Paleoenvironmental implications of two relative indicator rodent taxa during the Pleistocene to Holocene transition in south-eastern Washington state, USA

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ABSTRACT: Local pollen data, diminution of body size of three ungulate species, and decreased mammalian richness and evenness all indicate grass decreased in abundance during the Pleistocene–Holocene transition (PHT) in eastern Washington state, USA. This paleoenvironmental history suggests that the abundance of remains of Microtus sp. should decrease as remains of Peromyscus maniculatus increase in abundance during the PHT. These two taxa have well-known ecologies relative to one another. PHT sediments at the Marmes archeological site in south-eastern Washington state are sorted into three chronologically sequent, isotaphonomic analytical units. Relative abundances of remains of Microtus sp. and P. maniculatus shift across the analytical units in the predicted manner whether raw abundances or rarified abundances are considered. These results suggest relative abundances of remains of Microtus sp. and P. maniculatus recovered from other sites may be used as relative indicators of paleohabitats. Their abundances at Homestead Cave, Utah, shift as predicted from the Late Pleistocene through the Early Holocene.

KEYWORDS: paleohabitats; Pleistocene–Holocene transition; relative indicator taxa; rodents; Washington state.

Introduction

In paleoecology, so-called ‘indicator species’ are those that have well-known habitat requirements (Andrews et al., 1979). The extent to which the habitat requirements of any given species are known varies, however, from detailed and accurate to incomplete and of coarse resolution (e.g. Mead et al., 1992; Owen et al., 2000), a problem long recognized among paleozoologists (e.g. Findley, 1964; Lundelius, 1985). One way around this problem is to use two or three species whose ecological relationships relative to one another are well known, irrespective of what is known of their independent physiological tolerances and habitat preferences (e.g. Butler, 1969, 1972; Guilday, 1969). I use this alternative here, referring to the examined taxa as relative indicator taxa.

Ancient animal remains are often subject to taphonomic biasing and thus may provide inaccurate reflections of paleoenvironments (Andrews, 2006; Domínguez-Rodrigo and Musiba, 2010; Fernández-Jalvo et al., 2011). It is clear, however, that not all prehistoric collections are so severely biased as to not warrant study (e.g. Hadly, 1999; Terry, 2010a). Further, detailed taphonomic analyses can often account for such biases (e.g. Fernández-Jalvo, 1996; Andrews, 2000), and comparisons of collections subjected to similar taphonomic histories (assemblages that are isotaphonomic) may largely eliminate the influences of taphonomy or suggest those influences are trivial with respect to the environmental signal of interest (e.g. Grayson, 1991; Terry, 2010b).

In this paper I first describe the taphonomy and chronology of a temporally sequent series of three terminal Pleistocene–earliest Holocene deposits from the Marmes archeological site, located near the south-eastern border of the Columbia Basin in eastern Washington state, USA (Fig. 1). The faunal assemblages are isotaphonomic, so the relative abundances of two relative indicator taxa should provide accurate reflections of paleohabitats. Second, rather than infer paleohabitats based on the abundances of remains of the indicator taxa, I predict how those abundances should change during the Pleistocene–Holocene transition (PHT) based on independent paleoecological data. This serves to test both the validity of the relative indicator taxon approach and also the sensitivity of the two chosen taxa as indicators of paleohabitats.

Materials and methods

Mammalian faunal remains were recovered from 1-mm mesh screens during excavations of the Marmes archeological site (45FR50) in the 1960s (Fryxell and Daugherty, 1962; Fryxell and Keel, 1969; Rice, 1969, 1972). Recovery of small remains such as rodent teeth was exceptionally good (Lyman, 2012a). The final report on the recovered artifacts has been recently completed (Hicks, 2004); reports on small samples of the mammal remains have appeared intermittently since the completion of excavations in early 1969 (Gustafson, 1972; Caulk, 1988; Gustafson and Wegener, 2004). I recently identified all mammal remains recovered from PHT deposits making up the floodplain adjacent to and below the Marmes Rockshelter portion of the site, and PHT deposits within the rockshelter (Lyman, 2013a, 2013b, 2014). Analysis here focuses on remains from the floodplain deposits to ensure the isotaphonomic nature of the assemblages and because of the chronological coarseness of the rockshelter deposits (Lyman, 2014).

Taphonomy

There is no archeological evidence for change in mammal procurement strategies or technology during the accumulation and deposition of the faunal remains discussed here, but that may be an artifact of how materials have typically been analysed (e.g. Ames, 1988; Ozbun et al., 2004). There is no regional evidence that prehistoric human hunting significantly depleted local big-game populations (Lyman, 2010a); available evidence instead suggests that shifts in taxonomic abundances and prey body size were largely a result of fluctuation in paleoclimates (Lyman and Wolverton, 2002;
Butler and Campbell, 2004; Campbell and Butler, 2011). Most of the remains of the relative indicator taxa were, however, probably accumulated by non-human mechanisms.

The condition of the mammalian remains of concern here suggests that mammalian carnivores, owls, humans and fluvial action accumulated and deposited those bones and teeth (Lyman, 2010b, 2012b). Some of the rodent remains from the floodplain and from the rockshelter appear to have been lightly charred. Some of those remains may have originated in the rockshelter, only to be charred in a PHT crematorium within the rockshelter (Hicks, 2004). They were subsequently moved out of the rockshelter by humans who excavated burial and cache pits within the rockshelter and by burrowing mammals such as badgers (Taxidea taxus) that pursued ground squirrels (Spermophilus spp.) and wood-rats (Neotoma sp.) resident in rockshelter sediments. This interpretation is supported by the observation that some burned human remains, probably from the rockshelter crematorium, were recovered from floodplain deposits (Krantz, 1979).

Some of the rodent remains on the floodplain may have also been deposited by owls roosting in trees growing on the floodplain. Because it seems owls accumulated and deposited at least some of the small-mammal remains, a concern becomes whether a change in the species of owl involved changed over time. Such a change in predator could result in a change in the rodent fauna unrelated to paleoclimates (e.g. Grayson, 1981). There is no evidence suggesting that the three floodplain assemblages have individually unique taphonomic histories. Degree of fragmentation, extent of charring, skeletal part composition, and relative abundances of remains of large-, medium- and small-bodied mammalian taxa, all important taphonomic variables (Dodson and Wexlar, 1979; Hoffman, 1988; Kusmer, 1990; Lyman, 1994; Schmitt and Juell, 1994; Saavedra and Simonetti, 1998; Terry, 2004, 2007), indicate the three assemblages are isotaphonomic.

Chronology

Floodplain sediments of the Marmes site are similar to those in other river channels of western North America (e.g. Chatters and Hoover, 1986; Osborn, 1977) and comprise numerous relatively thin strata of fine sediment representing individual depositional episodes (Huckleberry et al., 2004). Individual strata in the floodplain deposits are lumped together into analytical units here because artifacts and faunal remains were not consistently recovered from individual floodplain strata during excavation. Radiocarbon ages for each analytical unit (Table 1) were calibrated to calendar years using Calib version 6.0 and the IntCal09 curve (Reimer et al., 2009). The possibility that materials from the three floodplain analytical units (see below) are somewhat mixed cannot be evaluated using vertical or stratigraphic provenance of radiocarbon ages because precise provenance data for individual samples were not consistently recorded (Fryxell and Keel, 1969; Sheppard et al., 1987; Hicks, 2004). Nevertheless, where data are available, greater ages are in deeper strata. Furthermore, minimal vertical movement of artifacts and faunal remains is indicated by the integrity of floodplain strata boundaries (www.archaeology.wsu.edu/county/franklin/45FR50/Appendices/AppendixB.html). Finally, radiocarbon ages on both charcoal and bones do not indicate deposition of ancient faunal remains in more recent deposits (e.g. Hebd et al., 2008).

The relative chronological order of the three floodplain analytical units is ensured by their superimposed positions (Huckleberry et al., 2004). Overlap in calibrated ages of each results from the vagaries of radiocarbon dating and the
The median calibrated age for each floodplain analytical unit is used for discussion purposes, but the duration of the deposition of the faunal materials included in an analytical unit probably extends several hundred years before and after that median age. The Marmes horizon analytical unit consists of two incipient A pedogenic horizons designated A1 and A2; these sediments were deposited 11,800–10,500 cal a BP; median age is 11,200 cal a BP, placing this analytical unit in the Early Holocene, but later than the Harrison horizon. The Harrison horizon analytical unit consists of three incipient A pedogenic horizons designated A3, A4 and A5; these sediments were deposited 12,600–10,500 cal a BP with a median age of 11,450 cal a BP, placing it in the earliest Holocene. Finally, a series of 11 incipient A pedogenic horizons were identified stratigraphically beneath the Harrison horizon and designated A6–A16 (Fryxell and Keel, 1969). Each of these deeper and more ancient A horizons was minimally sampled, so I have lumped them all together for analyses here. The A6–A16 analytical unit sediments were deposited 12,800–11,200 cal a BP; median age is 12,000 cal a BP, placing this unit within the latest Pleistocene given the boundary between the Pleistocene and Holocene of 11,700 cal a BP (Walker et al., 2009) (Fig. 2). Some calibrated ages in the A6–A16 analytical unit do not overlap at the 2-sigma level (Table 1). This is not unexpected given that 11 incipient A horizons are represented in that analytical unit and the individual ages derive from various of those A horizons.

A portion of the A6–A16 fauna probably accumulated during the end of a cool-moist interval dated at 13,200–12,200 cal a BP given two ages more than 12,200 cal a BP (Table 1). The Harrison horizon fauna probably represents the terminal Pleistocene and many of the remains were possibly deposited after 11,700 cal a BP. The Marmes horizon fauna probably represents only the Holocene. These statements reflect the placement of the temporal boundary between the Pleistocene and the Holocene (Walker et al., 2009); that boundary is arbitrarily placed relative to the continuum of climatic change over the last 15 millennia. The three faunas represent a dynamic, more or less continuous shift in past environments, but each fauna is also to some degree time-averaged. Nevertheless, each fauna represents a different segment of a continuum of environmental change.

**Paleoecology**

I use the number of identified specimens (NISP) to estimate abundances of the two relative indicator taxa. NISP values at...
best provide ordinal-scale estimates of taxonomic abundances whether the observed tallies or the relative (percentage) abundances they indicate are considered (Grayson, 1984; Lyman, 2008). Complete assemblages of identified faunal remains from the floodplain analytical units are summarized elsewhere (Lyman, 2013b, 2014). Here, to monitor change from one temporally and stratigraphically distinct fauna to another, I consider the abundances of only the two relative indicator taxa, Microtus sp. and P. maniculatus.

Rickard (1960) was one of the first to demonstrate the relationship of these two relative indicator taxa when he trapped small mammals along a transect that crosses vegetation zones in the Columbia Basin from semi-arid sagebrush (Artemisia sp.) steppe to cooler and more mesic grasslands with scattered shrubs. In short, he found that as grass increases, meadow voles (Microtus spp.) tend to increase in abundance while deer mice (P. maniculatus) decrease. That relationship between the two has subsequently been demonstrated multiple times in nearby areas (e.g. Capelli, 2005; Wittmer et al., 2007). Meadow voles are herbivorous and active day and night; deer mice are nocturnal granivores (Kritzman, 1977). The ecological reasons for the relative abundances of the two taxa probably include the facts that voles (~1.6 g body mass) prefer grassland habitats and displace smaller bodied deer mice (~1.3 g body mass) in those habitats (Feldhamer, 1979; Randall and Johnson, 1979). I assume this modern ecological relationship existed at the time of the accumulation and deposition of the faunal remains at the Marmes site.

All faunal remains were identified by direct comparison with modern reference specimens of known taxonomy. Identifications were to the finest resolution taxon possible and typically based on morphometric similarities of prehistoric specimens and reference specimens of taxa that occur in the general area of the site today. At present, four species of Microtinae occur in the immediate area or within 50 km of the Marmes site (Johnson and Cassidy, 1997): sagebrush vole (Lemmiscus curtatus), long-tailed vole (Microtus longicaudus), montane vole (M. montanus) and water vole (M. richardsonii). The first is readily distinguished from the other three by its morphologically distinct M3 and anterior portion of the m1; remains of this species were identified in the Marmes materials but are not included in this analysis. The water vole is significantly larger than the other three taxa; no remains of this taxon were identified among the Marmes mammalian remains. Only the shape of the incisive foramina distinguishes remains of the long-tailed vole and montane vole; teeth and other (non-cranial) bones of the two are not easily distinguished, and thus all remains of Microtus were identified only to genus.

Only one species of white-footed mouse (Peromyscus spp.) occurs in the site area today (Johnson and Cassidy, 1997): the deer mouse (P. maniculatus). Tooth morphology of species within the genus varies (Hooper, 1957) but there are taxonomically distinctive features, such as the presence or absence of an anteroconule on M1 (Rensberger and Barnosky, 1993). Furthermore, no species other than the deer mouse has been identified in late Quaternary mammal remains from eastern Washington. I identified Peromyscus remains from Marmes as deer mice based on a combination of modern geographical range and tooth morphology. Even if some of these remains are later found to represent other species, that will not significantly alter the interpretations outlined in what follows.

Independent paleoecological data

The northern half of the Columbia Basin was glaciated until about 15 000 years ago and much of the southern half of the basin was scoured multiple times by catastrophic floods, the waters of which originated behind glacial dams, the last flood occurring about 15 000 years ago (Chatters, 1998; Wigand and Hicks, 2004). The latter created pothole lakes and bogs that serve as excellent pollen accumulation sites. Analyses of the pollen content of several cores from these lakes and bogs form the basis of the following. Most analysts agree the PHT between 15 000 and 10 000 cal BP was a time of climatic warming, with evidence for an abruptly initiated period of cold-moist conditions about 13 200 cal BP, followed by an equally abrupt reversal back to the warming trend about 12 200 cal BP (Johnson et al., 1994; Mehringer, 1996; Wigand and Hicks, 2004). This cool–moist period ‘corresponds to the Younger Dryas Period of northern Europe’ (Wigand and Hicks, 2004, p. 55). Aridity and warmth increased gradually after the abrupt shift to warming and drying (Mehringer, 1996; Chatters, 1998; Wigand and Hicks, 2004; Huckleberry and Fadem, 2007).

During the cool–moist phase vegetation in the Marmes site area was composed of cool sagebrush (Artemisia sp.) steppe with scattered patches of mesic-adapted conifers (haploxylon pollen); grass was relatively abundant. About 12 200 cal BP, the abundance of grass and sagebrush increased relative to that of conifers (absolute abundances of grass and sagebrush decreased) and mesic-adapted conifers were replaced by a few individuals of xeric-adapted forms (diploxylon pollen) (Mehringer, 1996; Wigand and Hicks, 2004). Subsequently, conifers largely disappeared and grass abundance continued to decrease.

Remains of North American elk or wapiti (Cervus canadensis) from the Columbia Basin and dating to Marmes horizon times are larger than their modern counterparts (Lyman, 2010b). This large ungulate prefers grazing to browsing (e.g. McCrorquodale, 1991, 1993). It is likely that their Holocene diminution was at least in part a result of the decrease in available grass (McCrorquodale et al., 1989; Huston and Wolverton, 2011). Holocene remains of bison (Bison sp.), a well-known grazer (Meagher, 1986), from the Columbia Basin suggest this species, like its relatives on the Great Plains east of the Rocky Mountains (Hill et al., 2008), also became smaller in body size because of a decrease in grass (Lyman, 2004). And although palaeoecological data are few, it appears that bighorn sheep (Ovis canadensis), another grazer (Shackleton, 1985), underwent similar diminution in body size over the last 15 000 years or so (Lyman, 2009). Modern bighorn populations become stressed and may be extirpated as the abundance of grass decreases (Epps et al., 2004). Finally, total taxonomic richness and evenness of the three PHT floodplain faunas both decline locally, probably because of decreased forage quality and quantity (Lyman, 2014).

Predictions

Together, the palynological data and the mammalian data, both body size and taxonomic structure of faunas, indicate grass decreased in abundance and forage quality. Predictions as to how the two relative indicator mammalian taxa should respond are clear. The A6–A16 (oldest) fauna should reflect the cool–moist (Younger Dryas) event and relatively abundant grass. The Marmes horizon (youngest) fauna should reflect the subsequent warmer and more xeric time when grass was less abundant. The mid-aged Harrison horizon fauna should reflect the transition towards decreased grass. With respect to the two relative indicator mammal taxa, the habitat shifts suggest voles should decrease in abundance relative to the abundance of deer mice as the abundance of grass decreases.
I evaluate abundances of the two relative indicator taxa in two ways. First, the observed NISP per taxon per analytical unit is converted to percentage or relative abundances; only the two indicator taxa are included in the calculation such that if one taxon increases the other must decrease. Second, because the observed NISP of both taxa increases from the oldest to the youngest analytical unit, and because taxonomic abundances (both relative and absolute) are often a function of sample size (Grayson, 1984; Lyman, 2008), I used rarefaction to reduce sample sizes in the two larger analytical units, the Harrison and Marmes horizons (details in Lyman, 2014). This ensures that any shifts in abundances of the two taxa are not a result of changes in sample size. After 10 000 iterations, the mean rarefied NISP for each taxon for the Harrison and Marmes horizon assemblages was determined and used to calculate relative (percentage) abundances.

Results and discussion

Absolute and relative abundances, both observed and rarefied, of voles and deer mice across the three analytical units are summarized in Table 2. Although only three chronologically sequent data points are available, a clear trend in taxonomic abundances is evident. Voles decrease in abundance relative to deer mice whether the observed relative abundances (observed %NISP) values are inspected or rarified relative abundances (rarified %NISP) values are considered (Table 2). This is precisely what the independent paleoecological data derived from ancient pollen and independent faunal data suggest should be found. This result suggests that the relative indicator taxa approach is valid for the Marmes site faunal remains and for the two taxa considered here. Do these two taxa change relative abundances in other assemblages?

Unfortunately, the few nearby faunal records of PHT age or dating to the early and middle Holocene from which vole and deer mouse relative abundances might be determined either do not contain remains of either or both of the taxa (e.g. Gustafson, 1972), the remains were not identified to genus (e.g. Thompson, 1985), or the identified specimens are so few in number as to be potentially misleading (e.g. Rensberger and Barnosky, 1993). In the physiographic Great Basin, in western Utah, the late Quaternary rodent record from Homestead Cave (Grayson, 1998, 2000) is taphonomically similar to that of the Marmes site. The trend in PHT abundances of Microtus sp. and Peromyscus spp. at Homestead Cave mirrors the trend at the Marmes site. Voles decrease from about 15% relative abundance during the latest Pleistocene to about 2% relative abundance during the Middle Holocene; deer mice increase from about 85% to about 98% over this same time span. Independent paleoecological data in western Utah indicate increased aridity and decreased primary productivity at this time (references cited in Grayson, 1998, 2000). It seems, then, that when abundances of these two relative indicator taxa are sufficiently large (perhaps >25 NISP each), they provide a robust signal of shifts in paleohabitats.

Conclusions

When first studied by Gustafson (1972), the paleoenvironmental record for the Marmes site locality was of much coarser temporal and ecological resolution than today. Yet Gustafson (1972) accurately inferred a decrease in plant biomass during the PHT based on the few mammal remains he identified. The much more detailed and finer resolution paleoenvironmental history we know today permits nuanced analyses of the frequencies of relative indicator taxa of mammals. For example, the apparent decrease in local mammalian biomass at the end of the Pleistocene (Lyman, 2013b) prompted local Paleoindians to diversify their resource base to include a wide variety of fish and plant foods (Lyman, 2013a) and reflects a shift in relative abundances of at least some taxa.

Changing abundances of two relative indicator taxa – meadow voles and deer mice – in three chronologically sequent PHT-era deposits at the Marmes archeological site in south-eastern Washington reveal a relative decrease in meadow voles and an increase in deer mice. These shifts in relative taxonomic abundances are precisely what is predicted by independent paleo-palynological and mammalian data in the area. These results suggest these two taxa provide a robust paleoecological signal. Relative abundances of the two taxa in Homestead Cave in western Utah fluctuate in a similar manner. In sum, future research should continue to test the validity of these two taxa as paleoecological indicators, but when other paleoecological data are unavailable, the taxa may be used as a tentative first indication of local paleo-habitats.

Acknowledgements. The author has no conflicts of interest to declare. Study of the Marmes faunal remains is courtesy of the US Army Corps of Engineers, Walla Walla District and Washington State University, Museum of Anthropology. Research on the Marmes Site collection was funded by NSF grant BCS-0912851. M. Collins and D. Curewitz of the Washington State University Museum of Anthropology facilitated my access to the Marmes Site faunal collection. H. M. Gibb, E. M. McCarthy, D. Pierce, C. N. Rosania and A. K. Trusler provided assistance in the laboratory. G. Blomquist assisted with the rarefaction analysis. Early versions of this manuscript received valuable comments from M. C. Wilson and S. Wolverton.

Abbreviations. NISP, number of identified specimens; PHT, Pleistocene to Holocene transition

References


Table 2. Abundances of remains of voles and deer mice from the Marmes site floodplain.

<table>
<thead>
<tr>
<th>Analytical unit</th>
<th>Observed NISP</th>
<th>%Obs NISP</th>
<th>Rarified NISP</th>
<th>%Rarified NISP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microtus sp.</td>
<td>64</td>
<td>49.6</td>
<td>10.6</td>
<td>49.5</td>
</tr>
<tr>
<td>Peromyscus maniculatus</td>
<td>65</td>
<td>50.4</td>
<td>10.8</td>
<td>50.5</td>
</tr>
<tr>
<td>Harrison horizon</td>
<td>41</td>
<td>53.2</td>
<td>7.5</td>
<td>53.1</td>
</tr>
<tr>
<td>A6–A16 horizon</td>
<td>21</td>
<td>63.6</td>
<td>21</td>
<td>63.6</td>
</tr>
</tbody>
</table>

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