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A 14,100 cal B.P. Rocky Mountain locust cache from Winnemucca Lake, Pershing County, Nevada

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Abstract

The remains of approximately 1000 (MNI) Rocky Mountain locusts (*Melanoplus spretus*) from an archaeological cache pit in Crypt Cave, Winnemucca (dry) Lake, Nevada, date to between 14,305–14,067 calendar years before present (95.4 % confidence; 12,238 \pm 18 ¹⁴C yrs. B.P.). The age of this western Great Basin occupation along the shoreline of Lake Lahontan is consistent with occupation of several other

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Western North American terminal Pleistocene sites dating prior to 14,000 cal. B.P., including distinctive petroglyphs on the western shore of Winnemucca Lake dating as early as 14,800–13,200 cal. B.P.

Keywords: Great Basin, Archaeology, Peopling of the Americas, Food cache, Terminal Pleistocene

1. Introduction

Phil C. Orr (1952), Nevada State Museum and Western Speleological Institute, conducted archaeological excavations in a series of caves and rockshelters at Winnemucca (dry) Lake, Pershing County, Nevada, in 1952–1953 (Fig. 1). His excavations at Crypt Cave (26Pe3a), yielded remnants of a buried cache of adult Rocky Mountain locusts (Melanoplus spretus) dated to about 14,100 cal. B.P. (Fig. 1; Orr n.d.; 1952). This feature, with its locust contents, securely documents the earliest, directly dated evidence for human occupation of the Lake Lahontan basin in the Western Great Basin. The cache is coeval with early human occupations at Paisley Caves in south central Oregon (Jenkins et al., 2012; 2013; Fig. 1) and at Cooper's Ferry in west central Idaho (Davis et al., 2019) dating to before 14,000 cal. B.P. Crypt Cave occupants who used the cache may have been culturally related to the carvers of distinctive petroglyphs on the western shore of Winnemucca Lake dating as early as between about 14,800 to 13,200 cal. B.P. (Benson, et al., 2013a). Opportunistic foraging (in which people are able to adapt to a wide range of food choices as they become available) for large quantities of insects was common among subsequent Great Basin Archaic and ethnographic Native American cultures, and the presence of such a foraging strategy during this early period, together with data from other early sites, suggests these early peoples utilized a broad-based subsistence strategy involving seasonal storage.

1.1. Setting

Crypt Cave (elev. 1250 m) is a Pleistocene wave cut cave situated above a Lake Lahontan terrace along the northeastern shore of Winnemucca (dry) Lake. This cave shares this lake terrace with adjacent wave cut caves also containing early archaeological and paleontological deposits including Cowbone (26Pe3c), Guano (26Pe3d), and Fishbone (26Pe3e)

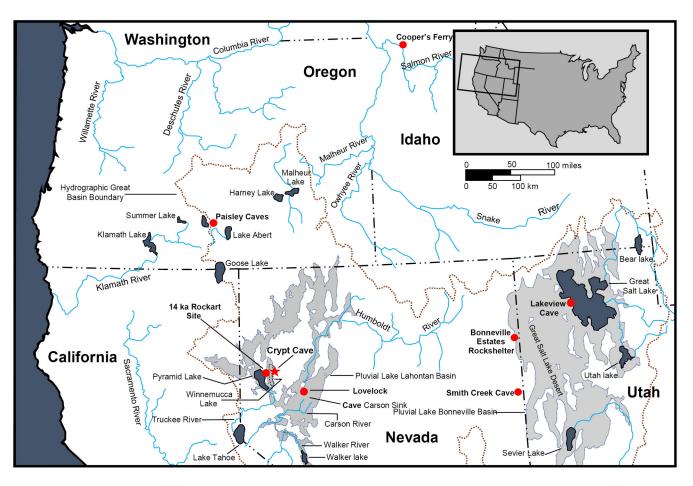


Fig. 1. Site location map for Crypt Cave and other locations mentioned in text.

caves (Orr 1952). Lake Lahontan, an endoreic lake, was comprised of a chain of seven sub-basins interconnected by sills with different elevations controlling sub-basin water inflow and outflow (see Supplementary Material). Lake Lahontan reached a maximum highstand of around 1335 m about 15,500 years ago (Benson et al., 2013b). Although the lake fell rapidly thereafter, δ^{18} O and total inorganic carbon (TIC) values in a core from the Pyramid Lake basin (Benson et al., 2013b) indicates water was flowing across a sill between the two subbasins and that a water body occupied the Winnemucca Lake Basin at the time the locusts were cached by the inhabitants of Crypt Cave (Fig. A1). The precise elevation of Winnemucca Lake at the time remains unknown, but it was likely at or above the 1177 m sill between the two sub-basins.

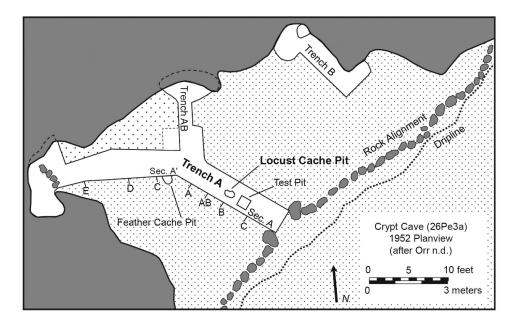


Fig. 2. Crypt Cave plan map.

Crypt Cave measures ~15.2 m wide by ~12.2 m deep and its interior height ranges between ~1.5 to ~3.0 m (Fig. 2) (Orr, 1952). Basal beach and lacustrine sand deposits (Level 5) contained ostracods, freshwater snails, and bones of cormorant (*Phalacrocorax auritus*), and the holotype of the American cheetah (*Miracinonyx trumani*) (Howard, 1958; Orr, 1969). The cheetah was dated to approximately 22,000 years ago (Orr, 1969). Although the cache pit intruded into Level 5, this level's fill was culturally sterile.

Radiocarbon data on basal sediments from Crypt Cave (Broecker and Orr, 1958) and on carbonate deposits that coat the cave (Table A1) reveal the earliest time that Pleistocene Lake Lahontan's surface dropped below the elevation of the cave and permitted human occupation. The age estimates for shells in the basal shoreline sediments indicate deposition before Lake Lahontan reached its highstand 15,500 years ago (Benson et al., 2013b), while the carbonate coating age estimates indicate water filled the cave until about 14,400 years ago. These age estimates suggest people moved into the cave relatively soon after the lake fell below its entrance.

The lowermost cultural unit (Level 4) was limited to the front of the cave. Sediments in this unit consist of redeposited lake sand and

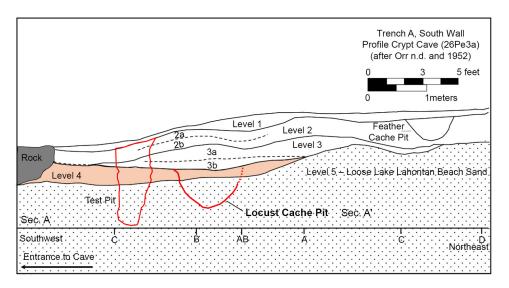


Fig. 3. Crypt Cave, Trench A stratigraphic profile with Orr (1952) field sketch of locust cache pit superimposed – Level 1: loose silt; Level 2: Compacted sediments with organics; Level 3: Loose silt with organics; Level 4: Hard compacted sediments with organics; Level 5: Culturally sterile (minus cache) Lake Lahontan loose beach sand.

silt entering the cave from the surrounding landscape through aeolian and colluvial processes (Orr, 1952; Fig. 3). This stratum was compacted, charcoal-stained, and included lenses of manure (artiodactyl), a horse splint bone (lateral metapodia), cactus areoles with spines, and a pointed greasewood (*Sarcobatus vermiculatus*) tool fragment (undated) associated with an open-twined tule (*Scheonplectus acutus*) mat-based bag fragment (~10,390 cal. B.P.) and a 2-ply cordage (cf. *Scirpus* sp.; ~6250 cal. B.P.) (Table A2; Orr, 1952; 1974). The date ranges on the cordage (~6250 cal. B.P.) and bag (~10,390 cal. B.P.) fragment suggest some intrusive mixing within the Level 4 deposits.

The locust cache pit (Fig. 4) was discovered in the southeast quadrant of the cave toward the cave opening in Excavation Trench A, Levels 4 and 5, (Figs. 2 and 3; Orr n.d., 1952). Based on Orr's crude illustrations, we estimate the oval bowl-shaped pit was about 90 cm in width. Depth is even more difficult to determine as Orr's (n.d.; 1952) profile sketch only shows the pit's profile within the culturally sterile Level 5, while his notes describe the pit as "originating in Level 4 (Orr n.d.). Based on all Orr's descriptive information we estimate the pit was about 60–80 cm deep. Assuming a depth of 70 cm, the pit had a storage volume of approximately 148 L. Both the size and volume

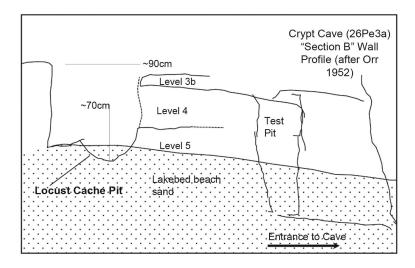


Fig. 4. Orr's (1952) sketch map depicting the locust cache in "*Sec.* B" of Trench A in Crypt Cave.

are consistent with "empty" and "reused" cache pits (i.e., non-burial pits or artifact caches) at other caves in the Lahontan Basin (Thomas, 1985). At Humboldt Cave, for example, the largest "empty" pit had an estimated volume of ~ 160 L (Heizer and Krieger, 1956). The grasshopper cache pit was backfilled with cultural Level 4 fill and then capped by a layer of "pure white" sand as a possible marker (Orr, n.d.). Although Orr (n.d.) noted the absence of a pit lining, one may have been employed to separate the locusts from the loose unconsolidated beach sands of Level 5 while the cache was in use. Many Holocene cache pits in Lahontan Basin caves and shelters contained linings of dried algal mats (see Supplementary Material), broken textiles, or grass used to separate the cache contents from surrounding cave sediments, especially those composed of sand and silt (Heizer and Krieger, 1956; Orr, n.d., 1974). Several caches in Crypt Cave and other caves in the area were described by Orr (1972) as being empty when discovered, and he interpreted these empty caches as having been used and abandoned by their owners. The total volume of the locust elements in the ~148-liter pit is less than ~750 ml (ml), so we speculate that most of the locusts the cache once contained were removed for consumption, with the remaining locust parts representing spillage. We identified six small algal mat fragments (Fig. 5) among the locust parts, but whether they

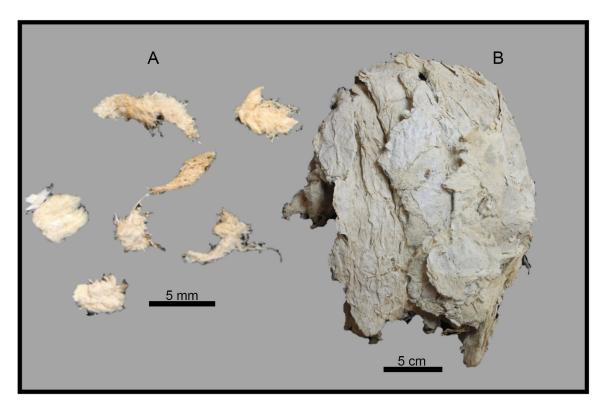


Fig. 5. Algal fragments recovered from the locust cache contents in Crypt Cave (left) compared with an algal mat containing cached tui chub (right) from Stick Cave (26Pe₃₁).

were associated with a pit lining or where incidentally collected along with the locusts from a paleoshoreline is uncertain.

The cache pit fill collected by Orr in 1952 (NSM specimen no. 26Pe3a/123) was curated at the Nevada State Museum in Carson City since its 1952 recovery. These contents contained a robust sample of the cache pit's silty sand matrix and the constituent elements remained unanalyzed until 2015 when this study was initiated. Although recovered locust remains are broken into body segments and parts, preservation of these desiccated pieces is excellent (Fig. 6).

2. Materials and methods

Six hind femora (Fig. A6) weighing a total of 50 mg were initially sent to Beta Analytic Inc. in 2015 for AMS dating (Table A3). Three additional AMS dates were obtained from UC Irvine the following year

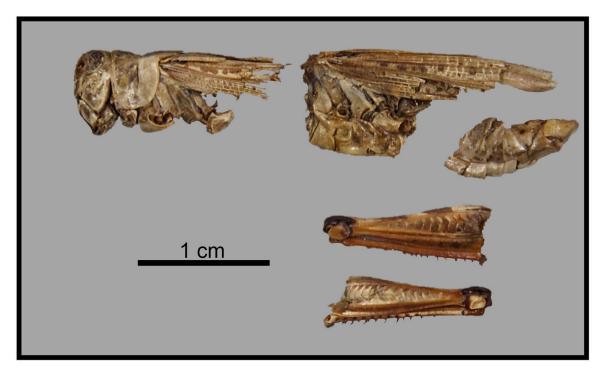


Fig. 6. Rocky Mountain locust (*Melanoplus spretus*) fragments recovered from Crypt Cave locust cache.

(Table A₃). Two bags containing locusts (Fig. A₇) recovered from Crypt Cave by Phil Orr were screened in M.S. Standard Sieve Series comprising of openings of 1.19 mm (14 mesh) and 420 µm (35 mesh) with a solid bottom to capture the fine lake sand mixed with insect debris and sorted on a lab tray (Fig. A8). Locust elements (e.g., left femora, heads, tibiae) were separated to establish the number of identifiable specimens per taxon (NISP). Next, minimum number of individuals (MNI) was determined based on possible matched pairs (a left femur must go with a right femur), and not actual matched pairs (impossible to find the original matched pairs) based on symmetry (see Reitz and Wing, 2008:207). Literature used to aid in the identification of locusts includes: Capinera et al. (2004) Field Guide to Grasshoppers, Katydids, and Crickets of the United States and Daniel Otte's (1981; 1985) The North American Grasshoppers Vol. I and II. Locust remains were initially compared with the comparative collection at the Nevada State Entomologists Office in Reno, Nevada. Additional samples of male terminal abdomina and femora were sent to the Entomology Department at Texas A&M for microscopic analysis and final identification (Fig.

A9). Other faunal identifications such as those of bone, hair and fur were made by use of personal and Nevada State Museum comparative collections. Macro botanical specimens were identified by the Desert Research Institute (DRI), Reno, Nevada.

3. Results

3.1. Radiocarbon dating the locust cache

The age of the locusts in the cache is controlled by four radiocarbon age estimates on locust femur cuticle (Table A3). The femora appeared pristine under microscopic examination but received acid-base-acid treatments to remove any carbonate deposits and soil humics that might be present (the acid-base-acid treatment is specifically designed to remove both). The base solutions showed little color, suggesting that contamination was not a major issue, and three variations of the pretreatment protocol yielded very similar ages, which would be unlikely if the samples were seriously contaminated. An analysis conducted using the OxCal v4.4.2 Rcombine function and IntCal20 produced an average age estimate of 12,238 ± 18 ¹⁴C yrs. B.P. (Fig. A2). The calibrated age range at 95.4 % probability is 14,305–14,067 cal. B.P. (14,305–14,274 [3.35 %]; 14,201–14,067 [92.1 %]).

3.2. Identifying Rocky Mountain locusts

Crypt Cave Orthoptera were identified as the extinct Rocky Mountain locust (*Melanoplus spretus* [Walsh]) based on a suite of internal and external attributes of male genitalia in comparison with figures of male genitalia of *M. spretus* in Gurney and Brooks (1959) as well as photographs of *M. spretus* male genitalia available from the Orthoptera Species File provided by Otte (Cigliano et al., 2021; Fig. A3). As noted by Gurney and Brooks (1959), *M. spretus* can be distinguished from other closely related species by the shape of the dorsal aedeagus valve, which is strongly recurved laterally and posteriorly. The distinctive aedeagus of the Crypt Cave locust's endophallus, however, is perhaps the most defining characteristic for identifying the specimens as *M. spretus* (Fig. 7).

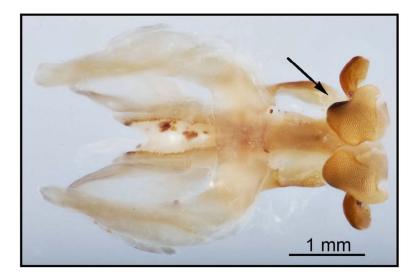


Fig. 7. Dorsal view of Crypt Cave male locust endophallus, with arrow pointing to aedeagus, with its definitive *M. spretus* structure.

Rocky Mountain locust remains in the Crypt Cave cache are comprised of disarticulated body parts which are largely fragmented and crushed rendering them unidentifiable as a result. These have a volume of ~ 500 ml. Another ~ 200 ml of the cache contained 5580 number of identifiable specimens (NISP) (Fig. 8). Complete and diagnostic fragments of right hind femora established the minimum number of individuals (MNI) at 979 (Table A4). Among the small bits of loose, crushed locust remains are four clusters comprised of crushed locust parts (Fig. 9). These clusters are intact, but very friable, and were undoubtedly larger at one time. Many of the bits and pieces of loose locust body parts recovered from nested sieves during analysis may have originated from disaggregated "locust cakes.".

Bruner (1893) observed that adult *M. spretus* femora were typically between 12 and 14.36 mm in length. The range of 41 diagnostic Crypt Cave femora is between 12 mm and 16 mm, with an average length 14.4 ± 1.0 mm). Based on Bruner's (1893) observations, the Crypt Cave femoral length data indicate that adult locusts, typical of a swarm, dominated the cache, with no indication of instars representing a local nesting area.



Fig. 8. Rocky Mountain locust (*M. spretus*) portion fragments recovered from Crypt Cave locust cache.

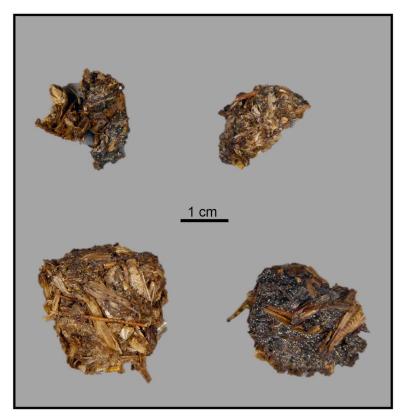


Fig. 9. Clusters of locust parts from Crypt Cave locust cache.

Other animal remains in the cache pit contents included pronghorn (*Antilocapra* sp.) hair, jackrabbit (*Lepus* sp.), probable tui chub (*Siphateles* sp.), a beetle (Coleoptera), a flesh fly (*Sarcophaga* sp.) and an isopod (Isopoda) (29 NISP; Table A5). We attribute the mammals to intrusive wall fall and cache pit backfill, but the fish vertebrae, beetle, flesh fly and the isopod might be unintentional constituents of the original locust harvest.

Eleven different plant taxa were also recovered from the cache pit contents (Table A6). *Juniperus occidentalis* (western juniper) was recovered from the locust cache; this species does not occur in the Winnemucca Lake Basin today. Its presence in the cache corroborates data provided by Wigand and Nowak (1992) suggesting that the eastern shore of Pleistocene Winnemucca Lake was more mesic than the present.

4. Discussion

4.1. Rocky Mountain locusts

The Rocky Mountain locust was North America's only true locust. Locusts are grasshoppers distinguished from other grasshopper species by the ability to undergo distinct phenotypic changes, possibly instigated, when these grasshoppers enter a gregarious phase and form dense migrating swarms (Song, et al., 2017). Although other North American grasshopper species might gather in large numbers and devastate crops, none of these localized outbreaks reached the magnitude, intensity, and impact on the landscape as did the historic 19th century Rocky Mountain locust swarms (Lockwood, 2004). Rocky Mountain locust swarms extended from the Midwest to central Canada during the latter half of the 19th century. Although relatively uncommon, these swarming events were devastating for Euro-American farmers, sometimes leading to settler deaths from starvation (Lockwood, 2004). For prehistoric and ethnohistoric foragers, on the other hand, such swarms could provide an extraordinarily rich food resource, particularly when the swarms fell into lakes and accumulated in windrows along shorelines (Madsen and Schmitt, 1998).

The Rocky Mountain locusts' historically documented/historical home range was principally along the eastern slope of the northern Rocky Mountains and western Great Plains in the U.S. and Canada. It extended into the Great Basin along the western slope of the Wasatch Range in Utah, as well as a northwestern pocket along the Snake River Plain in southwestern Idaho (Riley, et al., 1878). Based on historic distributional data and fieldwork, Riley, Packard, and Thomas (1878) plot *M. spretus* swarms extending as far west as the Humboldt River, approximately 100 km east of Winnemucca Lake. The Sierra Nevada apparently restricted westward swarm extensions into California's Central Valley and Pacific Coast.

4.2. Non-human locust capture and caching

The Crypt Cave cache was overwhelmingly comprised of whole, uncrushed locust body parts, suggesting they were not present in the cave as the result of foraging by owls or other raptors. However, it is possible the four small lumps of crushed locust parts could potentially be derived from owl pellets or raptor castings rather than human "grasshopper cakes." As a result, we examined whether predatory birds or other insectivorous animals may have been responsible for excavating a pit and filling it with intact and crushed locusts. Modern western Great Basin raptors, owls, rodents, and shrews were investigated as potential natural agents responsible for capturing and depositing the locusts in the site.

Raptors and owls are known from Winnemucca Lake, including nesting peregrine falcons (*Falco peregrinus*) (Hattori, 1982). Most, if not all, raptors and owls consume insects, including grasshoppers, as lower tier foods. Chitin in the insects' exoskeleton is largely indigestible, and these birds egest macerated portions of their prey's chitinous body parts within pellets or castings (Akai and Duke, 1998; Johnson et al., 1987). Insect chitin in pellets or castings typically co-occurs with hair, feathers, or bone from other prey species, but outbreaks of grasshoppers can result in raptor castings comprised entirely of chitinous grasshopper bits (Aughey, 1878; Johnson et al., 1987). However, most raptors do not roost inside caves (see Collopy, 1977; Johnson et al., 1987; Williford et al., 2009; Sibley, 2000; Haug et al., 1993), leaving owls, such as the western screech owl (*Megascops kennicotti*), and barn owl (*Tyto alba*) as the most likely possible avian vector, besides humans, responsible for the locust cache (Levinston, 1982; Gehlbach and Stoleson, 2010). Insect consumption in the latter, however, is rare (Earhart and Johnson, 1970).

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The locust cache was located near the center of Crypt Cave away from the cave margins where potential owl perches occur (Fig. 2). There is no suitable perch directly above the cache location and, from Orr's (1952) description of the sediments, there is no evidence of a pellet cone, which would be indicative of long-term use of the cache location by owls, similar to those found at sites like Homestead Cave where raptor deposits span the entire Holocene (Madsen et al., 2001). Most significantly, the locust cache was found buried in a pit, rather than on the flat surface of the cave floor, as would be expected if owls were responsible for the accumulation of locusts. Raptor food caches are typically elevated or surficial and are for daily use (Collopy, 1977; Sutton et al., 2016).

Hoard caching behavior is common in a variety of rodents, shrews, and other animals, but excavation of underground caches is mainly restricted to a few rodent species who cache food within their nests or tunnel complexes (Sutton et al., 2016). However, such storage chambers are much smaller than the ~ 60-liter locust cache pit (Vander Wall, 1990). Cricetid mice cache primarily vegetation, seeds, and nuts. However, some caches have contained small quantities of insects (Vander Wall, 1990:258). Moreover, most insectivorous and omnivorous mice, such as the northern grasshopper mouse (Onychomys leucogaster), cache seeds and fruits for winter sustenance following insect die offs in autumn, and thus do not typically include insects in their caches (Ruffer, 1964:51; Ingles 1965). Cache chambers excavated by heteromyids (i.e., kangaroo rats [Dipodomys sp.]) are typically ~ 15-25 cm in diameter by ~ 8 cm or more in depth (Vander Wall, 1990:253). The nearly 1000 locusts, from Crypt Cave, represented by remnant parts are well beyond the recorded caching behavior of rodents and other insectivores (Vander Wall, 1990; Zazula et al., 2006). All these potential rodent vectors have a limited foraging range, and the presence of algal mat fragments (Figs. A4 and A5) within the locust cache suggests they were collected along the shoreline of Lake Winnemucca which would have been beyond the foraging radius of these insectivores.

In sum, it is unlikely the Crypt Cave locust cache was the result of deposition by raptors, owls, or insectivorous rodents. By far the most parsimonious explanation for the pit full of locust remains in the cave is deposition by prehistoric human foragers. The production of grasshopper cakes was a common subsistence practice among ethnographic and prehistoric Native American groups in the Great Basin and we believe that the overriding cultural context for the locust clusters in the Crypt Cave cache pit suggests human involvement.

4.3. Native American grasshopper use

Historic grasshopper consumption by Great Basin Native Americans is well documented (Wheat, 1977; Fowler, 1986; Madsen and Kirkman, 1988; Sutton, 1988), and grasshoppers and crickets were commonly used ethnohistorically as a winter storage staple (Madsen and Madsen, 1987; Sutton, 1988; Michno, 2007). Washoe Indians, whose territory included the Truckee Meadows 55 km southwest of Winnemucca Lake, captured, dried, roasted, ground, and stored grasshoppers for later consumption (d'Azevedo, 1986; Jones, et al., 1967; Stewart, 1941). Curiously, some Northern Paiutes, whose territory included the Winnemucca Lake basin, denied eating grasshoppers (Melanoplus spp.) but consumed Mormon crickets (Anabrus simplex) and cicadas (Order Homoptera) (Fowler, 1989; Stewart, 1941). A means of preserving grasshoppers for later consumption included crushing or grinding them and forming the fragments or flour into "cakes," sometimes supplemented with berries or seeds and caching the cakes in storage pits (Bryant, 1849; Egan, 1917; Fowler and Fowler, 1971; Hill, 1978). Evidence of prehistoric Native American arthropod consumption occurs at other Great Basin archaeological sites throughout the archaeological record extending back to the terminal Pleistocene-early Holocene.

Lakeside Cave, Utah, a Lake Bonneville wave cut cave on the western shore of the Great Salt Lake, contained an immense quantity of migratory grasshopper (*Melanoplus sanguinipes*) remains (Madsen and Kirkman, 1988). This site is about 55 km west of the Rocky Mountain locust's home range along the western slope of the Wasatch Range, where Packard (1878) noted that its numbers at Lake Point (80 km southeast) in June 1877 were no greater than other, unspecified, grasshopper species (Riley et al., 1878). Grasshoppers were concentrated

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in older Lake Cave strata dating between about 5,500 and 5,150 cal. B.P. but also occurred throughout most of the younger deposits in reduced quantities. The authors also observed windrows of drowned migratory grasshoppers along the present shoreline of the Great Salt Lake resulting from a modern outbreak. Prehistoric Native Americans likely collected dead grasshoppers from similar windrows associated with past outbreaks and then processed and ate them in and around the cave. Human coprolites recovered from most of the strata within the cave contained grasshopper parts.

Paisley Caves, Oregon, yielded Mormon cricket remains in cultural deposits dated between 12,320 and 11,960 cal. B.P. (Blong et al., 2020). Jerusalem cricket (*Ammopelmatus* cf. *fuscus*) remains, a large arthropod common in the Great Basin, were recovered in "abundance" from deposits within the cave and from within a human coprolite.

Bonneville Estates Rockshelter, Nevada, another Lake Bonneville basin wave cut cave, yielded early orthopteran food remains (Hockett, 2015). In this instance, western longwing katydids (*Capnobotes occidentalis*) were directly associated with fire hearths dating between 9,500 and 13,000 years ago. Western longwing katydids, originally identified as migratory grasshoppers (*Melanoplus sanguinipes*), were also recovered from Smith Creek Cave in eastern Nevada, where Bryan (1979) associated them with the Baker Phase occupation between about 4,000 and 2,000 years ago.

In the western Great Basin, "cricket" parts were identified in human coprolites from Lovelock Cave (26Ch5) and three Pyramid Lake caves (26Wa275-Mogoose, 26Wa385-Thea Heye, and 26Wa525-Blazing Star) (Napton and Heizer, 1970). Although these coprolites were not dated and stratigraphic provenience is unstated, these sites were principally utilized between 5,000 years ago to the historic period (Northern Paiute).

Mantle's Cave, Colorado, yielded a cache pit containing a "great quantity" of grasshoppers (*Melanoplus* sp.) processed by mashing and then compacting their bodies "into a solid mass" as a preserved food (T. H. Hubbell correspondence in Jones [1948]). The Crypt Cave locust clumps are comparable to remnant grasshopper cake bits recovered from Mantle Cave.

5. Conclusions

The earliest securely dated evidence for human occupation in the western Great Basin is an unlined cache pit in Crypt Cave containing fragmented Rocky Mountain locusts dating to ~14,100 cal. B.P. during a Lake Lahontan low stand. Non-human vectors do not appear responsible for excavating this feature or caching locusts in it. The feature's age provides additional support for settlement of western North America prior to 14,000 years ago during the terminal Pleistocene and its use may have been roughly contemporaneous with the carving of petroglyphs along the shores of Pleistocene Lake Lahontan dating to as early as ~13,200-14,800 years ago. This cache appears to represent opportunistic Paleoindian foraging for adult Rocky Mountain locusts, likely in a one-off swarming event, around 14,100 years ago, with the locusts collected and stored for later consumption. Whole locusts may have been collected from windrows along the lakeshore almost entirely composed of drowned locusts, but live locusts may also have been hand collected and compacted into cakes.

* * * * *

CRediT authorship contribution statement

Evan J. Pellegrini: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing.
Eugene M. Hattori: Writing – review & editing, Resources, Supervision.
Larry V. Benson: Writing – review & editing, Formal analysis.
John Southon: Writing – review & editing, Formal analysis.
Hojun Song: Formal analysis.
Derek A. Woller: Formal analysis.

Competing Interest The authors have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability No data was used for the research described in the article.

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Appendix A. Supplementary data

Supplementary data to this article follows the References.

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Appendix A. Supplementary data

Isotopic and chemical data supporting the existence of a water body in the Winnemucca Lake Basin during the occupation of Crypt Cave. The prehistoric inhabitants of Crypt Cave would have benefited from a food base in close proximity and the presence of a marsh or shallow-lake system in the Winnemucca Lake Basin would have provided such a resource.

The hydrography of the Pyramid Lake (PL), Winnemucca Lake (WL), and Smoke Creek Desert (SCD) three-basin system is depicted in Fig. A1A. With an ever-increasing river discharge of the Truckee River, Pyramid Lake rises and eventually spills across the Mud Lake Slough (elevation 1177 m). Increasing discharge rates cause Winnemucca Lake to rise and reach an elevation of 1177 wherein it coalesces with Pyramid Lake. The combined water body then continues to rise until it overflows Emerson Pass Sill (elevation 1207 m), spilling water into the Smoke Creek Desert.

In the following, previously published values total inorganic carbon (TIC) data from cores PLC97-1 and PLC 97-3 and oxygen (δ^{18} O) values obtained on three well-dated Pyramid Lake sediment cores (PLC97-1, PLC 97-3, and PLC 92B), and surficial carbonate deposits are used to evaluate the possibility that the Winnemucca Lake Basin held water during the occupation of Crypt Cave. Data used in the following analysis, as well as published references to the data, are listed in Table A1.

Pyramid Lake has not overflowed since 1920, 14 years after diversion of ~55% of Truckee River discharge to the Carson Desert (Fig. 6 in Benson et al. 2002). 35 samples of TIC from Pyramid Lake box core PLB98-2 from this time interval indicate an average sediment δ^{18} O value of 0.0.14 ± 0.40 ‰ (Benson et al. 2002).

Increasing river discharge, resulting in a rising or overflowing lake, results in a decrease in the δ^{18} O value of lake water; the greater the rate of water input, the greater the decrease in δ^{18} O. Pyramid Lake most likely alternated between closed and open states during most of the past 3000 years (see Fig. 24 in Benson et al. 2002). This is supported by reconstruction of historical Pyramid Lake levels that indicates the lake would have been at or near its overflow level about $1/3^{rd}$ of the time between 1910 and 2000 (Fig. 7 in Benson et al. 2002). The effect of intermittent overflow on the δ^{18} O value of Pyramid Lake water, which was determined using δ^{18} O values of 300 late Holocene (2500-108 CE) TIC samples from PLC97-1, indicate mean and 1- σ values of -0.44 \pm 0.28 ‰.

The effect of continuous overflow of Pyramid Lake water to the Winnemucca Lake Basin was determined from δ^{18} O data on six late Holocene beachrock and carbonate encrustations that formed between 2930 and 180 CE. The samples were found to range in value from -0.18 to -1.57 ‰ with a mean value of -1.00 ± 0.49 ‰.

The effect of increased discharge of the Truckee River resulting in overflow to the Smoke Creek Desert, can be determined from δ^{18} O values of six carbonate samples from the Winnemucca Lake Basin (elevations ranging from 1203-1205 m). The δ^{18} O values range from -2.36 to -4.56 ‰ with a mean value of -3.31 ± 0.98 ‰.

In summary, the mean δ^{18} O value of intermittent flow to the Winnemucca Lake Basin is somewhat more negative than δ^{18} O values associated with a hydrologically closed Pyramid Lake Basin. However, constant overflow of larger amounts of water to the Winnemucca Lake Basin produces water with more negative δ^{18} O values, and overflow to the Smoke Creek Desert results in highly negative δ^{18} O values.

Figure A1B shows δ^{18} O values obtained on the TIC fraction of sediments in core PLC92B. The lowresolution record clearly indicates the timing of the Lahontan highstand (HS) at 15.6 kyr BP, and also indicates a rapid drop in lake level between 15.6 and 15.2 kyr BP, (0.32 m/yr, if it is assumed that the lake fell to ≤ 1207 m by 15.2 kyr BP). In any case, the δ^{18} O values of carbonate precipitated between 15.2 and 13.8 kyr BP remained at about a -3.5 ‰ level, indicating that the Winnemucca Lake Basin frequently held water until at least 13.8 kyr BP.

An increase in lake volume or overflow rate decreases the saturation state of carbonate minerals, such as calcite or aragonite, by reducing the concentration of dissolved Ca^{2+} and CO_3^{2-} , leading to a reduction in the amount of precipitated CaCO₃. In this paper, the amount of CaCO₃ is reported as % TIC, where

TIC represents 8.33% of the total CaCO₃ value. The amount of TIC can be used to detect a change in lake volume and the presence of overflow; e.g., TIC values approaching zero indicate rapid increases in lake volume or overflow rate, whereas substantial amounts of TIC in a sediment usually indicate a decrease in lake volume or existence of a closed-basin state.

The TIC record from PLC97-3 is depicted as a series of dots (Fig. A1C). During the period 15.2-13.0 kyr BP, the TIC data indicate a permanent body of water that may not have overflowed to the Smoke Creek Desert. Aragonite, a carbonate precipitate that forms in somewhat Mg²⁺⁻rich waters (Lippman, 1973), precipitated between 14.8 and 13.0 kyr BP, indicating a somewhat saline water body. The presence of oxygen-dependent ostracodes at 13.0 kyr BP indicates initiation of overflow to the Smoke Creek Desert (Benson et al., 2013).

Core PLC97-3 was at times affected by reworking and transport of older lake sediment (shaded area in Fig. A1C) derived from higher elevations in the basin (Benson et al., 2013). Sediment reworking resulted in the deposition of laminated, organic-rich, anoxic sediment. An initial examination of the core's sedimentology (Benson et al., 2013) indicated that the lake was deep between 16.23 and 14.78 kyr BP, that it fell between 14.78 and 14.52 kyr BP, and that it was generally shallow between 14.52 and 12.71 kyr BP. The following, however, offers an alternative interpretation of the data.

During Lake Lahontan's retreat from its 1335-m highstand level, evaporation would have increased the amount of dissolved Mg²⁺in the lake, resulting in the precipitation of aragonite. Reworking of the fine-grained fraction of pre-highstand sediments would not only have contributed organic carbon to the residual water body; fine-grained allochthonous carbonate would also have accompanied the erosive influx. As a result, carbonate-rich, fine-grained carbonate would have settled to the lake bottom giving the impression of a shallow-water body. Similar low-TIC values occur in core PLC92-B (TIC = 0.48 ± 0.12 % C) (Fig. A1B) during this time interval. Thus, the low concentrations of TIC recorded in PLC97-3 sediments may have exaggerated the apparent shallowness of the lake.

In summary, both parameters (δ^{18} O and TIC) indicate that a water body occupied the Winnemucca Lake Basin at the time (14,130 yr BP) the locusts (the "L" shown in Fig. A1) were cached by the inhabitants of Crypt Cave.

Radiocarbon Dating the Locust Cache. Four AMS radiocarbon dates were carried out on locust femurs: three at the Keck AMS lab at University of California Irvine and one at Beta Analytic (Table A3). Since a major component of locust cuticle is the biopolymer chitin, which resembles cellulose in many of its physical and chemical properties, the basic pretreatment chemistry applied to all of the samples was the same acid-base-acid sequence (ABA) commonly used for cellulosic plant material (Method A). Two of the three UC Irvine samples underwent additional processing to extract a clean stable isotope signal for chitin. Prior to ABA, they were sequentially sonicated in a 2:1 chloroform/methanol mixture, methanol, and ultrapure Milli-Q water, to remove lipids (Method B), and one sample also received a longer base treatment in the ABA (5 hours in 1M NaOH at 75°C vs 1 hour) to ensure complete removal of cuticle protein and muscle tissue (Method C).

Radiocarbon ages are shown as conventional ¹⁴C ages corrected for isotopic fractionation, with 1 sigma uncertainties that reflect scatter in repeated runs and uncertainties in the measurement of blanks and normalizing standards as well as counting statistics. Calibrated ages were determined using OxCal 4.4.2 software with the IntCal20 dataset and are shown as 95.4% confidence age ranges. Stable isotope values are expressed in the conventional delta notation and were measured relative to standards traceable to Vienna PDB and AIR and 1 sigma uncertainties of $\pm 0.1\%$ and $\pm 0.2\%$ for carbon and nitrogen, respectively.

The four radiocarbon determinations produced consistent results as shown by the OxCal Chisquared analysis, but the stable isotope and elemental data show some differences. The solvent- treated specimens exhibited less negative δ^{13} C values together with a shift to lighter δ^{15} N, and the most rigorous pretreatment Method C yielded the C/N ratio closest to the expected 8:1 value for pure chitin. The carbon isotope shifts are consistent with lipid removal by the solvents, and the δ^{15} N shift between Methods A and B may indicate that sonication during the solvent treatment helped to disrupt tissues and allowed even the short Method B base treatment to effectively remove proteinaceous material.

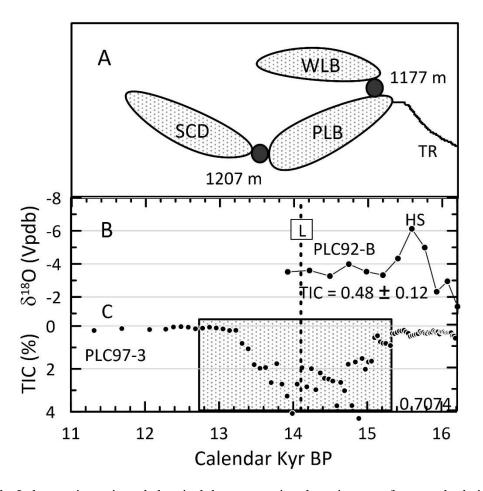


Fig. A1. Lake Lahontan isotopic and chemical data supporting the existence of a water body in the Winnemucca Lake Basin during the 14,100 cal B. P. occupation of Crypt Cave. A. Schematic of the interconnected Pyramid Lake (PLB), Walker Lake (WLB), and Smoke Creek (SCB) basins. Black dots indicate the Mud Lake Slough (1177 m) and the Emerson Pass (1207 m) locations. B. The δ^{18} O record of PLC92-B between 16.2 and 13.0 kyr BP. The Lahontan highstand is indicated by "HS" and the date on the locust cache is denoted by "L". C. The TIC record from Pyramid Lake core PLC97-3. The nearly zero values of TIC between 13.2 and 11.4 kyr BP indicate when the lake was overflowing the Emerson Pass Sill. The reduced TIC values between 16.0 and 13.2 kyr BP indicate when the water body in the Pyramid and Winnemucca Lake basins was below the Emerson Pass Sill.

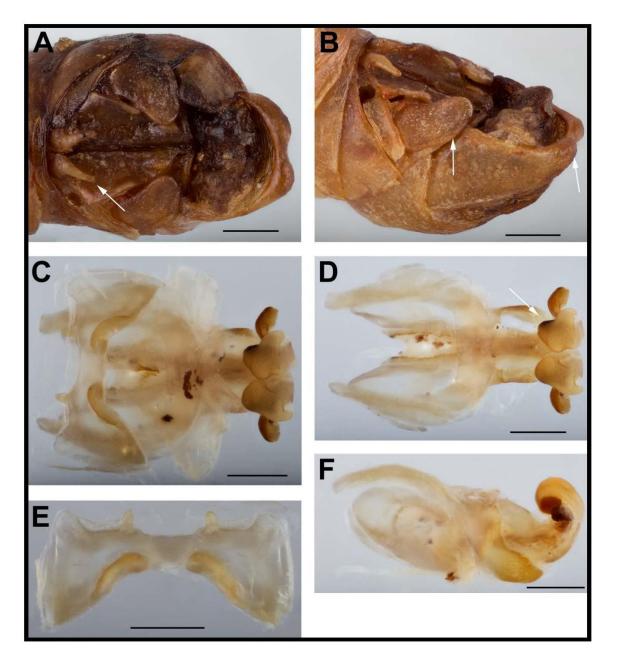


Fig. A2. Crypt Cave male locust genetalia, with 1 mm bar scale. A. Dorsal view with arrow pointing to furcula, *M. spretus* characteristic; B. Dorsal view with arrow pointing to cercus and subgenital plate, *M. spretus* characteristics; C. Dorsal view of the phallic complex; D. Dorsal view of endophallus, with arrow pointing to aedeagus, a *M. spretus* characteristic; E. Anterior view of epiphallus; F. Later view of endophallus.

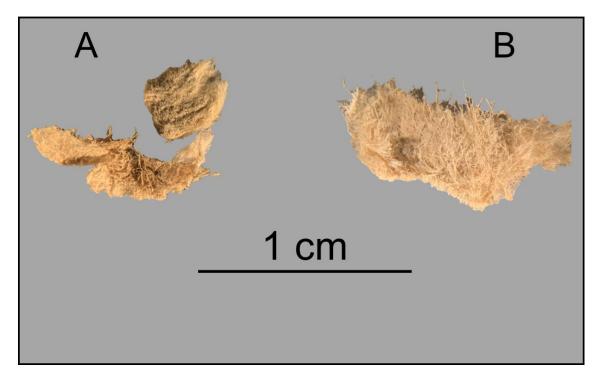


Fig. A3. Algal cache pit lining comparisons. A. Crypt Cave locust cache; B. Stick Cave (26Pe31) tuichub cache.

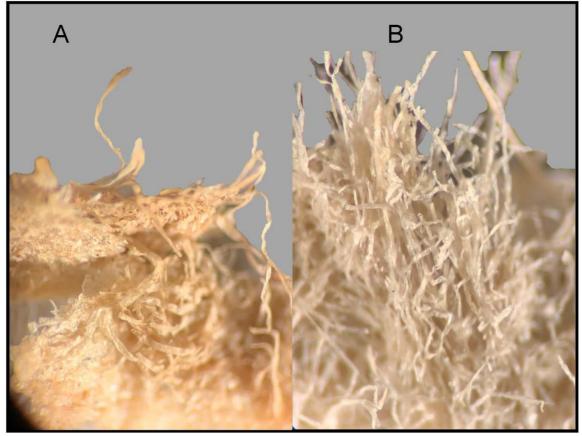


Fig. A4. Microscopic algal cache pit lining comparisons. A. Crypt Cave locust cache; B. Stick Cave (26Pe31) tui-chub cache.

Table A1. Radiocarbon dates on ca	arbonates coating and	l sediments flooring Crypt Cave.

Sample Type	6 I.N	T 1 3 T	Ele	¹⁴ C age	¹⁴ C err	Calib age	Calib err	Ref
	Sample No.	Lab No.	(m)	(ka)	(ka)	(ka)	(ka)	
New ¹⁴ C data from Crypt Cave carbonates								
Top of semi-horizontal carbonate layer	CC#1	UCIAMS 174249	1250	12.365	0.030	14.34	0.14	1
Carbonate coating west side of cave	CC#2	UCIAMS 174250	1250	16.230	0.040	19.58	0.08	1
Carbonate coating east side of cave	CC#3	UCIAMS 174251	1250	13.085	0.030	15.70	0.09	1
Outer surface of dendritic tufa east of cave	CC#4	UCIAMS 174252	1251	12.760	0.030	15.20	0.06	1
Outer surface of dendritic tufa west of cave	CC#5	UCIAMS 174253	1252	12.450	0.025	14.58	0.16	1
Old ¹⁴ C data from Crypt Cave Sediments]							
Shell from top of lake sediments	-1. C	L 364-BR	1250	18.70	0.70	22.62	0.83	2
Shell in lake sediments		L 364-BS	1250	19.75	0.65	23.73	0.78	2
Shell from sand below terrestrial deposits		L 289-P	1234	15.13	0.55	18.32	0.63	2
Shell in lake sediments		L 289-O	1234	15.67	0.70	18.97	0.81	2

Notes

Data from University of California-Irvine Keck AMS Facility
 Data from Lamont -Doherty Earth Observatory (Broecker and Orr,1958); 50% of Crypt Cave samples were dissolved prior to 14C analysis

Artifact	Material	14C Age	<u>+</u>	UCIAMS	Calibrated
		(B.P.)		No.	Age (cal. B.P.)
Open simple twined textile	Tule (Schoenoplectus acutus)	9230	25	181891	10,392
2-ply cordage (ss/Z)	cf. Scirpus sp.	5375	25	181892	6197

 Table A2. Crypt Cave Level 4 artifact radiocarbon dates.

Sample Name	Pretreatment	¹⁴ C Age	Cal. BP Age	δ ¹³ C	$\delta^{15}N$	C/N ratio
	method	(BP)	(95.4%)	(‰)	(‰)	(atomic)
UCIAMS 181882	А	12215 ± 35	14307 - 14040	-24.2	3.1	7.7
UCIAMS 181887	В	12200 ± 30	14295 - 14033	-24.0	-0.5	7.7
UCIAMS 181888	С	12255 ± 35	14760 - 14063	-23.3	-0.7	7.9
Beta 417651	А	12310 ± 40	14808 -14091	-25.1	N/A	N/A

Table A3. Crypt Cave locust cuticle dates and stable isotope results.

Body Part	NISP	MNI
Head w/Vertex	784	652
Thorax	71	64
Abdomen - Female	429	400
Abdomen - Male	189	180
Femur - Right	979	979
Femur – Left	957	957
Femur – Un- sided, non diagnostic	466	
Tibia – Not sided for MNI count	1776	
Total counted	5580	979

 Table A4. Crypt Cave locust NISP and MNI counts.

Animal	Taxon	NISP
Pronghorn	Antilocapra sp.	19
Jackrabbit	Lepus sp.	1
cf. Tui chub	Cyprinidae	6
Beetle	Coleoptera	1
Flesh Fly	Sarcophagidae	1
cf. Sowbug or Pillbug	Isopoda	1
	Total	29

 Table A5. NISP for Crypt Cave non-locust fauna in locust cache.

Plant	Taxon	Notes	Number
Greasewood	Sarcobatus c.f.	Fruits	3+
	vermiculatus		
Greasewood	Vermiculatus sp.	Twigs	1
Horsebrush	Tetradymia c.f.	Twigs	2
	canescens		
Wildheliotrope	Phacelia c.f.	Seeds	2
1004	crenulata		
Prickly Pear Cactus	Opuntia	Spines/Spine	7+
	polyacantha	clusters/seed	
Shadscale Saltbush	Atriplex c.f.	Leaves	2
	confertifoilia		
Ricegrass	Achnatherum	Seed coats	13
	hymenoides		
Giant Blazing Star	Mentzelia c.f.	Seeds	2
	laevicaulis		
Dogbane or	Apocynum	Small Stick	1
Milkweed	Cannabinum or		
	Asclepias sp.		
Sagebrush	c.f. Artemisia sp.	Bark fiber	6+
Western Juniper	Juniperus	Twiglets (1	10+
	occidentalis	with slight Z	
		twist)	
Cheat Grass	Bromus tectorum	Invasive/wall	1
		fall	
		Total	50+

 Table A6. Flora Recovered from Locust Cache.

Supplementary Data References

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