SCIENCE ADVANCES | RESEARCH ARTICLE

ANTHROPOLOGY

Late Pleistocene onset of mutualistic human/canid (*Canis* spp.) relationships in subarctic Alaska

François Lanoë[1,2]*, Joshua Reuther[2,3], Stormy Fields[4], Ben Potter[3], Gerad Smith[5], Holly McKinney[3], Carrin Halffman[3], Charles Holmes[3], Robin Mills[6], Barbara Crass[2], Ryan Frome[7], Kyndall Hildebrandt[2], Robert Sattler[8], Scott Shirar[2], Alida de Flamingh[9], Brian M. Kemp[7,10], Ripan Malhi[9,11], Kelsey E. Witt[12]

Large canids (wolves, dogs, and coyote) and people form a close relationship in northern (subarctic and arctic) socioecological systems. Here, we document the antiquity of this bond and the multiple ways it manifested in interior Alaska, a region key to understanding the peopling of the Americas and early northern lifeways. We compile original and existing genomic, isotopic, and osteological canid data from archaeological, paleontological, and modern sites. Results show that in contrast to canids recovered in non-anthropic contexts, canids recovered in association with human occupations are markedly diverse. They include multiple species and intraspecific lineages, morphological variation, and diets ranging from terrestrial to marine. This variation is expressed along both geographic and temporal gradients, starting in the terminal Pleistocene with canids showing high marine dietary estimates. This paper provides evidence of the multiple ecological relationships between canids and people in the north—from predation, probable commensalism, and taming, to domestication—and of their early onset.

INTRODUCTION

Interactions with large canids (*Canis* spp.; including wolf *C. lupus*, dog *C. familiaris*, and coyote *C. latrans*) form a key aspect of human life in Beringia and more generally in the Subarctic/Arctic. Most visible today is the mutualistic relationship between people and domestic dogs. When and how this relationship developed remains unknown. Beyond domestication, human-canid relationships have likely been iterative, complex, and multifaceted since the Late Pleistocene and encompassed ecological interactions as diverse as competition, predation, and symbiosis.

Large canids have been an integral part of northern ecosystems since at least the Late Pleistocene. Wolves were a major component of the glacial steppe and competed with people and other predators for access to resources (*1*–*3*). Their dietary flexibility enabled wolves to adapt to environmental change and survive the Pleistocene-Holocene faunal turnover, with limited extinction of some more specialized populations [e.g., *C. lupus* var. Beringia; (*4*, *5*)]. Coyotes likewise successfully adapted to Holocene environments in temperate North America (*6*, *7*) and have recently expanded into the Subarctic following anthropogenic environmental change (*8*).

Symbiotic relationships between people and large canids have occurred in the form of commensalism, taming, and/or selective breeding. Some or all of those eventually led to the domestication of dogs (*9*–*12*). The archaeological recognition of these phenomena remains unclear as each may have manifested by different anatomic, genetic, and/or dietary changes (*13*–*17*), as well as differential mortuary treatment (*18*, *19*).

Dogs were arguably domesticated during the terminal Pleistocene [~19 to 12 calibrated thousand years before the present (cal kyr B.P.)] in Eurasia (*20*–*25*). They may have accompanied initial human dispersal into Beringia and the Americas and may also have contributed to anthropogenic megafauna extinction (*26*, *27*). Although canid remains in Pleistocene sites are not uncommon in Beringia (*19*, *28*–*31*), evidence for domestication at that time remains mostly incidental or contextual. The earliest firm (anatomical and genetic), albeit indirect, evidence for dogs in Beringia dates no later than ~9.9 cal kyr B.P., by which time individuals of the American dog lineage were present in temperate North America (*18*, *22*, *32*). Direct evidence in Beringia appears ~9.0 cal kyr B.P. (*33*, *34*).

Evidence for dogs remains sparse or absent until the Late Holocene when they had become an integral part of life in the North (*35*) and, more specifically, in interior Alaska as hunting and transportation aids (*36*–*38*). In recent times, the Dene people of interior Alaska have also shared similar habitats with wolves (*39*) but generally respected and avoided both wolves and coyotes as hunting competitors and exerted limited predation on them (*40*–*45*).

Here, we focus on human-canid relationships in interior Alaska since initial settlement in the terminal Pleistocene (*46*) and through the Holocene, building a comprehensive database of archaeological and comparative paleontological and modern canid specimens. Interior Alaska is a key region of Beringia and, because of its dense concentration of early archaeological sites with well-preserved faunal assemblages, has been important in developing models of initial human settlement (*47*–*50*). We reconstruct the diets of large canids from paleontological, archaeological, and modern locales in the region and show how those diets expanded starting in the terminal Pleistocene. This expansion was probably related to human-canid symbiotic relationships in interior Alaska, including dog domestication. Eventually, those led to the mutualistic human-dog relationship characteristic of subarctic socioecological systems.

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[1]School of Anthropology, University of Arizona, Tucson, AZ, USA. [2]Archaeology Department, University of Alaska Museum of the North, Fairbanks, AK, USA. [3]Department of Anthropology, University of Alaska Fairbanks, Fairbanks, AK, USA. [4]Water and Environment Research Center, University of Alaska Fairbanks, Fairbanks, AK, USA. [5]Department of Anthropology and Geography, University of Alaska Anchorage, Anchorage, AK, USA. [6]Bureau of Land Management, Fairbanks District, AK, USA. [7]Laboratories of Molecular Anthropology and Microbiome Research, University of Oklahoma, Norman, OK, USA. [8]Tanana Chiefs Conference, Fairbanks, AK, USA. [9]Center for Indigenous Science, Carl R. Woese Institute for Genomic Biology, University of Illinois Urbana-Champaign, Champaign, IL, USA. [10]Department of Anthropology, University of Oklahoma, Norman, OK, USA. [11]Department of Anthropology, University of Illinois Urbana-Champaign, Champaign, IL, USA. [12]Department of Genetics and Biochemistry and Center for Human Genetics, Clemson University, Clemson, SC, USA.
*Corresponding author. Email: lanoe@arizona.edu

RESULTS

Morphology and genomics

We developed a database of 111 large canid specimens in interior Alaska, including 76 ancient (paleontological and archaeological) specimens, of which 8 are newly reported here; and 35 modern (wildlife collection) specimens (Fig. 1 and table S1). Ancient specimens originate from the middle Tanana River, an area rich in both residential archaeological sites and fossil locales; as well as locations elsewhere along the Tanana, Yukon, Copper, and Kuskokwim Rivers. Most (82%) ancient specimens have direct radiocarbon dates, 31 of which are newly reported here. The remaining specimens consist of archaeological specimens dated by stratigraphic association with other dated materials, a subset of which (9%) has both direct and indirect dates. Modern specimens (dated 1954–2006 CE) derive from multiple drainage basins and physiographic settings (lowlands and uplands) within interior Alaska, allowing us to evaluate potential geographic variation in isotopic values.

We identify ancient *C. latrans*, *C. lupus*, *C. familiaris*, and *C. lupus/familiaris* based on combined morphological and genomic analyses (50% of which are newly reported here), with no instances of mismatch between morphological and genomic identifications (table S1). Archaeological specimens include 17 dogs, 2 coyotes, and 8 unspecified canids; paleontological specimens include 31 wolves and 18 dogs; and modern specimens include 35 wolves.

Archaeological canids include seven individuals dated from the terminal Pleistocene to the Early Holocene (~13.7 to 8.0 cal kyr B.P.) (Fig. 2). Several lacked sufficient preserved genetic material and were further considered to be *C. lupus/familiaris* ($n = 4$). Others were identified as *C. lupus/familiaris* outside of known dog lineages ($n = 3$), including two specimens for which mitochondrial and whole genome data could be derived (Fig. 3 and figs. S1 to S3). The ~8100 cal yr B.P. (calibrated years before the present) Hollembaek perinatal individual (UA2018-088-211) grouped with modern wolves from Mexico and had a mitochondrial genome similar to ancient Siberian wolves and modern wolves from Russia and Finland. The ~12,000 cal yr B.P. Swan Point individual grouped with ancient arctic wolves from Zhokhov Island and had a mitochondrial genome similar to an ancient Belgian wolf and modern wolves from across Eurasia.

The size and morphology of Pleistocene and Early Holocene archaeological specimens vary (table S7). All measured specimens from Pleistocene individuals ($n = 4$) are within the size range of modern wolves at 1σ; specifically, the upper carnassial (P^4) from the Carpenter Quarry site is of a size characteristic of wolves per Janssens *et al.* (*51*) and substantially larger than those of the Zhokhov Island dogs (*33*). Of measured Early Holocene specimens ($n = 5$), one is within the size range of comparative wolf elements, and two are slightly smaller (85 to 95% in size). The mandible from Hollembaek's

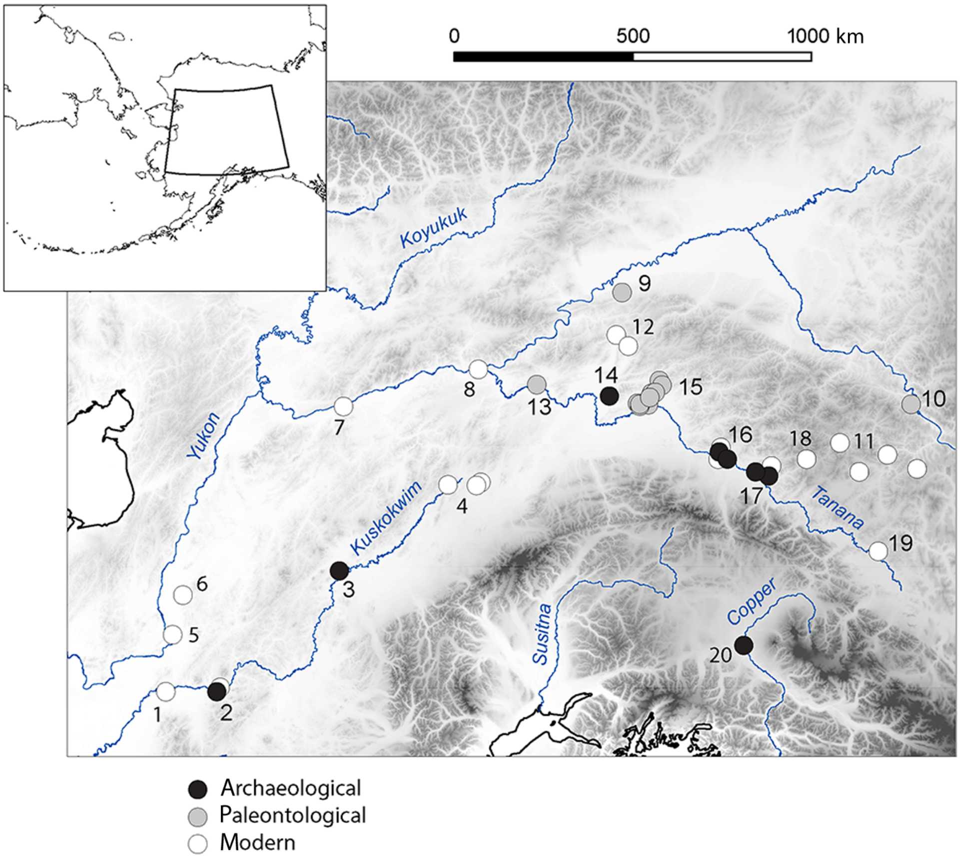

Fig. 1. Map of interior Alaska and location of specimens. 1: Discovery Ck.; 2: Kwigiumpainukamiut; 3: McGrath (Tochak); 4: Lake Minchumina area (Foraker R., North Fork Kuskokwim R.); 5: Holy Cross; 6: Shageluk; 7: Ruby; 8: Tanana; 9: Goldstream; 10: Eagle (Fort Egbert); 11: Fortymile area (Liberty Ck., Ketchumstuk Ck., and Joseph Ck.); 12: Livengood area; 13: Manley Hot Springs; 14: Minto Lakes; 15: Fairbanks area (Cleary Ck., Cripple Ck., Engineer Ck., Ester Ck., Fairbanks Ck., Gilmore, Gold Hill, and Goldstream); 16: Shaw Ck. area (Swan Point, Broken Mammoth, Carpenter Quarry, Quartz Lake, and Clear Ck.); 17: Healy Lake area (Hollembaek's Hill and Volkmar R.); 18: Upper Healy R.; 19: Little Beaver Ck.; 20: Glennallen (Ringling).

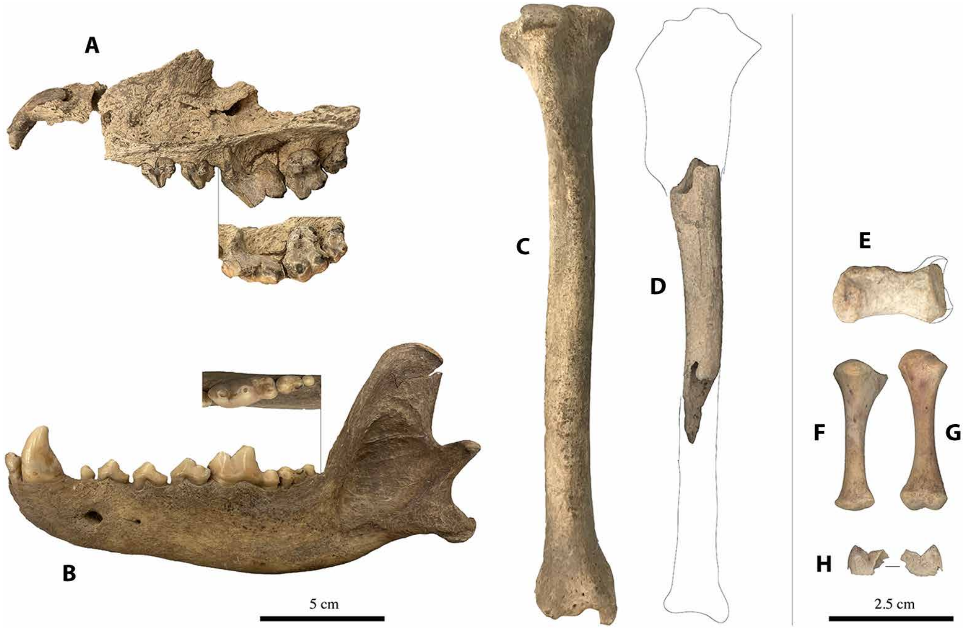

Fig. 2. Selected terminal Pleistocene/Early Holocene specimens (*C. lupus/familiaris*). Carpenter Quarry: adult maxilla/premaxilla (**A**). Hollembaek's Hill: adult mandible (**B**) and tibia (**C**). Swan Point: adult tibia (**D**). Hollembaek's Hill: adult pisiform (**E**); perinate tibia (**F**), femur (**G**), and dp^3 (**H**).

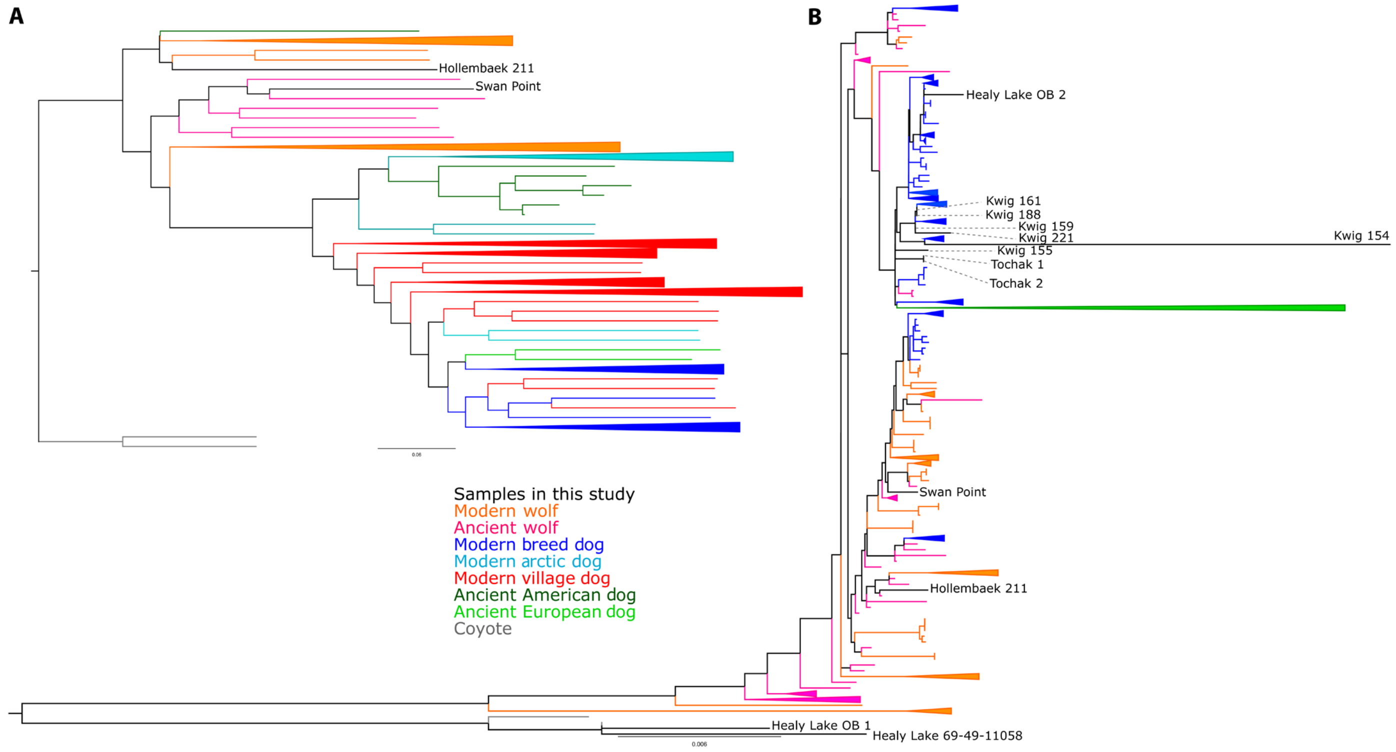

Fig. 3. Genomic relationship of specimens in this study with other large canids. (**A**) Whole-genome data and (**B**) mitochondrial genome data. The individuals from this study are labeled, and samples are color-coded by age, geographic origin, and taxon (more detailed graphs in figs. S1 to S3).

Hill is within the known length range for wolf at 1σ and substantially longer (>2σ) than those of Zhokhov Island dogs. It also appears to be substantially larger in height (>2σ of wolf variability) than length—a generally "stout" morphology argued by some to be characteristic of dogs (*52*), but by others to fit within the morphological variability of wolves (*51*).

The other 20 specimens from archaeological contexts date to the later Holocene (post-700 cal yr B.P.). It was possible to amplify DNA from 11 of the 18 specimens analyzed here (Fig. 3, figs. S1 to S3, and table S3). Species identification of nine specimens was confirmed by inter- and/or intra-amplicon sequences of informative sections of the mitochondrial genome, while two specimens (16-248 and 17-124) each produced only a single amplicon. Identified specimens include both coyotes ($n = 2$) and dogs ($n = 10$; includes one specimen reported in a prior study); two dog specimens (from the Tochak site) from the same archaeological context and with identical isotopic values cluster closely together and probably belong to the same individual. Six of the dog specimens, all from postcontact occupations at the Healy Lake and Kwigiumpainukamiut sites, group with modern European breeds. Another three dog specimens, including one from Kwigiumpainukamiut (UA97-99-155) and the two from the precontact Tochak site, do not group with either modern or known American lineages. Additional canid specimens ($n = 7$) that shared size, morphology, and context with specimens identified as dogs were further presumed to be dogs (table S1). One archaeological specimen ($n = 1$) was dated here to the modern period (post-1950 CE) and not identified further.

Of note, age reassessment (from calibration and modeling of radiocarbon reservoir effect) of paleontological dogs reported by Leonard *et al.* (*23*) ($n = 18$) makes many of them contemporaneous with the gold rush era in interior Alaska (starting approximately 1900 CE) rather than to strictly precontact times as assumed by the original authors (table S1). The partial mitochondrial DNA presented for a sample of those individual dogs ($n = 11$) still indicates Indigenous ancestry, but some European ancestry may also be present.

Stable isotopes and paleodiets

We provide stable carbon and nitrogen isotope values for all canid specimens, including 160 of which (71%) are newly reported here. Isotopic values cover a wide isotopic space in both δ^{13}C (−21 to −15‰) and δ^{15}N (4 to 16 ‰) (Fig. 4 and table S1). Wolves are for the most part contained within the isotopic variability of dogs, with consistently low δ^{13}C and δ^{15}N values. The few coyote specimens ($n = 2$) group with wolves. Specimens of unknown taxonomic affiliation (*C. lupus/familiaris*) are also contained within the dog variability but cover a wider isotopic space than wolves.

Canid isotopic values vary through time from Oxygen Isotope Stage 3 to the recent past (Fig. 5). Wolves' values are consistent through the entire period. There are no discernable changes that may be linked to climate variation within the Pleistocene, although Fox-Dobbs *et al.* (*1*) does indicate a slight increase in δ^{15}N during the Last Glacial Maximum (~23 to 19 kyr B.P.) compared to previous and later periods of the Pleistocene. In contrast, modern specimens show substantially lower average δ^{15}N (5.8 ± 0.9‰) values than Pleistocene specimens (7.8 ± 1.3‰). Dog values, restricted to the last thousand years, are consistently variable in both δ^{13}C and δ^{15}N. This isotopic variability and breadth appear to originate with specimens of unknown taxonomic affiliation (*C. lupus/familiaris*) from the Swan Point (dated 12,860 to 11,330 cal yr B.P.) and Hollembaek's Hill (dated to ~8100 cal yr B.P.) sites.

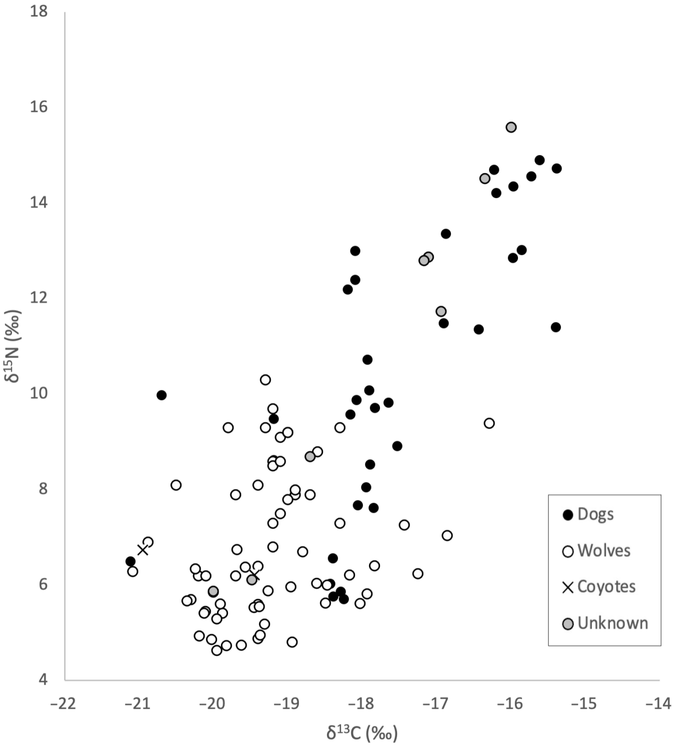

Fig. 4. Isotopic values of interior Alaska large canids.

Results of a dietary mixing model run on each canid specimen suggest considerable variation in canid dietary input through time and across taxa (Fig. 6 and table S1). Both wolves and coyote show fully terrestrial dietary estimates (at 2σ) throughout the entire period, with one exception, a modern wolf from the middle Kuskokwim River which shows high estimated salmon input (50 ± 14%). Dog diets instead range from salmon specialization (>60%) to fully terrestrial diet while also including some specimens with substantial (>20%) freshwater input. Some specimens of unknown taxonomic affiliation (*C. lupus/familiaris*) dated to the terminal Pleistocene and Early Holocene also had substantial estimated proportions of salmon (>50%) in their diet.

Dietary contributions of Late Holocene dog specimens vary by archaeological location. Salmon specialization (estimated input ranging from 51 to 86%) is notable in all 10 specimens from the Kwigiumpainukamiut site, on the middle Kuskokwim River; salmon input is also substantial (46 to 48%) in the dog at the Tochak site further upriver. Dogs along the middle Tanana River include individuals with probable fully terrestrial diet (>70%, $n = 8$), salmon specialization (68 to 81%, $n = 3$), and substantial salmon intake (20 to 41%, $n = 12$). Estimated freshwater input is most notable (40 ± 12%) in a dog from the Healy Lake site, on the shoreline of the eponymous freshwater lake. The single dog from the Ringling site, on the middle Copper River, appears to have been a terrestrial specialist (77 ± 9%).

Late Pleistocene and Early Holocene archaeological specimens fall into two distinct groups. Salmon specialization or substantial intake is restricted to specimens from the Hollembaek's Hill ($n = 4$, all dated to ~8100 cal yr B.P., estimated salmon input of 61 to 82%) and Swan Point ($n = 1$, 57 ± 8%, ~12,000 cal yr B.P.) sites. In contrast, two specimens from the Carpenter Quarry (~12,800 cal yr B.P.) and Hollembaek's Hill (~13,630 cal yr B.P.) sites seem to have fed exclusively (72 to 74%) on terrestrial sources.

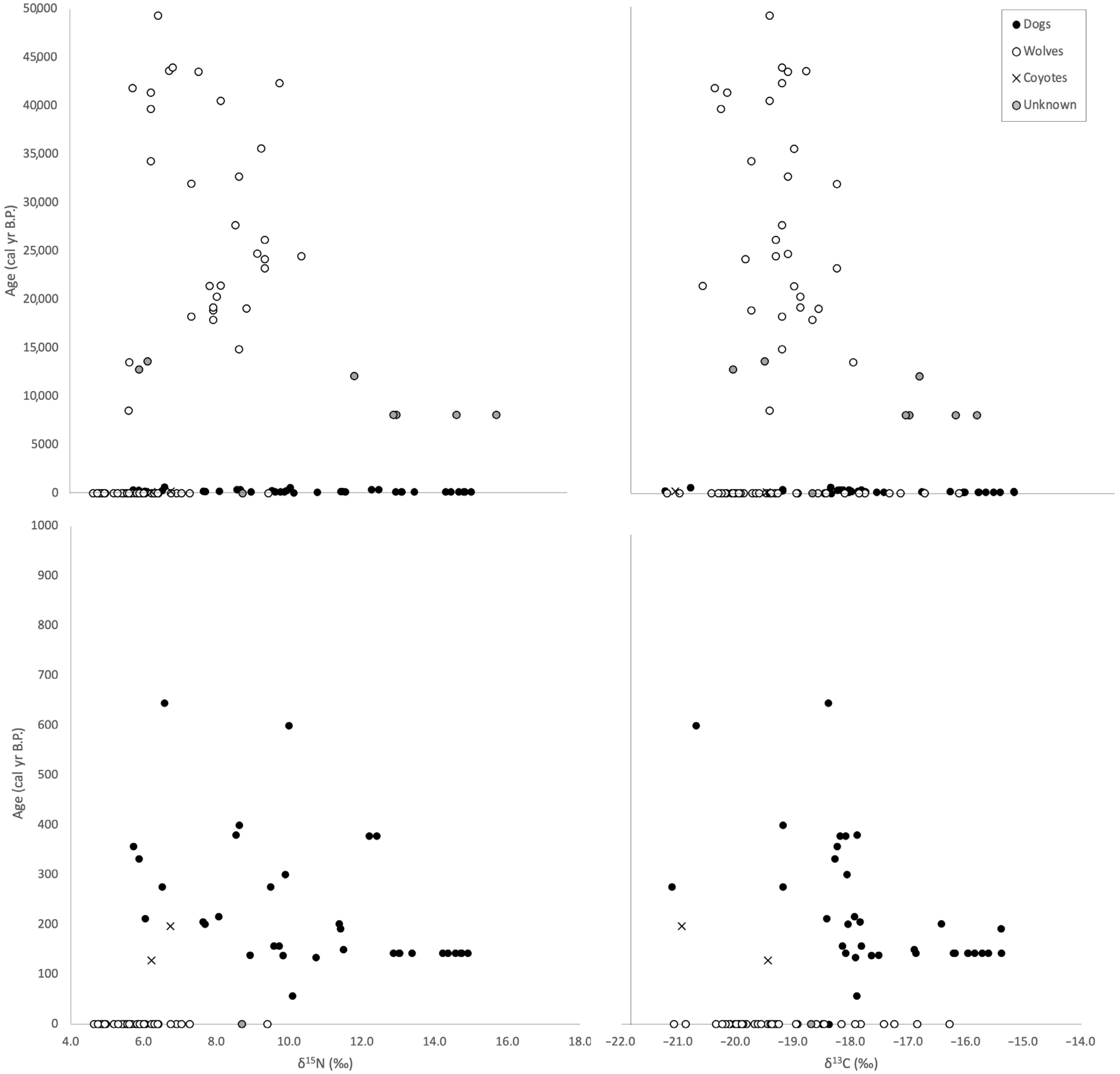

Fig. 5. Variation of canid δ^{13}C and δ^{15}N along a temporal gradient. Long (top) and recent (bottom) temporal scales.

DISCUSSION

Biogeography

The newly reported DNA information (mitochondrial and low-coverage genome) from two Pleistocene and Early Holocene canid individuals refines our understanding of past wolf biogeography. The relatedness of the Swan Point individual with ancient Siberian wolves, some of which date to more than 50 cal kyr B.P. (*53*, *54*), suggests some population continuity across the northern latitudes for at least 30,000 years. In contrast, the relatedness of the Hollembaek's Hill individual with modern North American gray wolves suggests that the wolves living in Alaska during the terminal Pleistocene and early Holocene were genetically diverse and that modern wolves found elsewhere in North America are also related to these early northern wolf populations.

Late Holocene canids identified as dogs contribute to our knowledge of dog lineages in the northern latitudes before and after European colonization. The close association between most post-contact dogs with mitochondrial sequences of European breeds corroborates evidence that, in some regions of the Americas [but not all, e.g., (*55*)], fast dog genomic turnover followed European

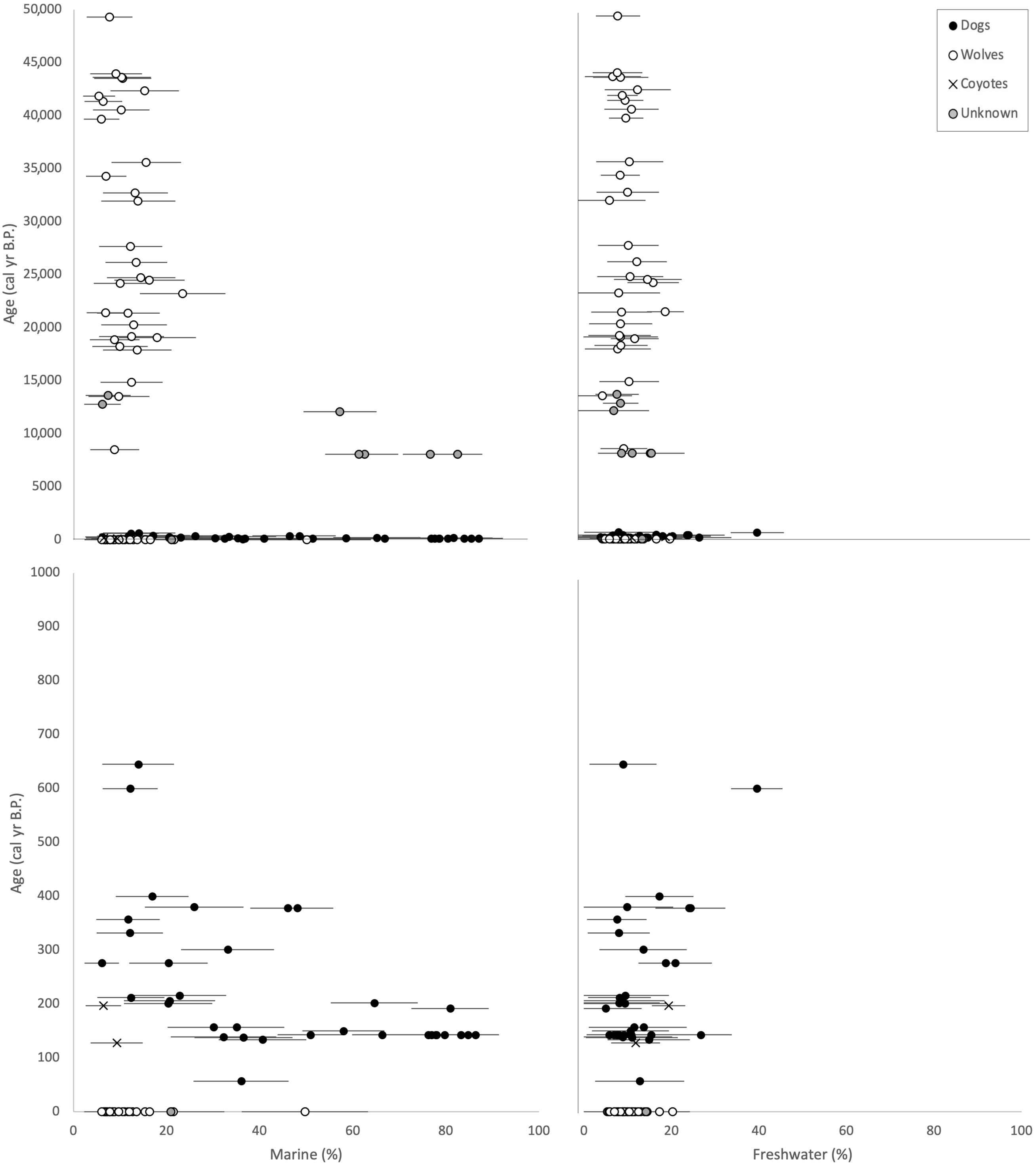

Fig. 6. Variation of estimated marine and freshwater contributions to canid diet (with 1 σ) along a temporal gradient. Long (top) and recent (bottom) temporal scales.

arrival (*22*). One other postcontact dog and two precontact dogs appear to be distinct from European dog lineages but do not cluster with known mitochondrial lineages in the Americas (A2b) or the Arctic (A1a, A1b, or A2a). This may be due to the recovery of limited amounts of mitochondrial DNA rather than a full mitochondrial sequence from these individuals.

Canid diets and relationships with humans

The diet of large canids in interior Alaska has been relatively constricted and focused on terrestrial resources from ~49.0 to about 13.6 cal kyr B.P., after which dietary variability increased to range from fully terrestrial to specialized marine diets. This variability is specific to canids from archaeological locales, as both paleontological and modern wolves consistently show fully terrestrial diets. Isotopic variation among wolves is limited, as noted by Fox-Dobbs *et al.* (*1*) who relate the slight Pleistocene variation in δ^{15}N to dietary changes within terrestrial sets of resources. The lower δ^{15}N of Holocene wolves can reasonably be attributed to environmental change starting in the Early Holocene (changes in aridity or increases in canopy cover) as observed throughout interior Alaska food webs (*56*–*58*). If wolves of interior Alaska consumed anadromous and freshwater resources, then it was episodic and left no substantial isotopic signature, with one exception from the middle Kuskokwim River known for its strong salmon runs (*59*).

In contrast, the dietary diversity of large canids recovered in archaeological sites likely reflects the multiple ecological relationships shared between canids and people including mutualism, other forms of symbiosis (commensalism), and antagonism (predation).

Dog dietary diversity in Late Holocene archaeological sites relates to the mutualistic relationship between Indigenous people of interior Alaska and their dogs (and possibly some early European settlers as well). Dogs were fed terrestrial, anadromous, and freshwater resources in varying proportions depending on archaeological locales. Dogs from sites on the Kuskokwim River and its strong salmon runs appear to have eaten more salmon, the proportion of which rises in sites further downriver. This relates to dogs' specialized salmon diets known from coastal sites near the mouth of the Kuskokwim River (*60*). Dogs from the middle Tanana River include individuals with specialized terrestrial diets, others with specialized marine diets, and yet others with mixed diets. This feeding strategy is consistent with the ethnographic record of interior Alaska that documents dog food as consisting of large game, small game, and fish depending on location (*44*, *61*). Some dog food items were shared with people, for instance, dried whitefish in the winter on the upper Tanana (*41*). Others were considered improper for human consumption, for instance, salmon harvested above the mouth of the Goodpaster River on the middle Tanana (*62*).

Dog food was needed to sustain those very present companions which were integral partners in the successful economic strategies of the Subarctic. Late Holocene dogs must have fulfilled the same obligations as documented ethnographically: hunting aids (for both large and small mammals); transportation (with packsacks); guarding; and as pets, particularly for children (*36*, *38*, *41*, *63*). This economic importance often came with a high level of respect from their human partners, with dogs carrying their own "luck" (*'engii'*) that could affect hunters' success (*64*), and documented instances of potlatches delivered on the death of a favorite dog (*65*, *66*). Dogs certainly seem to have been considered taboo for Northern Dene human food except during starvation periods (*41*, *67*). Dog food and care became more critical as their social roles expanded during the early Historic period, particularly to support the larger dog teams needed following the introduction of dog sleds in the early 20th century (*41*, *68*).

Early Holocene large canids documented at the Hollembaek's Hill site date from a time when dogs existed both to the west in Yakutia (*33*, *34*), to the south in the Midwestern United States (*18*, *22*), and probably (date not corrected for marine reservoir) in coastal Alaska (*69*). Available DNA information for one of the four Hollembaek's Hill individuals shows no relationship with known dog clades, and they appear to have varied in size from large (wolf-sized) to moderate, as did those known Early Holocene dogs (*18*, *33*). All four Hollembaek's Hill individuals fed on salmon over a large part of the year and as a large percentage of their diet, akin to Late Holocene dogs of the same area. This high salmon consumption would not occur in a situation of commensalism in which wild canids would have scavenged food remains; this is particularly true for the perinate canid individual whose mother, if a wolf, had to access salmon between times of conception and birth [February to June (*70*)], outside of salmon run season on the middle Tanana [July to November (*71*)]. High salmon consumption for the Hollembaek's Hill individuals rather implies reliance on stored salmon. Combined dietary, morphological, and contextual information thus suggests that Hollembaek's Hill individuals were pet wolves and/or domesticated dogs. Future genetic studies will likely clarify their relationships with other canid clades.

Late Holocene archaeological contexts include wild canids in addition to domesticated dogs. Here, we document the presence of coyotes, but potential wolf remains (not sampled in this study) are also known in sites at that time (*39*). Given their fully terrestrial diet, it is likely that coyote specimens in this study represent predation, akin to recent practices in which hunters occasionally harvested wolves both for population culls and fur but not for food (*43*, *72*–*74*). Such predation may have been facilitated by situations of commensalism in which canids became habituated to human settlements, as is known of both wolves and coyotes (*75*, *76*). It is also possible that those wild individuals were kept as pets and fed terrestrial resources.

The terminal Pleistocene archaeological canid specimens present a complex case. While DNA of the Swan Point individual, dated 12,860 to 11,330 cal yr B.P., shows no relationship with known dog clades, it clearly seems to have been fed salmon in similar proportions to later (Holocene) dogs of the middle Tanana. This novel marine dietary input is contemporaneous of the incorporation of salmon in human diet in interior Alaska starting ~12,950 cal yr B.P. (*77*–*80*). In contrast, both the contemporaneous specimen from Carpenter Quarry (12,840 to 12,750 cal yr B.P.) and the older Hollembaek's Hill specimen (13,750 to 13,510 cal yr B.P.) show fully terrestrial diets that are comparable to contemporaneous paleontological wolves, such as the Fort Egbert specimen in the Upper Yukon River region (*81*). Additional Pleistocene archaeological specimens in the region (not sampled in this study) also appear to show terrestrial diets: Britannia Creek further upstream the Yukon River [dated 12,940 to 12,700 cal yr B.P. (*82*)], based on a reported δ^{13}C value (−18.8‰ on a tooth; estimated at −19.9 ± 0.2‰ after correcting for nursing enrichment) on par with wild wolves; and Broken Mammoth on the middle Tanana River (dated 13,100 to 12,770 cal yr B.P.), based on the lack of radiocarbon dating offset with associated material [11,040 ± 80 versus 11,060 ± 90 ^{14}C B.P. (*28*); δ^{13}C not available].

The terminal Pleistocene in interior Alaska may have been a time of experimentation in terms of human-canid relationships. People may have domesticated canids that left no genetic trace in later dog lineages (including the American dog lineage). Alternatively, some wild canids may have been kept as pets and others hunted; some may have been fed salmon and others terrestrial resources, a dietary diversity seen in domesticated dogs a few millennia later. Yet in another scenario, salmon-feeding to canids (wild or domestic) started in the Younger Dryas but only became common during the Early Holocene. Regardless of the specific details, the onset of canid dietary expansion in the terminal Pleistocene reflects the increase of symbiotic human-canid interactions. While it eventually took different forms, it also marked the onset of the characteristic human-dog mutualistic system of the northern latitudes.

MATERIALS AND METHODS

Morphology and genomics

We strove to sample only one specimen per individual in (archaeological) cases where individuals appear to be represented by several specimens. All ancient specimens were morphologically identified as large canids (*Canis* sp.). Species-level identification was based on size and morphology when possible. A sample (28%) of ancient specimens (mostly paleontological) was identified by DNA in prior studies (*4*, *23*, *37*), and we followed Leonard *et al.* (*4*) in assigning the remaining Pleistocene paleontological specimens (28%) to *C. lupus*. In this study, we identified an additional 22 archaeological specimens (29%) by DNA at the University of Oklahoma ($n = 18$) and the University of Illinois at Urbana-Champaign ($n = 4$) (methods in Supplementary Text). We obtained selected osteological measurements following literature standards when possible (*83*) and compared them to published values (*7*, *33*, *51*, *52*) and/or comparative elements at the Zooarchaeology Laboratory of the Arizona State Museum and at the Mammalogy Department of the University of Alaska Museum of the North.

Stable isotope and paleodiets

Methods of collagen extraction and stable isotope measurement follow standards in the field (Supplementary Text). We ran a dietary mixing model [simmr, (*84*)] on each canid specimen. Canids have flexible diets, and potential dietary sources in interior Alaska are accordingly numerous, including ungulates (e.g., bison and mammoth), other terrestrial herbivores (e.g., rodents and gamefowl), freshwater animals (e.g., whitefish and waterfowl), anadromous animals (salmon), and terrestrial plants (e.g., berries). Taxon availability varied through the Late Pleistocene and Holocene in response to local extirpations and invasions (*85*). Isotopic values for each source taxon are also expected to have varied spatially and temporally with changing climates and vegetation zones (*1*, *2*, *86*). The diversity of potential sources and their internal isotopic variation forbids attempts to identify specific sources of canids' diet (*84*). Therefore, we combined potential sources with similar isotopic values into three broad categories: terrestrial herbivores (both mammalian and avian), freshwater resources, and anadromous resources. We added mammoth, which among terrestrial herbivores has a distinct isotopic signature (*87*), as a fourth source for iterations of the model conducted on Pleistocene canids. We excluded other potential source taxa on the basis that they are unlikely to have contributed substantially to canids' diet, including waterfowl (restricted and highly seasonal availability) and plants (unlikely to have contributed substantially to dietary protein).

Dating

The mixing model results suggested a notable (>30%) marine and/or freshwater dietary input for 28 (37%) ancient specimens. If available, we used associated indirect dates for these specimens ($n = 18$). For the remainder ($n = 10$), we applied ^{14}C corrections to account for a radiocarbon reservoir effect based on each specimen's dietary estimation (methods in Supplementary Text). All radiocarbon dates are calibrated with OxCal and IntCal20 (*88*, *89*).

Supplementary Materials

The PDF file includes:

Supplementary Text
Figs. S1 to S4
Legend for table S1
Tables S2 to S8
References

Other Supplementary Material for this manuscript includes the following:

Table S1

REFERENCES AND NOTES

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