Journal of Arid Environments 135 (2016) 1–8

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Dietary modifications of packrats in response to changing plant communities: Evidence from fossil plant cuticles spanning >55,000 years in Sonoran Desert packrat middens

Michael P. Borrelli [1], Camille A. Holmgren *

Department of Geography and Planning, SUNY Buffalo State, Buffalo, NY 14222, USA

ARTICLE INFO

Article history:
Received 27 May 2016
Received in revised form
22 July 2016
Accepted 3 August 2016

Keywords:
Baja California
Chaparral
Desert scrub
Neotoma
Pleistocene
Holocene

ABSTRACT

Plant cuticles in fecal pellets from 45 *Neotoma* middens from northeastern Baja California, Mexico were analyzed to explore woodrat dietary composition spanning >55,000 years. Pleistocene cuticles were dominated by the more mesic and/or chaparral-type extralocals *Juniperus californica*, *Nolina*, *Agave* cf. *deserti*, *Salvia,* and *Simmondsia chinensis. Cylindoputia*/*Opuntia* cuticles were abundant throughout both the Pleistocene and Holocene. Together, these species comprised the bulk of the woodrats' diet during the last ice age. The glacial-interglacial transition showed the replacement of extralocals in the diet by more xeric desert scrub species, especially *Acacia greggii*, *Larrea tridentata*, *Olneya tesota*, and *Prosopis glandulosa* var. *torreyana*. The main dietary species were all also highly abundant as macrofossils, suggesting preferential collection of favored foods. Interestingly, *J. californica* and *Nolina* cuticles persisted >1500 years after disappearing from macrofossils, while *O. tesota* cuticles appeared 4160 years earlier. It is possible that consumption of particularly prized foods at times they were less abundant left little material for incorporation into middens. Analyzing cuticles along with macrofossils from middens provides complimentary information about woodrat dietary preferences, helps refine the timing of species arrivals/disappearances, and shows how diets shifted with changing climatic conditions.

1. Introduction

Fossil rodent middens have been used extensively for developing late Quaternary vegetation histories in arid and semi-arid North and South America (Betancourt et al., 1990; Betancourt, 2004; Latorre et al., 2005). Middens are accumulations of seeds, leaves, twigs, flowers, fruits, and fecal material collected by the animals within ~30–50 m of their den (Finley, 1990; Vaughan, 1990). The materials are encased in crystallized urine and can be preserved for tens of thousands of years in caves and rock crevices in dry environments. The macrofossils in these deposits can be identified and radiocarbon dated to provide "snapshots" of the surrounding vegetation collected by rodents over a period of years to decades. Sequences of middens can be collated to reconstruct changing plant assemblages at a site, and various sites compared to investigate regional patterns of plant distribution, migration, and colonization, as well as identification of refugia and relict populations through time (Díaz et al., 2012; Holmgren et al., 2014; Lyford et al., 2004; Mujica et al., 2015). Middens also provide a rich source of materials for morphological, isotopic, and genetic analysis, as reviewed by Betancourt (2004).

In North America, middens are primarily made by woodrats, members of the genus *Neotoma*. Although most *Neotoma* species are considered dietary generalists, woodrats tend to concentrate on relatively few plant species within a given community (Verts and Carraway, 2002). Dietary preferences and collecting behaviors can introduce bias into midden records. This has been documented in studies of modern woodrat behavior, as well as comparisons of vegetation between modern middens and the surrounding landscape (Dial and Czaplewski, 1990; Frase and Sera, 1993; Lesser and Jackson, 2011; Lyford et al., 2004; Nowak et al., 2000; Vaughan, 1990). Dietary preferences vary among the different species of *Neotoma* and can even vary over the range of an individual species (Vaughan, 1990). In addition to cached food, woodrats accumulate other materials in their middens. These include twigs, bones, and cactus spines, some of which are used for midden structural

* Corresponding author.
E-mail address: holmgrca@buffalostate.edu (C.A. Holmgren).
[1] Present address: Pictometry International Corporation, Rochester, NY 14623, USA.

http://dx.doi.org/10.1016/j.jaridenv.2016.08.004
0140-1963/

elements and defense against predators (Finley, 1990; Spaulding et al., 1990; Wells and Berger, 1967). Thus, despite being influenced by rodent dietary preferences, middens fortunately still contain enough plant diversity to provide a good sample of the local vegetation.

A consequence of woodrat preferences, however, is that midden macrofossils are unlikely to provide a perfect representation of the suite of species in the landscape that surrounded paleomiddens. Instead, some species will be absent or underrepresented and others overrepresented in the middens compared to the local flora. Consequently, researchers have tended to rely more on the presence or absence of species than measures of relative abundance when interpreting midden plant assemblages. Although modern woodrat diets provide some indication of which plant species were likely consumed in the past, direct evidence has been lacking.

Recently, researchers in South America developed techniques for analyzing plant cuticles (epidermis fragments) preserved within the fecal pellets from fossil rodent middens, expanding the types of inferences that can be made using the midden record (Betancourt and Saavedra, 2002; Latorre et al., 2002). Plant cuticles consist of complex polymers and leaf waxes that are extremely resistant to decomposition and preserve the morphology of the underlying cells, including their micro-morphological features. These features include silica bodies, stoma, glands, hairs, and cell wall characters (Martin and Juniper, 1970; Taylor, 1981; Wooller, 2002). Examination of plant cuticles from fecal pellets allows researchers to determine the composition of the rodents' diet. In some cases, cuticles have included taxa not found as macrofossils in the same middens (Latorre et al., 2002). Cuticle analysis has the potential to establish which plants rodents were eating, to help identify potential biases in midden assemblages due to the rodents' dietary preferences, and to determine how diets may have shifted over time as plant communities changed.

We analyzed plant cuticles in fecal pellets from 45 middens to explore woodrat dietary composition and changes spanning >55,000 years. The middens analyzed were previously collected from Guadalupe Canyon, located along the eastern escarpment of the Sierra Juárez in northeastern Baja California, Mexico (Fig. 1). This work complements the recent study of the long-term vegetation and climatic history from the site by Holmgren et al. (2014) based on plant macrofossils from the middens. This low desert (<300 m) area of the Sonoran Desert yielded the greatest number of Pleistocene-aged samples of any published midden series from North America, thus providing a detailed record of long-term vegetation change for comparison with rodent diets. It is also located within a rich regional network of paleorecords (Fig. 1).

Our goals were to use cuticle analysis to 1) determine which plants species were being eaten by rodents, 2) compare the species found in the rodents' diets to the macrofossil record to better understand the impacts of dietary preferences, and 3) determine how woodrat diets changed over time in response to changing vegetation assemblages.

2. Materials and methods

2.1. Site description and middens

Guadalupe Canyon is located within the Lower Colorado River Basin, which is the hottest and driest subdivision of the Sonoran Desert. Modern vegetation here consists of desert scrub with nearly pure stands of the xeric-adapted shrubs *Larrea tridentata* (creosote bush) and *Ambrosia dumosa* (burro-weed) in the low-lying Laguna Salada Basin just to the east of the sampling area. The vegetation is more diverse among the boulders and low hills at the base of the canyon where the middens were collected. Here, *L. tridentata* and *A. dumosa* are joined by many small trees, shrubs, and herbs. The most abundant of these include *Acacia greggii* (catclaw acacia), *Bursera microphylla* (torote), *Cylindropuntia* spp. (cholla), *Encelia farinosa* (California brittlebush), *Ferocactus cylindraceus* (California barrel cactus), *Fouquieria splendens* (ocotillo), *Justicia californica* (chuparosa), *Lycium* sp. (wolfberry), *Olneya tesota* (ironwood), *Parkinsonia microphylla* (yellow palo verde), *Psorothamnus spinosa* (smoke tree), and *Prosopis glandulosa* var. *torreyana* (western honey mesquite). Above this in the canyon at ~1000 m, desert scrub transitions into chaparral and woodland.

The Guadalupe Canyon middens were all collected from <300 m elevation in the low hills and boulders near the mouth of the canyon and within a ~1.5-km radius centered around 32°09′30″N and 115°45′30″W. Out of 81 middens collected, 50 were selected for radiocarbon dating, with calibrated ages ranging from 680 to >55,000 yr BP (Holmgren et al., 2014). Five dated middens were excluded from analysis due to temporal mixing. Of the remaining 45 middens, 34 date from the Pleistocene and another 11 from the Holocene (last 11,700 years). Calibrated ages for the middens can be found in the Supplementary material and Holmgren et al. (2014). For this study, we analyzed cuticles from all 45 of these middens to compare rodent diets to the macrofossil record of vegetation at the site.

2.2. Past vegetation at site

Midden macrofossils show that a large number of extralocal species (i.e., species not occurring at the site today) moved downslope to the base of Guadalupe Canyon during the late Pleistocene (Holmgren et al., 2014). Many of the extralocals are indicative of more mesic pinyon-juniper-oak woodland and/or chaparral-type vegetation. These include abundant *Juniperus californica* (California juniper), *Agave* cf. *deserti* (desert agave), *Nolina* (beargrass), *Ephedra* (jointfir), and *Ericameria* cf. *cooperi/martirensis* (goldenbush), *Linanthus* (linanthus), and *Salvia* spp. (sage), as well as several other less abundant species. These woodland and chaparral species attest to greater effective moisture in the area during the late glacial.

The extralocal woodland and chaparral species were found in assemblages that also included several desert scrub species, including *Acacia greggii*, *Cylindropuntia*, *Encelia*, and *Ferocactus cylindraceus*, among others (Holmgren et al., 2014). Many other desert scrub species, however, were absent until later, with most arriving by the early Holocene ~10,000 yr BP. This suggests that many Sonoran Desert scrub taxa survived the late glacial within nearby drier microsites and were on hand and able to expand rapidly into the area as conditions became increasingly xeric at the end of the Pleistocene. Although changes in vegetation on the landscape are well documented by plant macrofossils from middens, we must turn to cuticles in the fecal pellets to determine if, and how, these changes are reflected in rodent diets.

2.3. Cuticle analysis

Six fecal pellets were randomly selected from each of the 45 radiocarbon-dated fossil middens for cuticle analysis. The six pellets were finely ground together in a mortar and pestle to homogenize the material, covered with ~100 ml of a 5% sodium hypochlorite (household bleach) solution and allowed to lighten for between one to four hours to aid viewing under the microscope. The ground material was then rinsed with water in stacked 40-mesh (425 μm) and 120-mesh (125 μm) sieves. A small amount of the material from the 120-mesh sieve was mounted on microscope slides with a drop of Hydromount. Although the amount recovered in the 120-mesh sieve varied, these methods yielded