This paper explores paleoenvironmental and paleoecological information that may be obtained from small-mammal assemblages recovered at central Alaska archaeological sites dated to the Terminal Pleistocene and Early Holocene (14,500-8000 cal B.P.). Small-mammal remains in these open-air sites are primarily related to deposition by natural death causes and as such provide information on site paleoenvironments and landscape heterogeneity. Their presence within archaeological occupations likely relates to anthropogenic disturbance and features that would have favored burrow construction. The co-occurrence of small-mammal remains and archaeological occupations provides a chronological framework of presence in the locality for most recorded small mammal species. Small-mammal remains document faunal turnover between Pleistocene and Holocene communities. The near-contemporaneity of species that strongly differ in their ecological requirements suggest that the Terminal Pleistocene and Early Holocene in central Alaska was a period of dynamic change that may have been characterized by patchy vegetation distribution, rather than the climax communities seen today. In addition to the biogeographical value of small-mammal remains, the paleoenvironmental information that they provide helps to characterize the ecology of early human settlers in the region and the processes behind human dispersal in Beringia and the Americas at the end of the Ice Age.

**Keywords:** Beringia; microtines; paleoenvironments; Pleistocene; Holocene

**Abstract**
This paper explores paleoenvironmental and paleoecological information that may be obtained from small-mammal assemblages recovered at central Alaska archaeological sites dated to the Terminal Pleistocene and Early Holocene (14,500-8000 cal B.P.). Small-mammal remains in these open-air sites are primarily related to deposition by natural death causes and as such provide information on site paleoenvironments and landscape heterogeneity. Their presence within archaeological occupations likely relates to anthropogenic disturbance and features that would have favored burrow construction. The co-occurrence of small-mammal remains and archaeological occupations provides a chronological framework of presence in the locality for most recorded small mammal species. Small-mammal remains document faunal turnover between Pleistocene and Holocene communities. The near-contemporaneity of species that strongly differ in their ecological requirements suggest that the Terminal Pleistocene and Early Holocene in central Alaska was a period of dynamic change that may have been characterized by patchy vegetation distribution, rather than the climax communities seen today. In addition to the biogeographical value of small-mammal remains, the paleoenvironmental information that they provide helps to characterize the ecology of early human settlers in the region and the processes behind human dispersal in Beringia and the Americas at the end of the Ice Age.

1. Introduction

Paleoenvironmental studies have proved fundamental in characterizing and understanding the major palaeoecological and biogeographical events associated with the Terminal Pleistocene and early Holocene (14,500-8000 cal B.P.) of Beringia, when Beringia served as a gateway for dispersal of animal and plant species between northeastern Eurasia and northwestern North
America. These migrants, including human populations, contributed to the emergence of radically new biotic communities.

In particular, human colonization of Beringia during the Terminal Pleistocene corresponds to one of the major steps of the story of human dispersal around the globe (Hoffecker et al., 2016). Archaeological and paleogenomic evidence together indicate that Beringian settlers originated from northeastern Eurasian populations (Llamas et al., 2016; Moreno-Mayar et al., 2018; Sikora et al., 2019) and became archaeologically visible during the Bølling-Allerød chronoperiod (14,500-12,900 cal B.P.) (Goebel and Buvit, 2011; Meltzer, 2009; Potter et al., 2018). The colonization of Beringia corresponds to the first evidence for recolonization of latitudes above 60°N after the Last Glacial Maximum and set the stage for the colonization of the Americas in the subsequent millennia (Goebel et al., 2008; Potter et al., 2018; Raghavan et al., 2015).

Dispersal of people in and through Beringia was part of and took place during a larger biotic turnover. Paleobiological studies have shown a biome shift from drier, steppe-like environments over most of Beringia, to wetter biomes characterized by tundra, along the coast, and forested environments, in the interior (Anderson et al., 2004; Blinnikov et al., 2011; Jones and Yu, 2010; Oswald et al., 2014; Wooller et al., 2018). Megafauna communities were accordingly affected with a decrease in number of species, the extinction of many grazing herbivores and hypercarnivorous predators (Guthrie, 2006; Mann et al., 2015), and their eventual replacement by dominantly mixed feeding and browsing herbivores and omnivorous and hypocarnivorous predators (Guthrie, 1982; Lanoë et al., 2017).

Causes of ecological change in Beringia at the end of the Pleistocene ultimately relate to global climate change associated with the end of the Ice Age and the beginning of the current interglacial period (Mann et al., 2018). More proximate drivers of environmental change may
have included regional climatic factors such as changes in atmospheric circulation and precipitation (Guthrie, 2001). In parallel, invasion and extinction of keystone ecological species such as ecological engineers and apex predators, including humans, may have triggered sudden biome shifts (Guthrie, 1984; Lanoë et al., 2017; Surovell et al., 2005; Zimov et al., 1995).

Research in Beringia has long focused on characterizing paleoenvironments and their evolution at a regional level, relying on proxies that provide information on past environments at a low spatial resolution, such as pollen (Edwards et al., 2000) and megafauna fossils (Guthrie, 1990, 1968a). A different set of proxies that provide paleoenvironmental information at a higher spatial resolution, such as macrobotanical remains (Zazula et al., 2007), insects (Elias, 2001), and sedimentological, pedological, biogeochemical, and genetic analyses of lacustrine and terrestrial sediments (Graham et al., 2016; Kaufman et al., 2016; Kokorowski et al., 2008; Reuther, 2013; Vachula et al., 2019; Willerslev et al., 2014), has shown the high degree of environmental heterogeneity in Beringia during the Terminal Pleistocene and Early Holocene.

Small-mammal remains constitute environmental proxies that, in contrast to large mammals, have seen considerably less attention in Alaska since pioneering studies of Repenning et al. (1964) and Guthrie (1968b). Because of their diminutive size, small-mammal remains don’t preserve well, are often overlooked in geological or archaeological contexts, and/or require a time-intensive sampling methodology. Even when recovered, such remains are seldom directly dated, particularly until recent methodological improvements in the dating of small bone samples. Instead, in Alaska their age has usually been inferred from stratigraphic association with geological layers, particularly in karstic contexts (Endacott, 2008; Georgina, 2001; Harington and Cinq-Mars, 2008; Morlan, 1989), and as a result they offer a very low chronological resolution.
Small-mammal remains have a high potential for providing paleoenvironmental information at both local and regional scales. In contrast to most large mammals, small mammals have small home ranges (typically below 0.5 Ha for herbivore species under 1.0 Kg [Haskell et al. 2002]) and are tied to micro-environments with specific hydric regimes and/or vegetation communities (Merritt, 2010). This high-resolution spatial paleoenvironmental information allows for a better understanding of the local environmental setting of archaeological sites. Changes in the small-mammal assemblage at a locality over time also indicate how regional climatic and environmental change impacts the local setting of a geological or archaeological site. At a larger scale, distribution of small-mammal communities across different localities provides information on the different components of a landscape and its homogeneity. This type of paleoenvironmental information is crucial for developing models of settlement and land use, and ultimately to address issues related to human ecology, economy, and geography.

In this paper we present and discuss paleoenvironmental information obtained from small mammals remains recovered from archaeological sites in the middle Tanana valley of Central Alaska dated to the Terminal Pleistocene and Early Holocene. The archaeological landscape of the middle Tanana valley is the best documented within Beringia and provides strong evidence for early dispersal in and through Beringia (Lanoë et al., 2018b; Potter, 2011; Potter et al., 2013). Paleoenvironmental information from small mammals contributes to establishing environmental contexts for these early settlers and subsequent populations, and its implications in understanding their economy and lifeways.

2. Materials & Methods
Small-mammal remains were recovered as part of archaeological excavations at sites in the middle Tanana valley (Table 1, Figure 1). Studied materials were restricted to layers dating to the Terminal Pleistocene (14,500-11,700 cal B.P.) and Early Holocene (11,700-8000 cal B.P.). Materials were collected from sediment screened at a mesh of 3.2 mm, in 5 or 10 cm levels. Due to their general rarity in Alaska aeolian sediments (Guthrie, 1968b), and because the main purpose of fieldwork was to retrieve archaeological materials, no specific sampling method was designed to systematically retrieve small mammal skeletal materials. Exceptions included small-mammal nests encountered whole during excavation, which were collected and screened in the laboratory in nested screens to a size of 63 μm.

Small mammals (<1.0 Kg) in central Alaska include vole and lemmings (Cricetidae), jumping mice (Dipodidae), squirrels (Sciuridae), pikas (Ochotonidae), shrews (Soricidae), bats (Vespertilionidae), and carnivorans (Mustelidae) (MacDonald and Cook, 2009). Species identification was conducted with the help of reference collections in the Mammal Collection at the University of Alaska Museum of the North in Fairbanks, and the Stanley J. Olsen Laboratory of Zooarchaeology at the Arizona State Museum of the University of Arizona in Tucson. Species identification of skeletal remains of Arvicolinae (Cricetidae) was limited to the lower first molar (m1), which is diagnostic to species for most of the Arvicolinae species expected in the higher latitudes of North America (Semken and Wallace, 2002). Exceptions include the m1 of *Microtus miurus* and *Microtus pennsylvanicus* that are of similar shape and can overlap in size (Morlan, 1989).

Remains were quantified using Number of Identified Specimens or NISP (Lyman, 2008), with quantification of skeletal remains of dipodids limited to the m1 for the sake of consistency with the similar-sized cricetids. No shrews, bats, or canivoran remains identifiable to species were
recorded. The presence of arctic ground squirrel (*Urocitellus parryi*) was assessed by the presence of their skeletal remains as well as their characteristic, ~10 cm-wide, burrow or krotovina (Zazula et al., 2007). Observations of bone surface modifications were conducted with a 20X hand lens on a sample of 305 cranial and postcranial elements, including 26 cricetid and dipodid m1, accounting for 37% of the total NISP as defined above.

3. Results

Skeletal remains of small mammals were recovered at five of the six archaeological sites studied for the time interval between 14,500 and 8000 cal B.P. (Table 2). Numbers of recovered specimens vary greatly between sites, ranging from a total absence of vole, lemming, and jumping mice at the Keystone Dune site, to as many as 6 per square meter at the Bachner site. On average, identified vole, lemming, and jumping mice specimens for the entire set of sites numbered 0.26 per excavated m$^2$, or 0.04 per m$^2$ per millennium of deposition.

Density of identified specimens is significantly lower than typically observed in karstic contexts. As a comparison, at Lime Hills Cave in southwestern Alaska 395 vole, lemming, and jumping mice remains were recorded with similar methods (3.2 mm mesh size, quantification of m1 only) over 17 m$^2$ of excavation and in stratigraphic layers spanning 10,000 to 20,000 years (Georgina, 2001), or a density of 1.16 to 2.32 identified specimen per m$^2$ per millennium of deposition. In contrast, studied loess sections near Fairbanks in central Alaska have yielded 31 vole, lemming, and jumping mice lower first molars in about 55 tons of Late Pleistocene loess, or about 60 m$^3$, using a mesh size of 0.6 mm (Guthrie, 1968b). Assuming loess deposition rates of 1 to 5 cm per century (Lanoë et al., 2018b), the Fairbanks loess sections provide densities of 0.05 to 0.26
identified specimens per m² per millennium of deposition. These densities are of the same order of magnitude as sites in the middle Tanana valley.

Species identified in this study include the brown lemming (*Lemmus trimucronatus*), the meadow vole (*Microtus pennsylvanicus*), the red-backed vole (*Myodes rutilus*), the singing vole (*Microtus miurus*), the taiga vole (*Microtus xanthognathus*), the tundra vole (*Microtus oeconomus*), the jumping mouse (*Zapus hudsonius*), and the arctic ground squirrel (*Urocitellus parryii*) (Figure 2). Several specimens could not be distinguished between meadow and singing vole. Other taxa were not identified.

Three of the species represented (arctic ground squirrel, brown lemming, singing vole) do not occur in the lowlands of the middle Tanana valley today (MacDonald and Cook, 2009, 2001). Five similar-sized species that do occur in the middle Tanana valley lowlands today, including the bog lemming (*Synaptomys borealis*), the flying squirrel (*Glaucomys sabrinus*), the long-tailed vole (*Microtus longicaudus*), the muskrat (*Ondatra zibethicus*), and the red squirrel (*Tamiasciurus hudsonicus*), are not represented in the assemblage. The arctic lemming (*Dicrostonyx torquatus*), recorded in undated Late Pleistocene loess of the lower Tanana valley (Guthrie, 1968b; Repenning et al., 1964), is not represented either.

A majority of vole and lemming m1 were recovered in (63.5%) or at the same level (24.3%) than anthropogenic features (pits or hearths), with only a few (12.2%) specimens “floating” in between archaeological occupations (Figure 2). At the Upward Sun River site, 54.5% of the recorded vole and lemming specimens were recovered in a pit associated with a cremation hearth and a burial that represents < 1% of the total area excavated at the site (Potter et al., 2014). At the Hollembaek site, 75.0% of the recorded vole and lemming specimens were recovered in an anthropogenic pit feature probably associated with trash management and that represents ~50%
of the total area excavated at the site (Reuther and Lanoë, 2018). At the Swan Point site, all
recorded vole and lemming specimens were recovered in association, within Cultural Zone 4b,
with two large hearths filled with mammoth (*Mammuthus primigenius*) ivory fragments and
mammoth and other animal bones (Lanoë and Holmes, 2016). All recorded vole and lemming
specimens at the Bachner and Cook sites, as well as 40.0% and 31.8% of those recorded at the
sites of Hollembaek and Upward Sun River (excluding those recorded in the pit features),
respectively, were recovered at the same stratigraphic level as archaeological occupations
(Figure 2). Lastly, the Keystone Dune site, characterized by an ephemeral archaeological
occupation with no anthropogenic feature and by comparatively high sedimentation rates (Lanoë
et al., 2018a), yielded no small mammal remains (m1 or other).

Jumping mice specimens were generally recovered deep in the stratigraphy (Figure 2). At the
Swan Point site where they are most prevalent, jumping mice remains were recovered as
complete skeletons including both cranial and post-cranial remains, often in nests consisting of
dry vegetation (Lanoë and Holmes, 2016). Like vole and lemming remains, jumping mice m1
and associated skeletons were primarily (90.5%) found in association with anthropogenic
features. At the Swan Point site, 87.5% of jumping mice specimens were recovered within
Cultural Zone 4b, including 38.1% in association with the same hearths where vole and lemming
remains were found. At the Hollembaek site, all jumping mice specimens were recovered
immediately underneath the same pit where vole and lemming remains were dominantly found.

Evidence of ground squirrel activity in the form of skeletal remains or burrows was recorded at
al sites except Keystone Dune (Figure 2). Their absence at Keystone Dune may result from the
homogeneous sand stratigraphy that hinders recognition of possible burrow outline and filling
(Reuther et al., 2016). Where it was recorded, evidence of ground squirrel activity occurred in
the lower portions of the stratigraphy in loess and/or sand, down to bedrock, in layers generally
dated to 12,000 cal B.P. or older (Figure 2). In addition to burrows, ground squirrel skeletal
remains were recovered at all sites except Keystone Dune (Lanoë and Holmes, 2016; Potter et
al., 2011).

Preservation of small-mammal remains (cranial and postcranial) was on average better than for
large mammals. Taphonomic observations at the Swan Point site show a scarcity of bone
breakage and a low impact of weathering and surface dissolution on the vole, lemming, and
jumping mice assemblage, compared to the large mammal assemblage, while preservation of
ground squirrel remains generally shows intermediate stages between those recorded for vole,
lemming, and jumping mice remains, and those recorded for large mammal remains (reported in
Lanoë and Holmes, 2016). At the Upward Sun River site, a high proportion of the vole,
lemming, jumping mice, as well as ground squirrel remains recovered in the hearth/burial pit
were combusted (reported in Potter et al., 2014, 2011).

Five radiocarbon dates were obtained on small-mammal remains or on materials associated with
small-mammal features from the Swan Point site (Holmes et al., 1996; Lanoë and Holmes,
2016). A jumping mouse element recovered in a nest 80-85 cm below surface was dated to 5590-
5330 cal B.P. (Beta-186682), in a layer otherwise dated to ~14,000 cal B.P. (Figure 2). Within
the same layer, charcoal fragments associated with 10-15 cm diameter (ground squirrel size)
burrows 75-80 cm below surface were dated to, 13,600-13,340 (Beta-71372), and 13,610-13,300
cal B.P. (Beta-56667), respectively; and a charcoal fragment associated with a ~4 cm diameter
(vole, lemming, or jumping mouse size) burrow 75-80 cm below surface was dated to 9540-9310
(cal B.P. (Beta-215328) cal B.P. (Figure 3). A charcoal fragment recovered in a burrow ~4 cm diameter
50-55 cm below surface was dated to 5580-5310 cal B.P. (Beta-190577), in a layer otherwise dated to ~12,000 cal B.P. (Figure 2).

4. Discussion

4.1. Modes of Accumulation

Small-mammal paleontological assemblages in the more commonly studied karstic contexts are primarily created by the action of avian and mammalian predators who sample small mammals in the vicinity of their denning/nesting site (Andrews, 1990; Morlan, 1989). In contrast, large mammal assemblages in open-air archaeological sites are primarily created by human predators who discard skeletal elements after consumption of the edible portions of a carcass.

The settings of the sites studied are unconducive to predator denning or nesting with a lack of rock outcrops and a paucity of large trees for the time period considered (Bigelow and Powers, 2001). The low density of small-mammal remains and their general lack of breakage makes them unlikely to be related to animal predation. In parallel, the low amount of weathering or surface dissolution suggests that small-mammal remains were not left on the surface or near surface contexts for extended periods for time like those of large mammals, but instead were deposited under the surface.

All the small mammal species recorded are at least seasonally fossorial and use burrows for hibernation, shelter, nest, and/or storage; non-fossorial species such as the red squirrel are not represented (MacDonald and Cook, 2009). Taphonomic observations, along with the recovery of nests much younger than the surrounding sediments, and the prevalence of burrowing in the sediment, suggest a large proportion of the small-mammal remains studied were deposited in
burrows, in which case the cause of death of the individuals would have been primarily related to
thermal or nutritional stress (Morrison and Galster, 1975). The ground squirrel assemblage
displays a taphonomic signature closer to the one observed for large mammal remains. Ground
squirrels are much larger-bodied than vole, lemming, and jumping mice, and in some cases may
have been acquired and consumed by the people that produced the archaeological assemblages
(see Potter et al., 2011; Yesner, 1996).

The location of recovery of small-mammal remains at the middle Tanana sites suggests that the
location of small-mammal burrows was strongly influenced by pre-existing anthropogenic
features and accumulation of artifacts. Small mammals may have been attracted by materials left
by people, such as ashes, animal bones and tissues, or feces, that provided food and nutrients.
Sediment disturbance by people may also have facilitated burrow excavation. Large branches
and roots contributed to the structure of modern Alaska burrows (Wolff and Lidicker, 1980);
discarded large archaeological artifacts and anthropogenic features may have provided the same
function in loess settings otherwise void of inclusions and with few or no large trees. The large
quantity of taiga vole remains in the anthropogenic feature at the Hollembaek site probably
reflects the local establishment of a taiga vole colony in these disturbed sediments shortly after
human abandonment of the site. Likewise, at the Upward Sun River site vole and lemming
skeletal remains, along with numerous ground squirrel remains, are located in and within 10 cm
underneath a human cremation hearth, above an underlying human burial (Potter et al., 2014),
and may reflect burrows excavated in the burial pit after initial abandonment of the site by
people.

In some cases, anthropogenic disturbance must also have impacted the preservation of small
mammal remains. Hollembaek site anthropogenic feature includes, in addition to taiga vole
remains, those of vole species (red-backed vole, singing vole) more typical of Late Pleistocene layers at this and other sites (Figure 2). Those specimens likely relate to the reworking of Late Pleistocene sediments during the construction of the feature. In parallel, combustion traces observed on the vole and ground squirrel remains in the Upward Sun River burial pit may correspond to indirect thermal alteration (Bennett, 1999; Stiner et al., 1995) from the subsequent superficial excavation of the pit and construction of the cremation hearth during reoccupation of the site by people (Potter et al., 2011), rather than to human consumption.

The creation of the vole, lemming, and jumping mice assemblage by causes mostly unrelated to predation makes it less likely to provide biased paleoenvironmental information than an assemblage created by mammalian or avian predators. Assemblages created by predators may reflect as much the predators’ dietary and habitat preferences than the range of micro-environments present at and around the sampling site (Andrews, 1990; Grayson, 1981). In contrast, assemblages created mainly by burrowing are composed of species and individuals that actually occupied the local site setting. Anthropogenic features may present avenues for bias by favoring species of small mammals that rely on ground disturbance, with for instance taiga vole in the Hollembaek site despite their being relatively uncommon in the region today (MacDonald and Cook, 2001).

Small-mammal burrowing depth varies across species. Recorded species of vole and lemming are characterized by shallow burrows that in Alaska are often located at the junction between litter and mineral soil (Wolff and Lidicker, 1980), with average reported depths of 10 to 15 cm below surface (Bee and Hall, 1956; Cole and Wilson, 2010; Wolff and Lidicker, 1980). Detailed burrow measurements for Kentucky prairie voles (*Microtus ochrogaster*) indicate that 93% of burrows volume occurs within the top 15 cm below surface (Davis and Kalisz, 1992). Jumping
mice and ground squirrel, in contrast, are known to excavate deep burrows down to 60 and over
100 cm below surface, respectively (Nowak, 1999; Whitaker, 1972).

4.2. Methods of Study and Chronological Control

Differences in the modes of accumulation of small mammal remains between karstic and open-
air sites is readily seen in the relative density of documented remains, with karstic sites
preserving 2 to 3 orders of magnitude more remains than open-air sites. On the other hand,
similar rates of recovery between archaeological sites of the middle Tanana valley and Fairbanks
loess studies suggest that a screen mesh size of 3.2 mm, however incomplete, provides a fair
chance of recovery of vole-sized remains that is comparable to studies conducted with a smaller
(0.6 mm) screen mesh size. It is also more readily manageable in archaeological excavations
which primary goal is not to retrieve small mammal remains. The lack of recovered shrew
remains reflects the limitations of this sampling strategy for very small mammals with slender
and minute elements, in contrast to larger and more robust rodent m1, particularly when still
encased within mandible bones.

The fossorial mode of accumulation of the small-mammal assemblage impacts any date
estimation for their recovered skeletal remains. The jumping mouse dated to 5590-5330 cal B.P.
at the Swan Point site was located ~50 cm below the sedimentological layers deposited at that
time, which falls within the range of known burrow depths for jumping mice. The charcoal
fragments dated to 5580-5310 and 9540-9310 cal B.P. were located ~20 and ~35 cm,
respectively, below layers deposited at that time, which also falls within the depth range of
jumping mice burrows. These charcoal fragments provide a maximum rather than actual age for
jumping mice populations, as individual mice likely incorporated charcoal from underlying layers in the infilling of their burrows.

Date estimates therefore need to take into account the stratigraphic layers in which small-mammal remains were recovered, radiocarbon dates, and potential burrow depths, ranging from up to 20 cm for vole and lemming, and up to 60 cm for jumping mice (Figure 2). Despite these limitations, open-air sites provide a more stable fossil environment than karstic sites, with higher sedimentation rates and comparatively little bioturbation and stratigraphic mixing, much reducing risks of contamination of asynchronous mammal communities. Dates for fossil individuals can reliably be estimated within a couple millennia as opposed to entire geological epochs (Table 4). The high occurrence of small mammal remains in anthropogenic features and archaeological occupations in general also provide avenues for developing targeted sampling protocols in these restricted areas. Open-air sites are routinely studied as part of archaeological excavations and while methods used by archaeologists are not suitable for very small mammals (e.g. shrews), archaeological research can contribute much to the biogeography and evolutionary history of “larger small mammals” such as vole, lemming, and mice.

4.3. Biogeography and Regional Paleoenvironments

Recorded species of small mammals through the Pleistocene-Holocene transition reflect species turnover that accompanied biome changes in Beringia/Alaska. Some species are only recorded during the Pleistocene between 14,000 and ca. 12,000 cal B.P. (brown lemming, singing vole, ground squirrel), others are only recorded in the Holocene after ca. 10,000-8000 cal B.P. (jumping mouse, meadow vole), and some span both the Pleistocene and Holocene (red-backed
vole, taiga vole, tundra vole). The presence of singing vole in a layer dated to 8000 cal B.P. at the Hollembæk site likely relates to anthropogenic disturbance of Late Pleistocene layer (see 4.1.).

The presence of singing vole and brown lemming in Pleistocene contexts concurs with the small mammal record in Full Glacial sediments in central Alaska, where these two species, along with the arctic lemming, are dominant (Guthrie, 1968b; Repenning et al., 1964); as well as with the karstic records from Lime Hills and Bluefish caves (Georgina, 2001; Morlan, 1989). Abundance of singing vole in particular has led Guthrie to associate the species with the steppe-like graminoid dominated biome that covered Beringia during much of the Late Pleistocene (Guthrie, 1968b). Both species are characteristic of open environments and are found today in alpine or arctic tundra only (Bee and Hall, 1956; MacDonald and Cook, 2009). Likewise, ground squirrels in the middle Tanana valley seem to have been a Pleistocene occurrence only until ca. 12,000 cal B.P. Evidence for a later presence is lacking, but they may have persisted in local patches exposed to high rates of disturbance until the Early Holocene.

Direct dates as well as interpretations based on burrowing habits suggest that the documented jumping mice may be of Middle Holocene in age. They are today characteristic of shrubby or herbaceous riparian zones (MacDonald and Cook, 2009) and along with the long-tailed and meadow voles with whom they share ecological requirements, as well as the bog lemming, they do not have any known Pleistocene occurrence in Beringia (MacDonald and Cook, 2009; Morlan, 1989) and are considered based on genetic studies to be post-glacial immigrants (Conroy and Cook, 2000; Cook et al., 2004; Malaney et al., 2013). Given these phylogeographic and paleontological premises, as well as the remainder of the local record for the singing vole, undetermined singing/meadow vole specimens recorded in ca. 8000 layers at the Hollembæk
Species present throughout the period studied have known Pleistocene and Holocene occurrences in Beringia (Georgina, 2001; Morlan, 1989) and are considered to have persisted in Beringia throughout the last Glacial-Interglacial cycle (Conroy and Cook, 2005; Cook et al., 2004; Galbreath and Cook, 2004). They are overall more generalist in their habitat requirements. The tundra vole occurs in habitats as diverse as tundra, shrubland, meadow, and bogs, but does tend to occur in habitats with little canopy (MacDonald and Cook, 2009). The red-backed and taiga vole occur in habitats as diverse as boreal forest, tundra, shrubland, and meadow, but do tend to occur in areas where trees are present (MacDonald and Cook, 2009). Indeed, the red-backed vole is by far the dominant species of vole in the middle Tanana valley lowland boreal forest today (MacDonald and Cook, 2001).

Overall, indicator small mammal species indicate environment openness as late as 11,000 cal B.P. (Table 4), as well as the presence of trees as early as 14,000 cal B.P. Pollen and macrobotanical records for the middle Tanana valley indicate that cottonwood/aspen *Populus* spp. trees were present as early as 14,000 cal B.P. and white spruce *Picea glauca* by 10,000 cal B. P. (Bigelow and Powers, 2001; Reuther et al., 2016). Trees at that time may have been sparse on the landscape in the form of stands or in open woodlands interspersed with patches of open grassland, rather than as the close-canopy forests characteristic of the current central Alaska lowlands (Anderson and Brubaker, 1994; Bigelow, 1997; Bigelow and Powers, 2001).

Soils associated with mature boreal forest did not develop in the region until 8000 cal B.P. (Dilley, 1998; Reuther, 2013). Likewise, carbon isotopic records for moose *Alces* sp. indicate their use of a relatively open habitat until 8000 cal B.P., after which point their carbon isotope
signature became more similar to ratios from boreal forest settings (Guthrie, 2006; Lanoë et al., 2017). The occurrence of jumping mice and meadow vole around that time may reflect a biogeographic association with the boreal forest and a dispersal at that time from North America. Species characteristic of old-growth forests such as flying squirrel and red squirrel (MacDonald and Cook, 2009) may have arrived at that time too. Though absent in the record, they are not fossorial and may have been present on the landscape without becoming part of the paleontological assemblage.

4.4. Sites Paleoenvironmental Settings and Archaeological Implications

The high diversity of small mammal species observed in the middle Tanana valley during the Terminal Pleistocene and Early Holocene points to the spatial and/or temporal diversity of environments that were present at that time, including grasslands, wetlands, and open woodlands. The association of species with different habitat requirements, such as singing vole and brown lemming, may reflect the local contemporaneous presence of different micro-habitats close to the site. Alternatively, accumulation of small-mammal remains by burrowing may have resulted in palimpsests related to small-mammal populations distant by as much as several centuries, where small-mammal remains recovered in the same layers may relate to successive communities that did not overlap in their use of the site. In this case, the co-occurrence of species using different micro-environments may indicate high landscape instability and rapid local environmental shifts.

Paleoenvironmental archives in the middle Tanana valley indicate that the Terminal Pleistocene and Early Holocene were characterized by a dynamic landscape (Mann et al., 2018). High rates of sediment input from aeolian or alluvial sources, frequent wildfires, megaherbivore grazing and
trampling, as well as lagged dispersal of tree species all contributed to maintain the vegetation at early successional stages, with little soil development until 8,000 cal B.P. (Bigelow and Powers, 2001; Reuther, 2013; Reuther et al., 2016). High rates of disturbance may have triggered rapid and frequent local vegetation shifts to which small-mammal populations, highly dependent on local environmental conditions, would have then adjusted by moving their home range.

The brown lemming is a species characteristic of wet environments, and is today primarily found in patches of wet tundra (Bee and Hall, 1956; MacDonald and Cook, 2009). Its presence at the Swan Point site ca. 14,000 cal B.P. and at the Upward Sun River site ca. 11,000 cal B.P. (Table 4) indicates the presence of wet micro-habitats in the vicinity of the sites. Both sites are currently located above muskegs with thick peat development and extant and desiccated ponds (Dilley, 1998; Reuther, 2013). The archaeological assemblages in layers dated to 14,000-12,000 cal B.P. include numerous remains of waterfowl such as swan, geese, and ducks (Lanoë and Holmes, 2016; Potter et al., 2011, 2008), as do nearby contemporary archaeological sites (Yesner, 1996). The presence of brown lemming at the sites suggests that the wetlands currently located nearby may have started developing as early as the Terminal Pleistocene as ponding and slack water environments between dunes and in floodplains (Reuther, 2013). Waterfowl processed and consumed by people may thus have been acquired locally (Potter et al., 2008).

The singing vole is a species characteristic of dry environments, and is today primarily found in patches of well-drained tundra (Bee and Hall, 1956; MacDonald and Cook, 2009). The presence of the singing vole at several sites of the Middle Tanana valley between 13,000 and 8,000 cal B.P. (Table 4) suggests the persistence during the Late Glacial and Early Holocene of local conditions reminiscent of the dry glacial steppes. Singing vole may have been particularly at ease in xeric, unstable patches with high aeolian sediment deposition contributing to maintain
vegetation in an early successional stage (Dilley, 1998; Reuther, 2013). Singing vole is indeed present in layers dated to ~13,000-11,000 cal B.P. at the sites of Upward Sun River and Cook (Table 4), which have yielded some of the highest known loess deposition rates of the region (Reuther, 2013). Likewise, arctic ground squirrels are usually found in open areas with early successional vegetation, primarily in the tundra, but also in patches within the lowlands that maintain early successional vegetation due to frequent disturbance, such as flood plains (Bee and Hall, 1956; MacDonald and Cook, 2009).

Regional conditions that favored environmental diversity and high alpha and/or beta small mammal diversity likely favored human settlement as well. People living in the middle Tanana valley during the Pleistocene-Holocene transition exploited resources from various habitats and as diverse as large grazers, such as horse (*Equus lambei*), mammoth (*Mammuthus primigenius*), bison (*Bison priscus*) and wapiti (*Cervus canadensis/elaphus*); waterfowl (Anatidae); gamefowl (Tetraoninae); and anadromous fish (Salmonidae); as well as trees and berry shrubs (Choy et al., 2016; Halffman et al., 2015; Lanoë and Holmes, 2016; Potter et al., 2014, 2013; Yesner, 1996).

In parallel, patchy distribution of resources made their location and seasonality more predictable than in more homogeneous landscapes, thereby reducing the search costs associated with hunting and gathering (Lanoë et al., 2018b). These conditions for a productive and efficient hunting and gathering economy may have been one of the dominant factors in the settling of the middle Tanana valley during the Terminal Pleistocene and Early Holocene, and may help explain the unusually rich archaeological record for this period.

5. Conclusion
Small mammal remains at Terminal Pleistocene and Early Holocene archaeological sites of the middle Tanana valley provide a welcome, if uncomplete, addition to the paleontological and paleoenvironmental record of that region. Small mammal remains are routinely recorded as by-products of archaeological projects that span several years of research, leading over time to the collection of a sizeable number of specimens. Specimen quality in archaeological contexts is similar to that observed in targeted paleontological projects for at least a portion of the small mammal clades, namely rodents. Specimens from archaeological contexts also benefit from a much tighter chronological control than typically observed at paleontological localities, providing valuable contributions to the understanding of the evolution and biogeography of these species.

Small mammal remains complement existing proxies documenting environmental change over time. In contrast to proxies such as pollen or large mammal remains, small mammal remains document more closely the environments local to archaeological sites. Such information is of large interest to understand subsistence and mobility behavior of past hunter-gatherers, particularly so in the characteristically heterogeneous environments of Terminal Pleistocene and Early Holocene eastern Beringia and central Alaska.

A better understanding of the processes leading to the accumulation of small mammal remains will benefit our knowledge of the formation and preservation of archaeological occupations in aeolian context. The tight association of small mammal remains and probable burrows with anthropogenic features raises questions of how post-depositional bioturbation may affect the spatial integrity of archaeological occupations. Future research should in parallel explore how the presence of small mammal remains may be indicative of human activities and anthropogenic modification of place.
Acknowledgments

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Access to the Hollembaek site was provided by the Hollembaek family. Excavation of the other sites was permitted by the Alaska State Historic Preservation Office. Access to comparative collections at the University of Alaska Museum of the North and the Arizona State Museum was provided by Curator Link Olson and Collection Manager Aren Gunderson, and by Acting Curators Nicole Mathwich and Matthew Rowe, respectively.

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Data Availability Statement
The data that support the findings of this study are available from tables and figures in the paper as well as cited references.

References


Guthrie, R. D. (1968a). Paleoecology of a Late Pleistocene Small Mammal Community from


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Yesner, D. R. (1996). Human Adaptation at the Pleistocene-Holocene (circa 13,000 to 8,000 BP)
Figure Captions

Figure 1. Map of the Middle Tanana valley and sites mentioned in text.

Figure 2. Simplified stratigraphy and location of recovered small-mammal remains at archaeological sites in the lowlands of the Middle Tanana valley. Dots indicate the depth of recovered remains (averaged for depth ranges), with arrows indicating the maximal reported burrow depth for these species. Numbers refer to the NISP for the associated species and depth.

All radiocarbon dates are previously reported in the literature (references in Table 1) except for Hollembaek’s, which are listed in Table 3. Starred (*) dates relate to averages of contemporaneous dates for the same occupation, while sets of dates relate to distinct occupations in compressed parts of the stratigraphies. LT: brown lemming; MM: singing vole; MMP: singing vole or meadow vole; MO: tundra vole; MP: meadow vole; MR: red-backed vole; MX: taiga vole; ZH: jumping mouse.
Figure 3. Rodent burrows exposed in the stratigraphy of the Swan Point site (A) and provenience of one of the radiocarbon dates (Beta-215328) associated with a rodent burrow (B).
<table>
<thead>
<tr>
<th>Site</th>
<th>Elevation (m asl)</th>
<th>Excavated Area (m²)</th>
<th>Sediment</th>
<th>Site Landform</th>
<th>Site Vegetation</th>
<th>Local Landform</th>
<th>Other Vegetation Present Locally</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bachner (XBD-155)</td>
<td>310</td>
<td>3</td>
<td>loess</td>
<td>bedrock bluff</td>
<td>well-drained mixed forest of white spruce, aspen, poplar, and paper birch; patches of dry grassland with sedges, grasses, and sagebrush</td>
<td>lake</td>
<td>black spruce forest; lakeshore vegetation with willow and alder</td>
<td>(Reuther, 2013; Wooller et al., 2012; this paper)</td>
</tr>
<tr>
<td>Cook (XBD-72)</td>
<td>310</td>
<td>10</td>
<td>loess (90%) sand (10%)</td>
<td>bedrock bluff</td>
<td>well-drained mixed forest of white spruce, aspen, poplar, and paper birch</td>
<td>floodplain</td>
<td>black spruce forest</td>
<td>(Reuther, 2013; this paper)</td>
</tr>
<tr>
<td>Hollenbaek (XBD-376)</td>
<td>360</td>
<td>12</td>
<td>loess</td>
<td>bedrock knoll</td>
<td>well-drained mixed forest of white spruce, aspen, poplar, and paper birch - patches of dry grassland with sedges, grasses, and sagebrush</td>
<td>floodplain</td>
<td>black spruce forest</td>
<td>this paper</td>
</tr>
<tr>
<td>Keystone Dune (XBD-363)</td>
<td>350</td>
<td>22</td>
<td>sand</td>
<td>sand dune</td>
<td>well-drained mixed forest of white spruce, aspen, poplar, and paper birch</td>
<td>alluvial terraces</td>
<td>black spruce forest</td>
<td>(Lanoë et al., 2018b, 2018a; Reuther et al., 2016)</td>
</tr>
<tr>
<td>Swan Point (XBD-146)</td>
<td>320</td>
<td>86</td>
<td>loess (80%) sand (20%)</td>
<td>bedrock knoll</td>
<td>well-drained mixed forest of white spruce, aspen, poplar, and paper birch</td>
<td>alluvial terraces</td>
<td>muskeg with black spruce, larch, and tussocks</td>
<td>(Dilley, 1998; Hirasawa and Holmes, 2017; Holmes, 2014, 2011; Lanoë and Holmes, 2016)</td>
</tr>
<tr>
<td>Upward Sun River (XBD-298)</td>
<td>260</td>
<td>240</td>
<td>loess</td>
<td>sand dune</td>
<td>well-drained mixed forest of white spruce, aspen, poplar, and paper birch</td>
<td>dune field and floodplain</td>
<td>muskeg with black spruce and tussocks</td>
<td>(Potter et al., 2014, 2011, 2008; Reuther, 2013)</td>
</tr>
</tbody>
</table>

Table 1. Sites geomorphological setting and present environment (aspen: *Populus tremuloides*; black spruce: *Picea mariana*; grass: Poaceae; larch: *Larix laricina*; paper birch: *Betula papyrifera*; poplar: *Populus balsamifera*; sagebrush: *Artemisia* spp.; sedge: *Cyperaceae*; white spruce: *Picea glauca*).
<table>
<thead>
<tr>
<th>Site</th>
<th>NISP</th>
<th>Excavated Area (m²)</th>
<th>Density (NISP.m⁻²)</th>
<th>Density (NISP.m⁻².yr⁻³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bachner</td>
<td>6</td>
<td>1</td>
<td>6.00</td>
<td>0.92</td>
</tr>
<tr>
<td>Cook</td>
<td>1</td>
<td>10</td>
<td>0.10</td>
<td>0.02</td>
</tr>
<tr>
<td>Keystone Dune</td>
<td>0</td>
<td>22</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Hollembæk</td>
<td>42</td>
<td>12</td>
<td>3.50</td>
<td>0.54</td>
</tr>
<tr>
<td>Swan Point</td>
<td>26</td>
<td>86</td>
<td>0.30</td>
<td>0.05</td>
</tr>
<tr>
<td>Upward Sun River</td>
<td>22</td>
<td>240</td>
<td>0.09</td>
<td>0.01</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>97</strong></td>
<td><strong>371</strong></td>
<td><strong>0.26</strong></td>
<td><strong>0.04</strong></td>
</tr>
</tbody>
</table>

Table 1. Recorded vole, lemming, and jumping mice lower first molars.
Table 3: Radiocarbon dates for the Hollembaek Site. Calibration conducted with IntCal13 and OxCal 4.3 (Bronk Ramsey, 1994; Reimer et al., 2013)

<table>
<thead>
<tr>
<th>Laboratory Number</th>
<th>Material</th>
<th>$^{14}$C Date B.P.</th>
<th>Calibrated Age B.P. (2σ)</th>
<th>$\delta^{13}$C (‰)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beta-294400</td>
<td>collagen, <em>Cervus canadensis</em></td>
<td>7330 ± 40</td>
<td>8290-8020</td>
<td>-20.8</td>
</tr>
<tr>
<td>UGAMS 26195</td>
<td>collagen, <em>Cervus canadensis</em></td>
<td>7020 ± 30</td>
<td>7940-7790</td>
<td>-21.3</td>
</tr>
<tr>
<td>UGAMS 26196</td>
<td>charcoal</td>
<td>7690 ± 30</td>
<td>8540-8420</td>
<td>-24.3</td>
</tr>
<tr>
<td>UGAMS 30764</td>
<td>charcoal</td>
<td>10,220 ± 25</td>
<td>12,090-11,810</td>
<td>-23.4</td>
</tr>
<tr>
<td>UGAMS 30765</td>
<td>charcoal</td>
<td>6680 ± 20</td>
<td>7590-7510</td>
<td>-23.1</td>
</tr>
<tr>
<td>UGAMS 30766</td>
<td>charcoal</td>
<td>7530 ± 20</td>
<td>8390-8340</td>
<td>-24.7</td>
</tr>
</tbody>
</table>
### Table 1

<table>
<thead>
<tr>
<th>Animal</th>
<th>Bachner</th>
<th>Cook</th>
<th>Hollembaek</th>
<th>Keystone Dune</th>
<th>Swan Point</th>
<th>Upward Sun River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brown lemming</td>
<td></td>
<td></td>
<td></td>
<td>14,000</td>
<td>11,000</td>
<td></td>
</tr>
<tr>
<td>Ground squirrel</td>
<td>&gt; 12,000</td>
<td>&gt; 12,000</td>
<td>&gt; 12,000</td>
<td>&gt; 12,000</td>
<td>&gt; 13,000-11,000</td>
<td></td>
</tr>
<tr>
<td>Jumping mouse</td>
<td>&lt; 8000</td>
<td></td>
<td></td>
<td>&lt; 9,500</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cf. meadow vole</td>
<td></td>
<td></td>
<td>8000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red-backed vole</td>
<td>8000</td>
<td></td>
<td>&gt; 12,000</td>
<td>14,000-12,000</td>
<td>11,000</td>
<td></td>
</tr>
<tr>
<td>Singing vole</td>
<td>12,000</td>
<td></td>
<td>&gt; 12,000</td>
<td></td>
<td>11,000</td>
<td>13,000</td>
</tr>
<tr>
<td>Taiga vole</td>
<td>8000</td>
<td>12,000</td>
<td>&gt; 12,000</td>
<td>14,000-12,000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tundra vole</td>
<td>12,000</td>
<td></td>
<td>&gt; 12,000</td>
<td>14,000-12,000</td>
<td>11,000</td>
<td>11,000-13,000</td>
</tr>
</tbody>
</table>

Table 1. Estimated ages cal B.P. of for small mammal presence at archaeological sites in the lowlands of the middle Tanana valley. The likely occurrence of meadow vole at Hollembaek is discussed in section 4.3.
Figure 1: Map of the Middle Tanana valley and sites mentioned in text.

84x43mm (300 x 300 DPI)
For Peer Review

Figure 2. Simplified stratigraphy and location of recovered small-mammal remains at archaeological sites in the lowlands of the Middle Tanana valley. Dots indicate the depth of recovered remains (averaged for depth ranges), with arrows indicating the maximal reported burrow depth for these species. Numbers refer to the NISP for the associated species and depth. All radiocarbon dates are previously reported in the literature (references in Table 1) except for Hollembaek’s, which are listed in Table 3. Starred (*) dates relate to averages of contemporaneous dates for the same occupation, while sets of dates relate to distinct occupations in compressed parts of the stratigraphies. LT: brown lemming; MM: singing vole; MMP: singing vole or meadow vole; MO: tundra vole; MP: meadow vole; MR: red-backed vole; MX: taiga vole; ZH: jumping mouse.
Figure 2 continued.
Figure 3: Rodent burrows exposed in the stratigraphy of the Swan Point site (A) and provenience of one of the radiocarbon dates (Beta-215328) associated with a rodent burrow (B).

192x90mm (300 x 300 DPI)