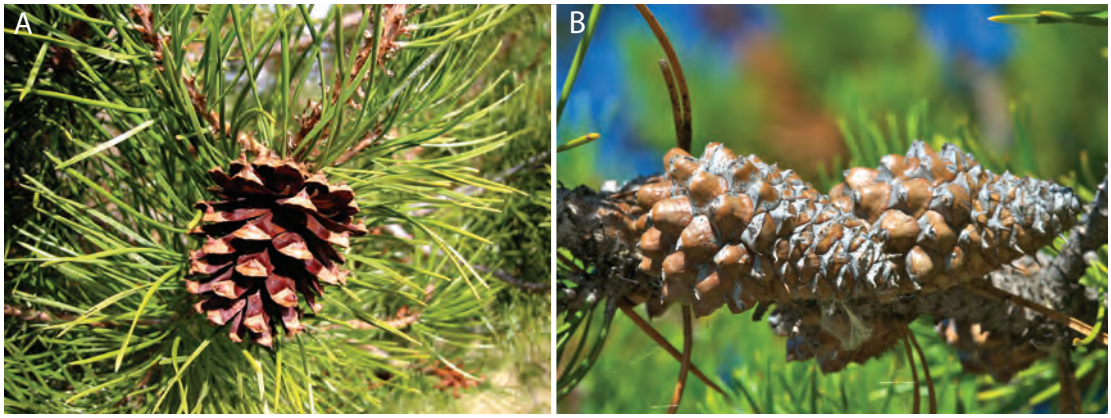


FIG. 12.10. Geographic variation in cone serotiny and cone-scale thickening of lodgepole pine ecotypes, varying by fire regimes and tree squirrel abundance. **A.** *Pinus contorta* var. *contorta*, shore pines, do not experience short-interval, high-severity fire, and have evolved cones that open on the branch annually. Photo: USDA. **B.** *Pinus contorta* var. *latifolia*, Rocky Mountain lodgepole pines experience frequent severe fires and have evolved cone serotiny. In conditions where seed predators are scarce, cone scales do not significantly thicken. Photo: Craig Benkman.

nous cones have evolved convergently in regions of severe fires that kill trees at landscape scale (as opposed to surface fires where mature trees can survive). Serotiny relates to cone traits that resist burning in crown fires. Serotinous cones neither open at maturity nor fall from the tree. Instead, they remain attached and closed, with scales tightly sealed by resin and seeds securely held in the cone, capable of surviving for years to decades (compare fig. 12.10A, B; Lamont et al., 2020). Although fire may kill the trees, heat from the fire melts the resins of the closed cones on those trees, and cone scales gradually open a few days after a fire passes. Seeds fall on freshly disturbed (burnt) soils, where they germinate and grow with little competition.

Serotiny develops in areas of primary winter precipitation where fuels build and fires are severe and frequent (Lamont et al., 2020) and in pines that are highly flammable and susceptible to crown fires (Schwilk and Ackerly, 2001). Tree and stand characters such as thin bark, low stature, flammable foliage, high resin loads, heavy shrub fuels, and early-successional status favor development of cone serotiny. Significant variation in degree of serotiny, from highly serotinous to nonserotinous, can occur within a pine species, reflecting geographic differences in fire regimes (fig. 12.10A, B; Lamont et al., 2020). The cooccurrence of severe fires and tree squirrels favors development of thick-scaled and/or serotinous cones (fig. 12.10C; Linhart, 1978; Talluto and Benkman, 2014).

Although piñon pines do not bear serotinous cones, we postulate that differing fire regimes between the western and central Great Basin may have affected piñon cone morphology. Notoriously difficult to evaluate, differences in fire regimes in piñon-juniper woodlands of the western Great Basin vs. central Great Basin suggest that natural selection on cone morphology from fire could be expected in the west. Although such conclusions are based on only a few reliable studies, Baker and Shinneman (2004) and Romme et al. (2009) suggest that fire regimes during the several centuries of pre-European settlement differ among three piñon vegetation community types—persistent woodlands (stable, midzone, dominant tree canopy, varying understory vegetation), piñon-juniper savannahs (dominant grasslands with sparse tree occurrence, rare for singleleaf piñon pine), and wooded shrub-

lands (stable shrub communities with temporal changes in tree presence varying with climate). The highest-confidence studies show that severe, crown- and tree-killing fires occurred most in piñon persistent woodland and wooded shrubland communities (Romme et al., 2009), with no evidence that surface fires burned at the landscape scale in these vegetation communities. Typically, the abundant understory fuel loads and high flammability of piñon trees enhances the severity of the fires, with whole trees even exploding in advance of the fire front. Given the slow postfire recovery of piñon, this evidence supports an expected long fire-return interval in persistent piñon woodlands and wooded shrublands (Baker and Shinneman, 2004).

The few reliable studies on historic fire regimes in Nevada and eastern California hint at the possibility that severe fires were historically more common in the western Great Basin than farther east. Studies of the historic fire regimes in the East Walker Watershed (western Great Basin) determined that high-severity fires burned frequently in this region, with return intervals as low as 8–50 years (Gruell, 1997; Baker and Shinneman, 2004). Studying central Great Basin piñon woodlands dating A.D. 1445–2006 in areas unaffected by human activities, Bauer and Weisberg (2004) found that fire regimes were of high severity but also small and infrequent, with a fire cycle of 427 years. They also concluded that the greater fuel available in more mesic woodland regions, such as the western Great Basin, caused fires to develop more frequently and these fires were severe.

A paleoecological study of Holocene piñon fire activity in the northern Great Basin corroborates high-severity fires in piñon woodlands and a positive correlation between piñon fires and periods with greater winter precipitation. Fire events in Idaho peaked during intervals of mesic climates, which supports the hypothesis that wet climates promote dense vegetation, high fuel loads, and frequent fires; fire-free intervals were associated with xeric climate periods (Weppner et al., 2013).

This combined evidence suggests that fire regimes in historic piñon woodlands could exert selective effects on cone morphology (serotiny or similar)—and piñon-juniper woodlands in the western Great Basin seem to have experienced more severe fires than their central Great Basin counterparts. This may be due to differing weather and climate. Table 12.7 documents that contemporary winter precipitation in the west is nearly twice that of the central Great Basin (due to the dominant winter Pacific storms), creating higher soil moisture during the growing season and an increased, rapid buildup of fuels. This appears to influence more severe and frequent fires in the west than in the central Great Basin (Biondi and Bradley, 2013).

Considered together, these factors suggest that piñon cone adaptations to fire may have evolved differently between the western and central Great Basin. We suspect that the higher severity, more frequent fires of the west exerted greater selection pressure toward thicker cones with a tendency to persistent closure or delayed opening than in the central Great Basin. Because no studies have evaluated such geographic differences in cone morphology, this remains a hypothesis to be tested.

Implications: We speculate that geographic differences in fire regimes and their potential effects on cone morphology translates into western piñon cones that are harder to open at maturity than those of the central Great Basin. If so, foragers harvesting ripe cones along the eastern Sierra Nevada corridor would have had greater difficulty opening the cones to extract seeds and would have to resort to afterripening techniques similar to those used to harvest unripe (green) cones. Central Mountains foragers harvesting ripe (brown) cones were, it seems, spared these more costly techniques.

Climate and Weather: Cool late summer temperatures favor cone production (Redmond et al., 2012; Bogdziewicz et al., 2021) with a significantly positive relationship between piñon cone production and spring-summer precipitation suggesting a limiting factor (Redmond et al., 2012; Khuu, 2017; Pearse et al., 2020). Although

TABLE 12.7

**Historic Climate Data for Western Great Basin and Central Great Basin Sites**

**A. NOAA COOP Station Summaries.** NOAA COOP weather station summaries (https://wrcc.dri.edu/). POR: period of record.

| Station, State, Range | Region | POR | Elev. (m) | Precipitation (annual) | Temperature (°C) | | |
|---|---|---|---|---|---|---|---|
| | | | | | Annual | Max. | Min. |
| Lee Vining, CA, Sierra Nevada | WGB | 1944–2016 | 2097 | 356 | 8.9 | 16.5 | 1.3 |
| Austin, NV, Toiyabe | CGB | 1887–2016 | 2012 | 312 | 8.8 | 16.1 | 1.4 |

**B. PRISM Climate Summaries.** Data extracted for the locations of the reference sites from the PRISM climate model, 30 arc-sec data, for the period A.D. 1981–2010 (Daly et al., 1994). PPT-ann: annual precipitation; PPT-DJF: precipitation December, January, February; PPT JAS: precipitation July, August, September; PPT SON: precipitation September, October, November; T-ann: annual temperature; Tmin-ann: annual minimum temperature; Tmin-DJF: minimum temperature December, January, February; Tmin JAS: minimum temperature July, August, September; Tmax annual: annual maximum temperature; Tmax DJF: maximum temperature December, January, February; Tmax, JAS: maximum temperature July, August, September. Data from Millar et al., 2021.

| | | | Precipitation (mm) | | | | | Temperature (°C) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | Region | Elev. (m) | PPT-ann | PPT-DJF | PPT-AMJ | PPT-JAS | PPT-SON | T-ann | Tmin-ann | Tmin-DJF | Tmin-JAS | Tmax-ann | Tmax-DJF | Tmax-JAS |
| Kavanaugh Ridge | WGB | 2993 | 701 | 351 | 87 | 48 | 41 | 3.3 | -3.6 | -10.2 | 4.4 | 10.2 | 2.4 | 19.5 |
| Lundy Canyon | WGB | 2906 | 695 | 349 | 84 | 47 | 46 | 3.5 | -3.1 | -9.6 | 4.9 | 10.0 | 2.1 | 19.2 |
| N Toiyabe Peak | CGB | 2996 | 633 | 196 | 190 | 75 | 33 | 2.4 | -4.2 | -11.0 | 4.0 | 9.1 | 0.5 | 19.6 |
| San Juan Creek | CGB | 3007 | 604 | 179 | 179 | 80 | 33 | 3.9 | -2.7 | -9.7 | 5.6 | 10.5 | 1.8 | 21.2 |

modern late summer temperatures have similar means at comparable elevations in the western and central Great Basin, the proportion of spring and summer precipitation differs greatly (table 12.7). Although annual precipitation is higher in the west, the central region experiences roughly twice as much spring-summer precipitation. Millar et al. (2021) interpreted similar regional differences in summer precipitation in tree growth (limber pine) throughout the past millennium.

Hygroscopic closing of mature pinecone scales depends on humidity and may also affect cone behavior. Under dry atmospheric conditions, cone scales open and seeds can disperse; when humid, cone scales close and seeds remain inside (fig. 12.11; Dawson et al., 1997). As a result, in regions of higher humidity, seeds remain longer in the cone and require drying to open and extract. Under the contemporary climatic regime, autumn precipitation and relative humidity during the cone ripening and processing period is somewhat greater in the western than central Great Basin (table 12.7), but we are unaware of any specific studies investigating either factor in Great Basin piñon populations.

Implications: Likely climate and weather impacts lead us to propose that regional differences in cone production could result, further implying that Central Mountains Archaic communities had access to more abundant piñon seed crops with cones easier to open than those living in the western Great Basin.

Human selection: Finally, we consider the possibility that Archaic human foragers themselves influenced the evolution of piñon reproductive characteristics through intentional piñon harvest practices repeated over millennia.[49] To be effective as natural selection (as well as in intentional domestication), several factors must co-occur: a trait or set of traits (e.g., thin cone scales, large seeds) needs to be preferentially selected repeatedly over a long period of time (relative to the generation length of the organism selected); the trait must have a genetic basis (that is, inherited); and individuals with the desired trait(s) must differentially reproduce and survive relative to individuals that lack the desired trait(s). Further, populations under selection need to be isolated to some degree from gene flow (pollen and seed immigration) from populations not under selection. How does this stack up for piñon and human use?

From evidence presented in preceding sections, especially in regard to cone and seed predators and fire regimes, piñon cone traits appear to be highly heritable, tightly coupled to fitness (survival and reproduction), and subject to rapid evolution when selection is strong (Smith, 1970; Vander Wall and Balda, 1981; Tomback, 1982; Benkman and Siepielski, 2004). Talluto and Benkman, (2014), working with Rocky Mountain lodgepole pine, simulated effective influence of fire and tree squirrels on evolution of cone traits within as few as 2000 yrs. Thus, there appears ample reason to consider that Archaic human foragers might have affected the evolution of piñon traits. The problem: what direction might their selection actions have taken, and/or did competing processes negate a directional effect?

Several different directions can be considered: First, we assume foragers collected cones (differentially harvested cones) from trees that had thin scales, large seeds, avoided cone predators, produced large numbers of cones bearing large number of seeds/cones, and that such cones were produced regularly (low to no masting). In this case, cones would be differentially removed from the population that bore those traits, leaving trees (cones/seeds) not bearing these traits to reproduce. In this case, humans would be acting similarly to tree squirrels and evolution would progress toward populations of piñon trees bearing cones with more protection from predation (human and otherwise) and stronger masting.

Another direction for forager-related evolution seems equally feasible. That is, forager selection might have favored the increase in piñon populations of human-desired traits by differentially increasing the number of desired seed-bearing genes that were effectively planted. Processing, storage, and use of piñon seeds by foragers gave ample opportunity for seeds to be inadvertently (or intentionally) lost from consumption and dispersed in the landscape. This is likely in that piñon seeds remain viable, especially for a year or more, and that many situations existed where seeds would be lost. The latter activities include cone removal from trees, cone drying, seed extraction, cone and seed storage, and seed transport for food. Some or all of these could lead to preferential reproduction of trees bearing forager-desired traits. In this situation, foragers would be acting similarly to birds such as Clark's Nutcrackers, which, although they prey on piñon seeds, also act as highly important dispersal and planting agents.

A final possibility is that both forces were at work as a result of human foraging, and the net evolutionary direction was null or weak if only a slight advantage one way or the other occurred.

Implications: Natural selection on cone traits by Archaic foragers, while likely unintentional, is an additional potential factor influencing cone morphology and masting in Great Basin woodlands. Although we cannot put high probability on the direction of selection, without further knowledge, the different cone and masting traits that exist between the western Great Basin and central Great Basin suggest that humans did not effectively lead to predator-avoidance traits in central Great Basin piñon populations, and rather potentially favored the evolution of desired traits in that region.

[49] We thank Dave Rhode for suggesting that human foragers may have exerted selection pressure on piñon cone evolution, and thus should be considered among other factors.


FIG. 12.11 Hygroscopic cone-scale opening. **A.** When cones fall from trees of non-serotinous pine species, they remain open as long as weather is dry. **B.** If weather becomes rainy or humid, cone scales close and are difficult to open. The example shown is lodgepole pine.

## CONCLUSIONS

We have enumerated several known and potential differences in ecological factors that affect piñon cone and seed production throughout the Great Basin and conclude that evolutionary processes, predatory impacts, climatic fire variability, and masting processes differed significantly within the Great Basin. We think that human foragers responded to these factors with significantly different strategies for their piñon harvests that were appropriate to their own environmental conditions, and in so doing, may have themselves exerted novel selection forces that influenced the direction of piñon evolution.

Central Great Basin: We hypothesize that piñon trees in central ranges are characterized by thinner cones, more seeds/cone, lower rates of seed and cone predation, and considerably lower interannual variability than in the piñon woodlands of the western Great Basin. Although total cone production does not depend on either cone morphology or cone-procurement methods, we suggest that the overall piñon cone production was vastly more stable and capable of a readily feasible harvest in the central than in the western Great Basin (at least during the climate conditions of the past millennium and likely before). If so, then Central Mountains Archaic communities were usually free to harvest pinecones and seeds as they ripened and experienced less competition from mammalian and avian competitors.

Steward's (1938) landmark warning of boom-and-bust cycles of piñon unpredictability was likely exaggerated for the woodlands of the Shoshone, Toiyabe, Toquima, and Monitor ranges. With fewer alternative resources than landscapes to the west, Central Mountains Archaic foragers focused on piñon as a primary food source almost immediately after it arrived.[50]

Western Great Basin: When compared to piñon trees of the central Great Basin, we propose that those in the western Great Basin had thicker cones, fewer seeds/cone, cones that remain closed longer at maturity, higher seed and cone predation, and greater interannual variability in cone production with irregular heavy mast years and intervening lean years. If true, the cumulative impact of these ecological factors would have led to more energy expenditure required to harvest, store, and consume piñon seeds along the valleys and ranges directly east of the Sierra Nevada. Combined with evolutionary and climatic processes, pressure from squirrels, corvids, crossbills, bears, and other piñon predators forced human foragers to draw upon difficult, costly, and time-consuming methods to successfully harvest unripe cones and risky afterripening practices to avoid lower quality seeds.

These multiple ecological factors likely made piñon seeds more difficult and expensive to obtain in the Inyo-Mono (western Great Basin) region, where alternative higher-value resources were abundant. We agree with Bettinger (1976a: 82–83) that among the Owens Valley Paiutes "pinenuts probably ranked no higher than third in terms of overall contribution to the diet"—well below dense stands of tule, cattail and other hydrophytes, mollusks, fish, and migratory waterfowl of the riverine landscape and also less important than the low shrubs, seed-bearing grasses, and artiodactyls of the desert scrub community.

The Upshot: This combination of ecological factors (many of which remain to be empirically tested) is consistent with the available archaeology of the Great Basin. This may explain the enigma of why the stone circles presumably associated with piñon processing (and perhaps ground stone frequencies) are vastly more common in the west.

For approximately 7000 years, foragers of the Central Mountains Archaic largely harvested ripe piñon seeds, yet rarely needed to build the processing features required when piñon was scarce. By contrast, western Great Basin foragers

[50] We also acknowledge that the Comstock hypothesis (above) resulted in an overemphasis of piñon in precontact subsistence. The impacts of 19th century ranching and mining damaged valley bottom resources (especially grasses and geophytes) more than the upland piñon stands, Shoshonean consultants in the 1920s and 1930s could recall few such lowland harvests from personal experience, but they readily remembered piñon harvests firsthand because they still participated in them since childhood (sometimes as wage labor).

were forced to resort to the more expensive unripe cone harvesting that generated an abundance of archaeological processing features, some of which date back more than 4000 years.

We see no eclectic evolutionary progression from brown- to green-cone intensification. It is hardly necessary to fall into the "ecological Indian" fallacy (Krech, 1999; Smithers, 2016) to argue, as we do, that indigenous foragers are ecological observers of the highest order (Knopf and Däwes, 2020; Newman, 2021; see relevant unpublished paper by Teeman[51]). We think it inconceivable that Great Basin foragers required millennia to figure out the range of possible ways to harvest piñon cones (including the timing of cone ripening and collection, interannual crop variability or masting, competition with cone/seed predators, requirements for storage and afterripening). They knew how to predict lean harvests more than a year in advance, and doubtless shared this knowledge socially through communal pronghorn and jackrabbit hunts and fandangos. Depending on local conditions, harvesting options were built in—sometimes more intensive harvesting was required, sometimes not. They knew what the corvids, crossbills, and squirrels knew because their community survival depended on crafting such knowledge into resilient mixes appropriate to the changing landscapes at hand.

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