Journal of California and Great Basin Anthropology | Vol. 43, No. 1 (2023) | pp. 59–82

Rethinking Pinyon Procurement in the Ancient Great Basin: An Ecological Hypothesis

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Julian Steward believed that single-leaf pinyon pine ("pinyon pine" hereafter; Pinus monophylla*) was the most important long-term plant resource for Great Basin Shoshoneans, wherever it occurred. Assuming that pinyon pine reproductive ecology was constant across the Great Basin, Steward set the stage for generations of anthropologists to universally assume that the unpredictable cycling rendered pinyon a notoriously erratic resource throughout the Intermountain West. And because pine nut harvests were unpredictable, this uncertain food source prevented Great Basin family clusters from participating in the settled village life typical of other hunter-gatherer "bands." We question Steward's uniformitarian assumption: What if boom-and-bust pinyon reproductive cycles were not universal and, instead, evolutionary processes generated significant regional variability in cone and seed procurement across the Great Basin? We argue that significant ecological differences separate pinyon pine woodlands between the western and central Great Basin and these differences carried major implications for pinyon procurement by people living there. We propose that regional ecological factors help account for the startling disparities in the archaeological distribution of pinyon processing facilities across the Great Basin.*

Of the three dozen different plant species consumed by the Western Shoshone, Julian Steward regarded pinyon pine as by far the most important (Steward 1938:19, 104, 230–31). The problem was that pinyon harvests were "unpredictable" and erratic (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). Descriptions of notoriously unpredictable pinyon pine productivity were prominent in Steward's (1955) argument against the presence of permanent suprafamilial associations ("bands" in the sense of Elman Service 1962). Steward contended that unreliable seed yields (particularly pinyon pine) failed to allow family clusters to participate in true village life because social contacts remained largely ad hoc due to the irregular abundance of surplus food. Steward unwittingly set the stage for generations of anthropologists to universally assume that pinyon pine reproductive ecology is identical across the Great Basin, with unpredictable cycling between good and poor seed years rendering pinyon a notoriously erratic resource.

In this paper, we question this uniformitarian assumption and propose an alternative hypothesis that derives from a deeper understanding of pinyon pine ecology. What if one-size-fits-all, boom-and-bust pinyon cycling was not universal, and instead evolutionary processes generated significant variability in cone and seed procurement across the Great Basin? We argue here that significant ecological differences separated the pinyon pine woodlands of the western Great Basin (WGB) from those of the central Great Basin (CGB), carrying major implications for pinyon procurement practices of people living there.[1] We hypothesize that regional and interacting ecological factors impacting pinyon cone harvesting and processing practices help explain the startling disparities in the archaeological evidence.[2]

PINYON HARVESTING STRATEGIES BASED ON CONE MATURATION

Archaeologists and many others have long attempted to characterize exactly how Great Basin communities gathered and processed pine nuts (Bettinger 1999; Bettinger and Baumhoff 1983; Chamberlin 1911; Dutcher 1893; Egan 1917:241; Fowler 1989:49–53; Hoffman 1878:473; Kelly 1932, 1964; Lanner, 1981:102; Lowie 1909, 1924; Madsen 1986:29; Muir 1894; Simms 1985a, 1985b, 1987:121–124; Steward 1933, 1938; Stewart 1941; Wheat 1967). Beginning with McGuire and Garfinkel (1976), most Great Basin archaeologists have generically compressed these various practices into categories based on the stage of cone maturation—that is, *brown cone* and *green cone* strategies.

The brown cone strategy describes pinyon nut harvesting that begins when the cones are fully mature, brown, woody, and loosely attached to the branches, usually in mid-late September (Hoffman 1878:473). Nuts already fallen from the trees are picked up and ripe pine cones are pulled from trees with poles, sometimes struck with a stick to free the loosely enclosed nuts. Caloric returns from this simple technology are relatively high, on the order of 850 to 1,500 cals./hr. (Simms 1985a:Table 3, 1985b). If mats are placed under cone-bearing trees (Lanner 1981:102; Steward 1933:241) that rate can rise to more than 4,000 cals./hr. Only a handful of wetland plant taxa generate return rates comparable to brown-cone procurement of pinyon nuts (Zeanah 2002:237).

The contrasting green-cone strategy harvests begin when the seed cones are still immature, green, fleshy, pitch-covered, tightly closed, and strongly attached to the branches, commonly 2–4 weeks before maturity (Dutcher 1893; Steward 1933:241–242, 1938:28). John Muir well summarized this strategy (Muir 1894; see also Rhode 1988):

> 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].

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."

McGuire and Garfinkel (1976:84) were the first archaeologists to rank-order the brown cone and green cone procurement strategies, defining a cultural evolutionary sequence that took place ~A.D. 600 when "a whole new regimen of pinyon harvesting, including the roasting of green cones" began. 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).

Despite minimal comparative evidence, diet breadth and transport models suggest that brown cone harvesting should have been included in the diet early in prehistory (Zeanah 2002). Some have argued that the presumed higher costs of green cone harvesting caused this practice to be delayed until increased residential activity within the pinyon-juniper woodlands occurred (Barlow and Metcalfe 1996; Hildebrandt and Ruby 2006; Jones and Madsen 1989; Rhode 1990; Zeanah and Simms 1999).

EXPLAINING ANCIENT PINYON PINE PROCUREMENT

With the green-brown cone strategies in mind, two contrasting hypotheses have emerged to explain long-term patterns of pinyon procurement in the Great Basin (Fig. 1).

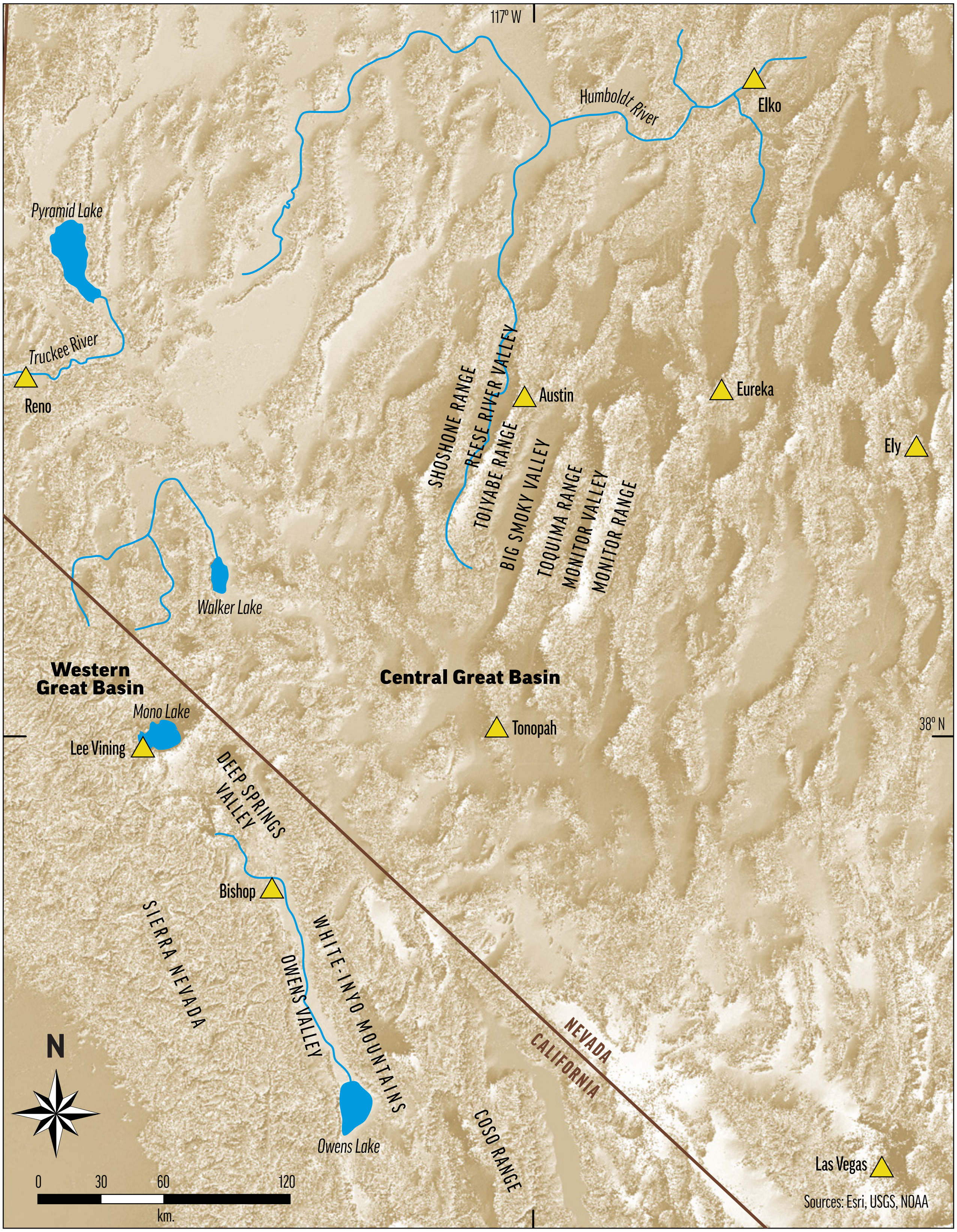

Figure 1. Nevada and eastern California, indicating the western Great Basin and central Great Basin regions and other locations referenced in this study.

Early Intensive Pinyon Use

This hypothesis holds that full-scale pinyon exploitation—the kind described by Steward and attested to archaeologically throughout the Great Basin—was routinely practiced in the Intermountain West soon after pinyon arrived in central Nevada, roughly 5,000–6,000 years ago (Thomas 1971, 1973, 1981), and more recently in the WGB. This hypothesis holds that Great Basin hunter-gatherers should have added pinyon to their diet whenever and wherever the nuts were locally available. Optimal foraging models hold that use of any particular food resource (including pinyon pine nuts) can only be understood in the context of other foraging options at the time (Kelly 1997; Rhode 1980; Simms 1987). This caveat includes other behavioral options (including childcare or participating in rituals), but to date, most attention has focused on trade-offs involved in field processing and transport costs to camp.

Great Basin foragers rapidly learned the various ways for procuring and processing pine nuts soon after the pinyon pine arrived in their region; they relied on pinyon nuts as their primary food source for subsequent millennia. Others have proposed similar early and significant exploitation of pinyon elsewhere in the Great Basin (Basgall and Delacorte 2012; Basgall and McGuire 1988; Cunnar et al. 2019; Hildebrandt and Ruby 1999; Lechner and Giambastiani 2009; Madsen 1981; McGuire and Garfinkel 1980; Reynolds 1996, 1997; Rhode 1987:218–219).

Late Intensive Pinyon Use

Bettinger (1999:65) proposed an alternate hypothesis that "intensive pinyon 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." This hypothesis is supported by considerable archaeological research in the Owens Valley, California (Bettinger 1975, 1976a, 1977, 1989, 1994, 1999, 2015; Bettinger and Baumhoff 1982, 1983; Delacorte 1990; Giambastiani 2007; McGuire and Garfinkel 1976). Although people lived in the lower pinyon woodland for millennia, this hypothesis holds that pine nuts remained a secondary resource in the WGB because people relied more heavily on other food sources. These foragers opportunistically took pinyon seeds using a simpler, less costly brown-cone (ripe cone) strategy to supplement their diet. The hypothesis of late intensive pinyon dependence specifically links the switch to labor-intensive green-cone (immature cone) procurement strategy to Numic-speaking processors, who out-competed pre-Numic travelers and subsequently spread out of the WBG across the rest of the Great Basin.

OPERATIONALLY DEFINING PINYON ARCHAEOLOGY

Great Basin archaeologists exploring these two hypotheses have routinely classified habitation sites within the pinyon-juniper woodland as "pinyon settlements," "pinyon camps," and so forth—all characterized by flaked stone tools and debris, milling gear, stone circles, and often pottery (e.g., Basgall and Giambastiani 1995; Bettinger 1975, 1976a, 1989; Delacorte 1990; Hildebrandt and Ruby 2006; Madsen 1986:31–32; Reynolds 1996; Simms 1989:17–18; Thomas 1971, 1973). Archaeologists tend to interpret one or more larger rock-ring features in the pinyon-juniper woodland as house foundations for fall and/or winter dwellings. Small circular groupings of stones that lack internal living areas are typically taken to be remnants of green-cone processing features or caches (hence implying a green-cone strategy). The presence of millingstones and handstones in the pinyon-juniper zone is often seen as representing pine nut processing in which roasted pinyon nuts were hulled, ground into flour, and cooked.

Numerous difficulties arise from these vague arguments and assumptions linking the behavioral and archaeological correlates of pinyon procurement for both competing hypotheses sketched above.

Rock Rings

Most archaeologists agree that many of the stone circles within the modern pinyon-juniper woodland are likely related to pinyon procurement but have long struggled with operationally distinguishing between domestic house foundations and rock-encircled features for pinyon processing (e.g., Bettinger 1975; Thomas 1988, 2020:411–415, 820–830; Thomas and Bettinger 1976). These simple stone circles range across a functional continuum from rough-and-ready features intended for hunting disguise to well-constructed house foundations, often with doorways, designed to hold a non-stone superstructure in place.

Thomas' (1971, 1973) regional randomized survey of the central Reese River Valley documented 11 stone circles made of small boulders, with the circles ranging from 2 to 4 m. in diameter (1971:149–150). The follow-up survey of the pinyon ecotone of the lower Toiyabe Range (east side of the Reese River Valley) mapped 32 more stone rings ranging from 2 to 6 m. in diameter (Hatoff and Thomas 1976; Thomas et al. 1976; Williams et al. 1972). Bettinger (1976b) excavated one of these, a Western Shoshone house with a terminal occupation dating to A.D. 1880–1890. Although we concluded that nearly all the Reese River rock rings were domestic house foundations on the basis of their size and structure, Wells (1983) and Giambastiani (2007) suggested instead that most were more likely built for pinyon cone storage.

Bettinger's (1975) randomized Owens Valley survey (WGB) recorded 128 circular floors, most of them stone-encircled and ranging from 1 to 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 pinyon-nut caches—but he did not attempt to distinguish between them because of the multiple ambiguities involved (1975:145–46).

Delacorte (1990:85–89) grappled with the same issue for the 37 rock rings recorded in his Deep Springs Valley survey (WGB), where the maximum diameter averaged ~4 m. and ranged from 1.1 to 9.0 m. (1990:85, Table 4.3). He concluded that these rings served diverse functions, some as foundations for wood or brush domestic structures (after Steward 1933:263–66, 1941:334–35), others as caches (Steward 1933:242, 1941:332) or features for processing pinecones (Bettinger 1989). Delacorte added that some of the rock-ringed features likely served multiple functions through time, constructed initially as domestic structures, then later reused as pine-nut roasting facilities. Whereas a feature's size or location might preclude some functions—extremely small rings could hardly have served as house foundations (Bettinger 1975:145–46; 1991:665)—Delacorte felt that excavation was required to define specific function(s).

Bettinger (1975:145–46) 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." The truth is that today, Great Basin archaeologists are no closer to defining these baseline distinctions (without detailed excavations) than they were nearly five decades ago.

Milling Gear

Archaeologists generally regard millingstones and handstones recorded in the pinyon-juniper woodland as somehow related to pine-nut processing, but readily acknowledge that they could have been used for multiple other functions.

The randomized regional sampling of the Reese River Valley was puzzling because only a handful of millingstones occurred among the 2,500 finished artifacts encountered. The puzzle became more complicated when McGuire and Garfinkel (1976:Table 1) observed that although grinding stones were scarce at Reese River, they were "ubiquitous" in Owens Valley (Bettinger 1975, 1976a) and elsewhere in the pinyon-juniper woodlands of the WGB—hardly in keeping with the hypothesis that promoted pinyon as the staple Great Basin resource whenever and wherever it occurs (Thomas 1973; Thomas et al. 1976; Williams et al. 1972).

Bettinger (1999) and Zeanah (2002) compounded this millingstone enigma by comparing regional distributions and frequencies of grinding stones and rock ring features:

- If the foraging communities of the Reese River (CGB) and Owens Valley (WGB) relied so heavily on prehistoric pinyon procurement (as Steward had documented for the ethnohistoric period), and
- if millingstones and rock rings are somehow diagnostic of pinyon procurement, then why does the CGB 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 Delacorte 1990; Delacorte et al. 1992; Giambastiani et al. 2012; Kelly 2001; Lechner and Giambastiani 2009; Madsen 1986; Simms 1985a:169; Zeanah 2002).

Testing competing hypotheses regarding the nature and antiquity of pinyon procurement is complicated by multiple issues that cloud direct linkage of pinyon procurement behaviors to their archaeological diagnostics. As noted, this is because pinyon harvesting has routinely been defined in the archaeological record by the presence of millingstones and rock rings within the contemporary pinyon-juniper woodland (Bettinger 1976a; Delacorte 1990). Hildebrandt and Ruby (2006) argued that Bettinger, Delacorte and others made the mistake of combining rock rings and millingstones together as if they meant the same thing. Instead, Hildebrandt and Ruby found that millingstones went through the entire sequence (and could represent brown cone harvest/processing), but rock rings (the majority of which were smaller than house rings, built on rock outcrops and so forth) were mostly used after 1,500 B.P. and probably represented green-cone caches. Hildebrandt and Ruby note they found many more rock-ring caches (without charcoal) than active green-cone processing features (with charcoal). These investigators documented a chronological sequence for these two feature types, with the caches representing a passive technique where the green cones can ripen, and people could return to them later. Although this technique was risky, it cost very little to produce many such caches.

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). Current efforts toward analyzing starch from pinyon and other plants hold great promise for assigning specific functions to individual groundstone artifacts (Louderback et al. 2021; Rhode and Richey 2020), but the problems are far from resolved.

Subsequent attempts to distinguish stone circles used for house foundations from those employed for pinyon after-ripening or as cone/nut caches remain sketchy (Simms 1989:18; Thomas 2023:Chap. 12; Vierra 1986). This problem compounds the undeniable fact that whereas millingstones and rock rings are somehow related to past pinyon procurement, nobody has satisfactorily explained the radically different frequencies and distributions between the CGB and WGB—both known to be prime pinyon-dependent regions in the past.

Complexities in Cone and Seed Biology: Modern Forestry Perspectives

Modern forestry practices help to shed light on some of these conundrums. Contemporary forestry and nursery institutions require large quantities of conifer seeds to provide seedlings for reforestation (Edwards 1980; Karrfalt 2008; Kolotelo 2006; Linhart and Mitton 1979). Public agencies, such as the USDA Forest Service, and private forestry companies employ standard sequences in collecting conifer seeds that require considerable knowledge about cone and seed biology for the species and geographic region. Comparing these to the processing practices of Great Basin Shoshoneans can be informative.

Modern seed processing cycles begin with an assessment of the maturing cone crops. Collecting cones from natural stands and seed orchards requires precise timing of cone maturity to avoid losing seeds to natural dispersal, predation, or decay, and to ensure the greatest seed viability. Sampling cones and seeds for their condition is done prior to full maturity (generally August to September; Edwards 1980). Year-to-year variability in cone productivity that characterizes conifer species is also a critical monitoring element for seed-collection programs.

Collecting ripe cones in a "good cone-crop year" is the most efficient because the seeds can be rapidly dried and shaken out. However, when pressing research or conservation concerns dictate that seeds be obtained regardless of the crop size or condition, as well as in light-cone years, it is necessary to collect before natural predators get the seeds. In extreme cases, ripening cones are bagged in mid-summer on the tree in wire cages to allow ripening *in situ*. Unripe cones can be collected and "after-ripened," which requires experience and careful 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). Misjudging the timing or conducting the after-ripening procedures incorrectly results in cones remaining sealed closed ("case-hardened"), and the seeds will not mature.

Consider a recent example from a research project in which one of the authors (Millar) has been involved in the study of genome sequencing of Great Basin bristlecone pine (*Pinus longaeva*; https://whitebarkfound.org/our-work/genome-projects/bristlecone-pine-genome-project/). Logistically, only a single year was available to collect cones from the White Mountains, Cal. (WGB) population and obtain the few seeds needed to sequence the genome. The seed crop that year was meager. Grantfunding obligations required that a very old 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 (first year, immature cones) in trees early in spring and frequently through the 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 a few young unripe cones in mid to late summer to test maturity. Those early cones were 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 collected and after-ripened. This cone produced a few viable seeds that became the DNA material for sequencing. This example illustrates the challenges in obtaining even a few viable seeds using low-technology methods.

Post-collection handling also requires careful attention to assure high-quality seeds. Freshly picked cones contain moisture, which 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 moisture problems. Seed collection facilities usually promote uniform drying by field-storing 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 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 used to dry them (Karrfalt 2008). These sacks cannot be stored in direct sunlight because overheating damages cones, but they cannot remain wet for extensive periods because that encourages growth and spread of fungi. If mature pinyon 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 (slicing the cone vertically and observing the appearance/size of seeds), and internal seed condition through cutting tests (slicing individual seeds and observing the internal condition of seeds; 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—commonly cool-to-frozen and dark for longest storage. Even with optimal preparation and storage conditions, however, viability (potential to germinate and produce a seedling) of stored seeds varies by species, from weeks to decades. Pinyon seed viability 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 Bassett 1983).

Because pine nuts are used in contemporary cooking, common food-safety storage recommendations are also informative. Pinyon 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 for up to 12 months. Regardless of the nuts being shelled or unshelled, if the nuts turn rancid, they are still edible, although many consider them unpalatable. These modern practices highlight the complexities of combining the science of cone and seed biology with experience and subjective judgment.

AN ECOLOGY-BASED PINYON PROCUREMENT HYPOTHESIS

We propose that just as in modern forestry nurseries, foragers routinely employed multiple strategies over the weeks of cone and seed maturation, varying their practices depending on the year and condition of the cone crop. Here we advance a multi-dimensional ecological hypothesis that proposes significant regional differences in pinyon cone and seed morphology, competitive seed predation, interannual cone production and masting, fire regimes, and climatic factors within the Great Basin. We suggest that the regional differences in these interacting factors had significant and cumulative implications for pinyon procurement strategies in Owens Valley (WGB) compared to Monitor Valley and the rest of the CGB. These differences and their implications might help explain why stone circles and millingstones are vastly more frequent in the WGB than in the CGB.

ECOLOGICAL VARIABILITY IN PINYON REPRODUCTION AND WOODLAND CONDITONS ACROSS THE GREAT BASIN

Pinyon trees reach sexual maturity in ~25–35 years, but do not produce large seed crops until trees are ~100 years old (Krugman and Jenkinson 1974; Meeuwig et al. 1990). Pinyon pines require two years to produce a mature seed cone with ripe seeds. Buds destined to become seed cones are initiated in mid spring (~May) approximately 2.25 years before cones are fully mature. In spring of the following year pollination occurs (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, but cones and seeds do not mature until the following growing season. Second-year cones are much larger than first-year conelets, and 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 cones and seeds become capable of falling off the tree. 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). Like most pine species, pinyon 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).

We describe five conditions that we hypothesize differ significantly between the WGB and CGB, and if so likely affected ancient foraging practices: (1) diversity and abundance of pinyon cone and seed predators; (2) interannual variability in cone production (masting); (3) cone morphology, size, seed number, and seed-coat thickness; (4) fire regimes and cone morphology; and (5) climate and weather effects. We suggest that these ecological factors, individually and cumulatively, resulted in significantly greater unripe (green) cone harvesting by foragers living in the WGB and far greater reliance on ripe (brown) cone harvesting by people in central Nevada. While some of these conditions have not been well documented, we propose them for further validation.

Regional Differences in Diversity and Abundance of Pinyon Cone and Seed Predators

Conifer cones and seeds are important sources of nutrition for mammal and bird species, and pinyon pine is no exception. Non-human seed predators damage and remove pinyon seeds, with widespread and cumulative impacts that reduce the volume of nuts available for competing human use. We believe that the differences in number of seed predator species, their modes of foraging, and local abundances across the Great Basin are critical to understanding the strong competition for pinyon nuts faced by humans and their decisions about harvesting strategy.

The WGB supports far more species of pinyon seed predators than the CGB. Table 1 lists the presence/absence of 29 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 pinyon pine is no exception. Although studies have been done on pinyon insects, no comprehensive evidence exists to indicate differences in their numbers, abundances, or significance between the Great Basin regions. Of the remaining 29 bird and mammal predators, 26 occur in the WGB and 15 in the CGB. Only three species (Woodhouse's Scrub Jay [*Aphelocoma woodhouseii*]), (cliff chipmunk [*Neotamias dorsalis*], and rock squirrel [*Otospermophilus variegatus*]) are found in the modern CGB and not in the WGB; one additional species (black bear, *Ursus americanus*) may have occurred in the paleohistoric CGB as well as WGB and was extirpated ~90–140 years ago (Lackey et al. 2013). However, documentation of the newspaper and journal references on which these claims are made is not provided, making the basis for range extension of black bears across Nevada unsupported. Pinyon nuts are an important component of bears' diet, especially before hibernation. Most important among the differences are tree squirrels (*Tamiasciurus* spp.), which occur in the WGB and not in the CGB. Tree squirrels are highly evolved, voracious cone predators and seed consumers; a

Table 1

MAJOR PREDATOR SPECIES OF PINYON PINE CONES AND SEEDS IN THE WESTERN AND CENTRAL GREAT BASIN

TAXON– Scientific Name	TAXON– Common name	Western Great Basin[a]	Central Great Basin[a]	Importance to Pinyon seed predation	Predation context: Tree (T), Ground (G)	References
Insects						
Diverse Species		ukn[b]	ukn[b]	Very important	T, G	Christiansen and Whittam 1993; Forcella 1978, 1980; Jenkins 1984; Negron 1995
Birds						
Nucifraga columbiana	Clark's Nutcracker	+++	++	Very important	T, G	Audubon Guide to North American Birds 2022; Hutchins and Lanner 1982; Vander Wall 1988; Vander Wall and Balda 1981
Gymnorhinus cyanocephalus	Pinyon Jay	+++	++	Very important	T, G	Audubon Guide to North American Birds 2022; Balda and Bateman 1971; Vander Wall and Balda 1981
Aphelocoma californica	Western Scrub Jay	+++	absent	Very important	T, G	Audubon Guide to North American Birds 2022; Bardwell et al. 2001; Beedy and Pandolfino 2013
Aphelocoma woodhouseii	Woodhouse's Scrub Jay	absent	+	Moderately important	T, G	Audubon Guide to North American Birds 2022
Cyanocitta stelleri	Steller's Jay	+++	absent	Moderately important	T, G	Audubon Guide to North American Birds 2022; Beedy and Pandolfino 2013
Loxia curvirostra	Red Crossbill	+++	absent to rare	Very important	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	Moderately important	T, G	Beedy and Pandolfino 2013
Mammals						
Tamiasciurus douglasii	Douglas's tree squirrel	+++	absent	Highly important	T, G	Benkman and Siepielski 2004; Smith 1970; Steele 1999
Callospermophilus lateralis	Golden-mantled ground squirrel	+++	+++	Moderately important	T, G	Bartels and Thompson 1993; Hutchins and Lanner 1982
Peromyscus maniculatus	Deer mouse	+++	+++	Moderately important	G	Hollander and Vander Wall 2004
Peromyscus sonoriensis	Pinyon mouse	+++	+++	Moderately important	G	Hollander and Vander Wall 2004
Neotamias speciosus	Lodgepole chipmunk	+++	absent	Moderately important	T, G	Hall 1946; Jameson and Peeters 2004; Hollander and Vander Wall 2004
Neotamias dorsalis	Cliff chipmunk	absent	+++	Moderately important	T, G	Hall 1946; Jameson and Peeters 2004; Hollander and Vander Wall 2004
Ammospermophilus leucurus	White-tailed antelope ground squirrel	+++	++	Moderately important	G	Hollander and Vander Wall 2004
Neotamias umbrinus	Uinta chipmunk	++	++	Moderately important	T, G	Hall 1946; Jameson and Peeters 2004; Hollander and Vander Wall 2004
Neotamias amoenus	Yellow-pine chipmunk	+++	absent	Moderately important	T, G	Hall 1946; Jameson and Peeters 2004; Hollander and Vander Wall 2004
Neotamias minimus	Least chipmunk	+++	+	Moderately important	T, G	Hollander and Vander Wall 2004
Perognathus mollipilosus	GB pocket mouse	+++	+++	Moderately important	G	Hollander and Vander Wall 2004
Ursus americanus	Black bear	+++	?[c]	Moderately important	T, G	Goodrich 1991; Kuhn and Vanderwall 2007; Lackey et al. 2013
Dipodomys panamintinus	Panamint kangaroo rat	+++	absent	Moderately important	G	Hollander and Vander Wall 2004
Dipodomys ordii	Ord's kangaroo rat	+++	+++	Moderately important	G	Hall 1946; Jameson and Peeters 2004; Hollander and Vander Wall 2004

Table 1 (*Continued*)

MAJOR PREDATOR SPECIES OF PINYON PINE CONES AND SEEDS IN THE WESTERN AND CENTRAL GREAT BASIN

TAXON– Scientific Name	TAXON– Common name	Western Great Basin[a]	Central Great Basin[a]	Importance to Pinyon seed predation	Predation context: Tree (T), Ground (G)	References
Neotamias panamintinus	Panamint chipmunk	++	absent	Moderately important	T, G	Hall 1946; Jameson and Peeters 2004; Hollander and Vander Wall 2004
Neotamias senex	Shadow chipmunk	++	absent	Moderately important	T, G	Hall 1946; Jameson and Peeters 2004; Hollander and Vander Wall 2004
Sciurus griseus	Western gray squirrel	++	absent	Minor importance	T, G	Matson et al. 2010; James Patton (personal communication 2020); Verts and Carraway 1998
Otospermophilus beecheyi	California ground squirrel	+++	absent	Minor importance	G	Smith et al. 2016
Otospermophilus variegatus	Rock squirrel	absent	+	Minor importance	T, G	Oaks et al. 1987
Canis latrans	Coyote	+++	+++	Minor importance	G	Hall 1946; Jameson and Peeters 2004; Lendrum 2017
Megascops asio	Screech owl	++	++	Minor importance	G	Shuford and Fitton 1998
TOTAL, excluding insects (29)		**26**	**15[c]**			

[a] +++ is more abundant, + is less abundant.

[b] Although seed and cone insects are very important predators on pinyon pine, and although information exists on some of them, we have no comprehensive understanding of the differences between the WGB and CGB.

[c] Although bears are absent today from interior Nevada, including the region we identify as the central Great Basin, there is some evidence bears may have been in the prehistoric Great Basin (Lackey et al., 2013). This evidence is unsupported, however, and for now we exclude them from the CGB.

single squirrel can remove (and destroy for other purposes) 80% of the unripe cones developing on a single pine tree (Fig. 2; Benkman et al. 1984). Other cone predators found only or in greater abundance in the WGB further reduce the number of cones that come to maturity, including corvid and crossbill bird species. In sum, we propose that a larger number of predator species, and the greater abundance, efficiency, and capacity of several key species (tree squirrels, Clark's Nutcrackers, and black bears, Fig. 3) leads to far greater consumption of both immature and ripe pinyon seeds in the WGB than the CGB.

From this, we infer that human foragers in that region were likely more vulnerable to competition for mature cones as well as ripening cones than their CGB counterparts. To procure adequate pinyon supplies, foragers in the WGB would be forced to harvest increasingly more unripe cones before their competitors got them. Because significant pinyon seed-predator species are relatively more rare in the CGB, human foragers had greater opportunity to secure adequate pinyon seeds—including those from ripe cones, which had the highest quality seeds. On this basis, we infer that CGB foragers regularly could—and did—delay harvest until the cones fully ripened, thus choosing the lower-cost strategy.

Regional Differences in Pinyon Cone Masting

Unlike earlier anthropologists who assumed that Basin-wide boom-and-bust cone cycling ("masting") rendered pinyon seeds an erratic and unpredictable resource base, our ecological hypothesis emphasizes annual fluctuations in pinyon cone productivity as an evolutionary mechanism that evolved in regions of high seed predation to compensate for losses to predators and to ensure that pinyon trees had adequate seeds for regeneration (Koenig 2021).

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). Predator satiation—by far the oldest, continuously accepted factor for the evolution of masting (Koenig 2021; Salisbury 1942; Zwolak et al. 2021)—addresses masting as an adaptive 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 provides more seeds than existing predators can consume

Figure 2. 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) In the western Great Basin, Douglas's tree squirrels scatter-hoard cut cones into small holes in the ground below trees; (c) Douglas's tree squirrels harvest unripe pinecones from branches and allow them to drop to the ground; (d) Fresh pine branch tips clipped by Douglas's tree squirrels in late spring to serve as a food source (fresh cambium) until cones can be retrieved when snow melts. Here the branch tips remain after the snow has melted.

(saturating the predator population) and allows adequate surplus seed for tree reproduction (Buonaccorsi et al. 2003). Predator populations that increase in high-crop years crash in subsequent years of low fruit production. Erratic timing of mast years stymies the evolution of predator populations from synchronizing with fruit production (Pearse et al. 2020).

Given an evolutionary capacity for masting in a species, the favorable sequence of years required for a mast crop to develop can be triggered at large landscape scales by proximal conditions (Ascoli et al. 2021; Hacket-Pain and Bogdziewicz 2021). Annual and seasonal weather are the most important proximate factors determining whether a mast crop is produced or not; bud initiation and fruit development may be "cueing up" for a large crop only to be "vetoed" by unfavorable weather conditions during the fruit development season (Fig. 4; Ascoli et al. 2021). Erratic intervals between mast years correlate with large scale regional climate models, such as ENSO (El Niño-Southern Oscillation), as well as annual weather that favors or inhibits fruit production (Koenig 2021; Wion et al. 2021).

Figure 3. Black bear (*Ursus americanus*) is another important consumer of pinyon cones and seeds. Black bears occur in the Western Great Basin and not in the Central Great Basin: (a) Bear tracks in the sand of the Bodie Mountains, east of the Sierra Nevada pinyon woodlands during the cone-ripening period; (b) and (c) large amounts of cones and their seeds are consumed by bears, as shown from hulls remaining in their scat. (Fig. 3c photo credit: David Rhode.)

We suggest that significant differences in pinyon cone and seed predation (Table 1) triggered evolution of strong masting behavior in WGB pinyon woodlands, and weaker or no masting in the CGB. If so, the western woodlands only occasionally produced heavy pinyon seed crops and were interspersed erratically with lean or intermediate crop years. While aware of no published evidence for this hypothesis, unpublished observations confirm strong masting in the WGB (Arnaldo Ferreira [USFS, regional geneticist], personal communication to CIM, 2022; Millar, 30 years of unpublished observations in the WGB). Pinyon pinecone reproduction at the species level is described variably, such as (1) pinyon is recognized as a masting species, with trees producing "good cone crops" every 3–7 years (Meeuwig et al. 1990); (2) pinyon pines produce "large crops" in 1 to 3 of 10 years (Forcella 1981); and (3) "years between cone crops" in pinyon are 1–2 years (Bonner and Karrfalt 2008; Krugman and Jenkinson 1974).

If substantiated, differential pinyon masting has critical implications for Great Basin human foragers. We hypothesize that during sparse cone-crop years in the WGB, Inyo-Mono foragers were forced to harvest unripe cones to outcompete the numerous, abundant, and diverse non-human cone and seed predators. Consequently, this early harvest required that WGB foragers resort to costly after-ripening and drying techniques to release seeds and assure mature nutritive quality. Because CGB foragers lived where evolutionary forces minimized pinyon masting, producing stable annual cone production, we propose that CGB human foragers could regularly rely on harvesting fully ripened, woody cones bearing mature

Figure 4. Maturing pinyon cone crop thwarted by abiotic conditions late in the second year. A moderate cone crop had been developing in pinyon pine woodlands during 2020 and 2021 in the Wassuk Range, Western Great Basin. In mid-summer 2022, however, weather conditions occurred that caused the crop to abort prior to maturation, as seen by the three small, closed cones in the center. Cones remained case-hardened and produced useless, immature seeds throughout the population. The three larger, open cones around the small ones are healthy and mature, contained ripe seeds, and are shown for comparison. The large cones derived from the successful 2022 crop in central Nevada.

seeds. The lack of significant seed-predator competition further ensured that adequate numbers of cones and seeds were available on pinyon trees throughout the cone-maturation period for mature cone harvesting of the most nutritive seeds. We suggest that the relative ease of collecting ripe cones typically obviated any need to harvest or after-ripen immature cones.

Differential Cone Morphology

Pinecone 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 influence the direction of cone morphology in ways that thwart predators. Pines growing in regions of strong predator pressure evolve thicker cones that are tightly attached to the stem and often at an oblique angle, have fewer and reflexed scales (sharper tips pointing outward as “armor”), and fewer viable seeds but with seed coats twice as thick (Fig. 5; see also, Benkman and Siepielski 2004; Gurnell, 1983; Linhart 1978; Smith 1970). Tree squirrels in particular affect the evolution of these defensive cone traits in pine species, for instance in limber pine (*Pinus flexilis*) and whitebark

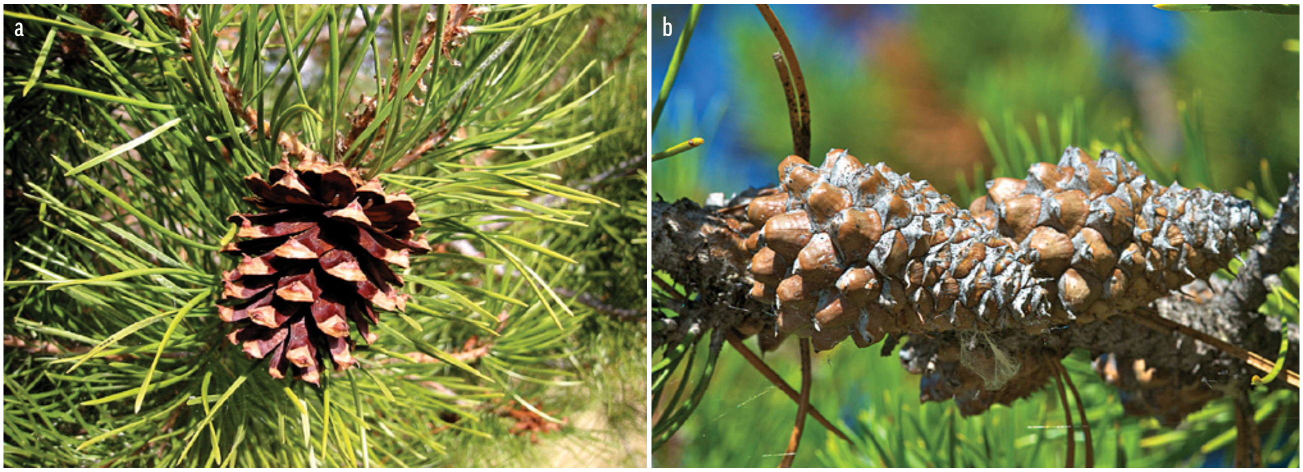

Figure 5. Geographic variation in cone serotiny and cone-scale thickening of lodgepole pine ecotypes, varying by fire regimes and tree squirrel abundance: (a) *Pinus contorta* var. *contorta*, shore pines, do not experience short-interval, high severity fire, and have evolved cones that open on the branch annually (photo credit: Walter Siegmund, CC BY-SA 3.0 http://creativecommons.org/licenses/by-sa/3.0/, via Wikimedia Commons); (b) *Pinus contorta* var. *latifolia*, Rocky Mountain lodgepole pines, experience frequent severe fires and have evolved cone serotiny. Where they grow in the presence of fires and seed predators, such as tree squirrels, they develop thickened as well as serotinous scales (photo credit: Craig Benkman).

pine (*P. albicaulis*) in the Great Basin (Siepielski and Benkman 2007).

We hypothesize that regional variation in cone and seed morphology has evolved in pinyon pine woodlands of the Great Basin. In the WGB, where millennia of evolutionary pressure was exerted by cone and seed predators, we expect pinyon cones to be heavier and thicker, armed with defenses to prevent opening or chewing, strongly attached to the stems, and containing fewer, smaller seeds per cone. In the CGB, where predator pressure was minimal, this protection would not evolve; from the tree fitness standpoint, cones would evolve that easily drop off the tree at maturity, open readily, contain seeds that disperse easily, and hold many, large seeds per cone. We know of no studies that have evaluated geographic variation in pinyon cone morphology, either in the Great Basin or beyond, and offer this as an hypothesis for testing.

If this hypothesis holds, cone-morphology adaptations that evolved to thwart cone and seed predators would have impacted human foragers as well. In the WGB, where cone morphology was adapted to resist predators, human foragers would also find pinyon pinecones a high-cost food source and be likely to rank pinyon lower than other resources. Further, heavily armored, difficult to open cones in that region would require after-ripening processes similar to those employed for green cones. By contrast, foragers in the CGB, where cone and seed predators were sparse, found cones that were easy to open and did not require costly after-ripening activity.

Fire Regimes and Cone Morphology

Not unlike cone-predator pressure, fire regimes are natural-selection forces that influence the evolution of cone morphology (Lamont et al. 2020). Throughout the genus *Pinus*, serotinous cones have evolved convergently in regions of high-severity fires—i.e., those that kill trees at the landscape scale as opposed to surface fires that mature trees can survive. Serotiny refers to cone traits that resist burning from high severity crown fires. Serotinous cones neither open at maturity nor fall from the tree. Instead, they remain attached to the branch and closed, with scales tightly sealed by resin and seeds securely held in the cone, capable of surviving for years to decades (Lamont et al. 2020). Although fire kills the trees, heat from the fire melts the resins of the closed cones, and cone scales gradually open a few days after a fire passes. Seeds, whose viability is protected from overheating by thick scales, fall on freshly disturbed (burnt) soils where they germinate and grow with little competition.

Serotiny develops in areas of primary winter precipitation where fuels accumulate, and fires are severe and frequent (Lamont et al. 2020). Vulnerable pines are highly flammable and more 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 the development of cone serotiny. Significant variation in degree of serotiny, from highly serotinous to non-serotinous, can occur within species, reflecting geographic differences in fire regimes (Lamont et al. 2020). The co-occurrence of severe fires and tree squirrels further favors the development of thick-scaled, and/or serotinous cones (Fig. 5; Linhart 1978; Talluto and Benkman 2014).

Although pinyon pines do not bear serotinous cones, we postulate that differing fire regimes between the WGB and CGB may nonetheless have affected pinyon cone morphology in ways that would have influenced seed procurement. Although notoriously difficult to evaluate, differences in fire regimes in pinyon-juniper woodlands of the WGB vs. the CGB suggest that natural selection on cone morphology from fire would be expected to be strongest in the west. The few reliable studies on historical fire regimes in Nevada and eastern California indicate that severe fires have been historically more common in the WGB, with return intervals as low as 8–50 years (Baker and Shinneman 2004; Gruell 1997). By contrast, in CGB pinyon woodlands, Bauer and Weisberg (2009) found historic fire regimes during A.D. 1445–2006 were of high severity but 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 WGB, caused fires to occur more frequently and those fires were severe. The highest-confidence studies show that high severity, crown- and tree-killing fires occurred most often in denser pinyon woodlands community types, with no evidence that surface fires burned at the landscape scale in those areas (Baker and Shinneman 2004; Romme et al. 2009).

This combined evidence suggests that differing historical fire regimes may have led to different regional pinyon cone-morphologies in the WGB vs. the CGB. We suspect that the higher severity, more frequent fires in the west exerted greater selection pressure toward thicker cones with a tendency toward persistent closure or delayed and difficult cone opening in the WGB than in the CGB. We hypothesize that foragers harvesting ripe cones in the WGB would have had greater difficulty opening pinyon cones to extract seeds and would have had to resort to after-ripening techniques like those used to harvest unripe cones. Central mountains foragers, by contrast, harvesting thinner, unarmed cones, would have been spared these more costly techniques. Because no systematic studies have evaluated such geographic differences in cone morphology, this remains another testable hypothesis.

Climate and Weather

We further hypothesize that variations in climate across the Great Basin led to further regional differences in pinyon cone production. Cool late summer temperatures favor cone production (Bogdziewicz et al. 2021; Redmond et al. 2012) with a significantly positive relationship between pinyon cone production and spring-summer precipitation (Pearse et al. 2020; Redmond et al. 2012). Although modern late summer temperatures have similar means at comparable elevations in the WGB and CGB, the proportion of spring and summer precipitation differs greatly between those regions (Millar and Thomas 2023:Table 2). Although annual precipitation is higher in the west, the central region experiences roughly twice as much spring-summertime precipitation. Millar et al. (2021) interpreted similar regional differences in summer precipitation in tree growth (for limber pine) throughout the past millennium.

At the most local areal and short temporal scale, hygroscopic closing of mature pinecone scales may have also affected cone procurement practices between the WGB and CGB. Under dry atmospheric conditions, pinecone scales open and seeds disperse; when conditions are humid, cone scales close and seeds remain held inside (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 contemporary climatic conditions, autumn precipitation and relative humidity during the cone ripening and processing period are somewhat greater in the WGB than the CGB, but we are unaware of any specific studies of either factor in Great Basin pinyon populations. Such proximal atmospheric conditions, if severe, would compound the challenges to pinyon foragers more in the WGB than in the CGB.

RE-EVALUATING PAST PINYON PROCUREMENT STRATEGIES

This brings us back to the competing hypotheses regarding early vs. intensive pinyon use in the Great Basin. Given the nuanced and shifting pinyon procurement strategies of modern forestry institutions, we agree with Simms (1987:124) that pinyon procurement is better 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." So viewed, pinyon maturation was considered by foragers as an ecological process, not an abrupt transition from green to brown, and intensive green-cone harvesting does not necessarily provide a "maximum yield" relative to the brown-cone strategy. This is more a matter of adjusting diet breadth to suit the conditions at hand. Brown pinyon cones should always be taken upon encounter. Green cone strategies are only added to the subsistence strategy when the people intensify production. In some places and times they did, and other places and times they did not.

Despite variable duration, technology, and rates of caloric return for the specifics of harvesting pine nuts, we think that the range of practices analogous to those used by modern forestry practitioners likely existed from the arrival of pinyon in the CGB ~6,000 years ago (Cole et al. 2013; Grayson 2011:253–58, Fig. 8.16; Wigand 2002). In years with locally abundant pinyon crops, there would have been little reason to collect 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, we suspect that Great Basin harvesters knew precisely how to proceed—either by moving to better locations with higher cone productivity or by harvesting immature cones where they lived.

The available archaeological record also supports early intensive pinyon procurement wherever it was appropriate. Although Bettinger (1976a:86, 1989) and Delacorte (1990:235) hypothesized that intensive, green-cone strategies and residential pinyon camps universally post-date 1,350 B.P., archaeological surveys in Papoose Flat (central White-Inyo Mountain Range) and the Coso Range suggest that green-cone pinyon processing likely pre-dates this estimate by two millennia. Reynolds (1996:155, 1997) found a surprisingly high number of Little Lake and later points associated with rock-ring sites and milling equipment, suggesting that green-cone pinyon 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 suggesting intensified use of upland resources (particularly pinyon) and green-cone processing during the Elko interval. Hildebrandt and Ruby (2006) emphasized that Coso Range sites with rock rings (identified as pinyon caches and pinyon camps) tended to date much later than sites lacking rock rings. Statistically significant associations with rock rings contrasted with the pattern for millingstones, which were strongly 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 [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 [which was] more than a casual resource prior to 1,350 B.P." (Hildebrandt and Ruby 2006:26, 29).

We see green-cone procurement as a time-transgressive process, and find the evidence compelling that Great Basin foragers for millennia have been ecologists of the highest magnitude. They understood the nuances of their environment and exploited the variability of staple resource species accordingly. Given their ecological knowledge and attention to food resources, we think it highly unlikely that foragers required several millennia to learn mid-season (i.e., immature cone) pinyon harvesting strategies. Foragers most likely took advantage, on a year-to-year basis, of the simplest ways to optimize pine nut harvests either early or late season.

CONCLUSIONS

We have enumerated several known and potential differences in ecological factors that affect pinyon cone and seed ecology, and hypothesize that evolutionary processes, predatory impacts, climatic fire variability, and masting processes differed significantly across the Great Basin. We suggest that human foragers responded to these differences with strategies appropriate to their local environment, and in so doing may have even exerted novel selection forces themselves that influenced the direction of pinyon evolution (Millar and Thomas 2023).

We further hypothesize that pinyon woodlands in the CGB are characterized by trees with thinner cones, more seeds/cone, lower rates of seed and cone predation, and considerably lower interannual variability in cone crop size than trees in pinyon woodlands of the WGB. Although cone production does not depend exclusively on cone morphology or cone procurement methods, we suggest that the overall pinyon cone production was vastly more stable and capable of a readily feasible harvest in the CGB than the WGB. If so, then Central Mountains Archaic communities were commonly able to harvest mature pinecones and seeds and experienced less competition from mammalian and avian competitors than western foragers.

We suggest that Steward's landmark concern with boom-and-bust cycles of pinyon unpredictability was likely wrong for the woodlands of the Shoshone, Toiyabe, Toquima, and Monitor ranges. With fewer alternative resources than landscapes to the west, central Nevada foragers could focus on pinyon as a primary food source almost immediately after the species arrived in the region, 5,000–6,000 years ago.

We propose that in comparison with pinyons in the CGB, pinyons in the WGB had thicker cones, fewer seeds/cone, cones that remained 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. The cumulative impact of these ecological factors would have led to more costly energy expenditures to harvest, store, and consume pinyon seeds along the valleys and ranges directly east of the Sierra Nevada. Combined with evolutionary and climatic processes, pressure from squirrels, corvid birds, crossbills, bears, and other pinyon predators forced human foragers to draw upon difficult, costly, and time-consuming methods to successfully harvest unripe cones and risky after-ripening practices to avoid lower quality seeds.

We argue that these multiple ecological factors made pinyon seeds more difficult and expensive to obtain in the Inyo-Mono 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 (less important than the low shrubs) the seed-bearing grasses and artiodactyls of the desert scrub community.

This combination of ecological and climatic factors, many untested, is consistent with Great Basin archaeology. Together these factors may explain the enigma of why the stone circles, at least some of which were likely associated with pinyon processing, are vastly more common in the WGB than the CGB. For approximately 6,000 years, foragers in central Nevada largely harvested ripe pinyon seeds, and rarely needed to build the processing features required when pinyon cones were scarce, as in the WGB woodlands. By contrast, western Great Basin foragers were forced to resort to more expensive, immature-cone harvesting techniques that generated an abundance of archaeological processing features, some of which date back more than 4,000 years.

We find no evidence for an Indigenous intellectual progression from brown-to-green-cone intensification. We think it highly improbable, given the dietary importance of pine nuts, that Great Basin foragers required millennia to learn the ecological behaviors of pinyon cone reproduction and woodland ecology. Those foragers likely knew well how to predict lean harvests more than a year in advance and doubtless shared this knowledge socially through communal pronghorn and jack rabbit hunts and fandangos. Depending on local conditions, the best harvesting options were exploited—sometimes more intensive harvesting was required, sometimes not. We argue that Indigenous foragers were ecological observers of the highest order (Knopf and Däwes 2021; Newman 2021; Teeman 2021). They understood local pinyon ecology, and their community survival depended on crafting such knowledge into resilient mixes appropriate to the changing landscapes at hand.

NOTES

[1]By "western Great Basin" (WGB) we refer to the geographic corridor of valleys and ranges directly east of the Sierra Nevada hydrologic crest, extending along the eastern Sierra

Nevada, and from the Bodie Mountains to the southern Owens Valley. By "central Great Basin" (CGB) we refer to the uplands of the Shoshone, Toiyabe, Toquima, and Monitor ranges, and the valleys/basins around them.

[2]More details are available in Thomas (2023:Chapter 12) and Millar and Thomas (2023).

ACKNOWLEDGMENTS

We thank Drs. David Charlet (College of Southern Nevada, Henderson, Nev.), Donald Grayson (University of Washington, Seattle, Wash.), David Rhode (Desert Research Institute, Reno, Nev.), and Robert Westfall (USDA Forest Service, Albany, Cal.) for thoughtful reviews of an earlier version of this material. Millar also thanks Donald Grayson for discussions regarding black bears in the Great Basin, and for pointing out that conclusions on the prehistoric range of bears in central Nevada are not supported by the data available. James Patton of the University of California, Berkeley provided information on the western gray squirrel. We are especially grateful to the three anonymous reviewers whose thoughtful comments made this a far better contribution, and we are grateful to Dr. Seetha Reddy for working with us on the revised draft. We acknowledge the assistance of Lorann S. A. Pendleton and Diana Rosenthal-Roberson (both at the American Museum of Natural History) for help in preparing this manuscript.

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