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The effects of resources and population expansion on female–male protein consumption among hunter-gatherers

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ABSTRACT

This paper investigates the effects of terrestrial vs. marine resources and population expansion on sex differences in the consumption of protein among hunter-gatherers. We propose that differences in protein consumption emerge under conditions of greater specialization on terrestrial resources and population expansion. Consistent with this hypothesis, hunter-gatherers in pre-contact Texas display more pronounced sex differences in δ^{15}N isotope values when they exploit terrestrial and riverine resources rather than coastal and estuary resources. Further, where foragers harvest terrestrial and riverine resources, sex differences in δ^{15}N isotope values first decline and then increase coincident with population expansion on the Texas Coastal Plain. In coastal ecosystems, sex differences in δ^{15}N isotope values remain minimal as population expands. These patterns support the hypothesis that population expansion and associated changes in the production of resources may create incentives for more or less overlap in the dietary niches of males and females. The direction of change depends on the resource options that foragers select to scale-up their production of food.

1. Introduction

Researchers have long studied sex differences (or lack thereof) in the production and consumption of resources among human societies (e.g., Jiménez-Brobeil et al., 2021; Haas et al., 2020; Hervella et al., 2018; Umezaki et al., 2016; Ogilvie and Hilton, 2011; Marlowe, 2007; Wood and Eagly, 2002; Hayden et al., 1986; Ember, 1983; Bender, 1978) and, specifically, among-hunter-gatherers (see e.g., Eerkens et al., 2022; Haas et al., 2020; Hervella et al., 2018; Fauvelle and Somerville, 2024; Cashdan et al., 2012; Codding et al., 2011; Marlow, 2010; Marlowe, 2007; Bliege Bird et al., 2009; Zeanah, 2004; Lillie, 2003; Hayden et al., 1986; Bender, 1978).[1] Much of the hunter-gatherer research focuses on: (1) Investigations of sex differences in foraging behavior and the life history strategies that maximize the fitness of males vs. females, respectively (e.g., Eerkens et al., 2022; Eerkens, 2022; Wood et al., 2021; Codding et al., 2011; Marlowe, 2007; Bliege Bird et al., 2009; Zeanah, 2004). (2) Investigations of the emergence of inequality in terms of the consumption of resources, often associated with increasing community size and evidence of status differences (e.g., Fauvelle and Somerville, 2024; Hervella et al., 2018; Rose, 2008; Lillie, 2003; Hayden et al., 1986). In this paper, we build on this work and a recent model of population expansion to ask a different, macroecological question. Do terrestrial vs. marine resources and long-term population expansion have effects on the geography of sex differences in protein consumption among hunter-gatherers?

To structure our investigation, we begin from the general biosocial perspective proposed by Wood and Eagly (2002) that differences in female–male diets emerge at the intersection of biological, ecological, and social structures. From this perspective, in order for differences in protein consumption to emerge among human foragers, males and females must continually construct partially non-overlapping dietary niches. The dietary niche is the social–ecological space, defined by a set of resources x_i, that an individual consumes and the proportion of total consumption that each resource comprises. Individuals may procure these resources or they may receive them as part of food transfers.

We hypothesize that the dietary niches of males and females differ in (1) terrestrial ecosystems and (2) these differences amplify when foragers experience population expansion driven by intensification. These two conditions create partially non-overlapping dietary niches

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[1] In this paper, sex refers to a set of biological attributes that are associated with physical and physiological features (e.g., external anatomy). Gender refers to the socially constructed roles, behaviors, and identities of individuals that vary with cultural context. We use the terms sex or male–female throughout the paper because the analysis focuses on physical features and their correlation with potential differences in resource consumption.

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in which males and females are more likely to create different trophic positions. We anticipate this because, in such settings, females and males should experience social and ecological structures that create different locations of food consumption and/or time constraints on their fitness maximizing strategies (e.g., maximize prestige vs. minimize variance in the consumption of calories). These factors may lead to males and females eating different proportions of foods in alternative locations (e.g., inside vs. outside of camp) and, perhaps, male imposed social limits on access to some protein resources. To evaluate this hypothesis, we conduct a meta-analysis of archaeological radiocarbon and published data on human bone stable isotopes from the Texas Coastal Plain (TCP) and, secondarily, Central Texas to estimate differences in the dietary niches of individuals. Our results contribute to understanding the social–ecological contexts that may lead to sex differences in resource consumption.

2. Dietary niches and the Ideal Specialization Model

Our hypothesis combines two strands of scholarship. First, multiple studies indicate that sex differences in trophic position can, but do not always, occur among subsistence oriented foragers and farmers (e.g., Eerkens et al., 2022; Fauvelle and Somerville, 2024; Umezaki et al., 2016; Nelson et al., 2012; Berbesque et al., 2016, 2011; Berbesque and Marlowe, 2009; Rose, 2008; Lillie, 2003). Based on our synthesis of this work, we propose that sex differences in trophic positions occur in settings where populations produce and consume more terrestrial, as opposed to marine, resources.

In an ethnographic study, for example, Umezaki et al. (2016) find significant differences in the consumption of protein among males and females in highland New Guinea. Among rural communities in which men control the distribution of the primary protein source (i.e., pigs) and woman spend much of their time gardening and processing carbohydrates, the authors find that females consume significantly less protein than males (Umezaki et al., 2016). However, in communities where females have access to markets, the differences in protein consumption decrease markedly. This occurs because females control access to garden produce, which may be converted to cash, and the cash used to purchase tinned fish (Umezaki et al., 2016). Similarly, researchers working among Hadza hunter-gatherers find that females prefer carbohydrate food over meat, consume less meat than males, and eat in camp more frequently than males (Berbesque et al., 2016, 2011; Berbesque and Marlowe, 2009). In both of these ethnographic cases, females spend much of their time producing carbohydrates and often consume foods apart from males. The change in protein consumption among the market integrated communities of Highland New Guinea is particularly intriguing. Males and females still produce different resources and eat apart, but protein differences decline because females participate in markets that provide access to fish from distant ecosystems. The intersection of ecological and social structures (i.e., market access) impacts the presence of female–male differences in protein consumption.

Archaeologically, Rose (2008) reports sex differences in protein consumption using stable isotopes from human bone over time along the middle Mississippi River of North America. Rose finds little evidence of osteologically identified sex differences among mortuary sites during the Middle Woodland Period. However, Rose observes significant sex differences at some sites beginning in the Late Woodland Period and at most sites during the Mississippian Period (Rose, 2008). A key change in the economy of the Middle Mississippi River Valley occurred during the Late Woodland. Paralleling the ethnographic cases noted above, during this time period, economies increasingly centered on gardening and the consumption of carbohydrates, a trend that continued into the Mississippian Period as the population of the region expanded (e.g., Freeman et al., 2024c; Milner and Boldsen, 2023; Milner, 2004). Like in Highland New Guinea, protein resources are restricted in North America to fish from rivers, and animals, such as deer. These resources may have been more difficult for females to consume regularly as their time was increasingly allocated to gardening, grinding, and, potentially, eating apart from males.

Along the river systems of Eastern Europe, Lillie (2003) finds sex differences in protein consumption among foragers, with males consuming more protein than females. In California, stable isotope evidence suggests that males tend to consume larger quantities of protein, and/or from higher trophic positions than females among inland but not necessarily coastal mortuary sites (Eerkens et al., 2022; Fauvelle and Somerville, 2024). The differences in female–male diets observed among inland sites associate with evidence that inland populations consumed a higher proportion of terrestrial resources than populations along the coast, where individuals consumed more marine resources and sex differences appear absent. Finally, in the coastal settlements of Norse Greenland, where populations subsisted on large quantities of marine prey, researchers find little evidence of sex differences in protein consumption (Nelson et al., 2012).

The studies cited above suggest that in terrestrial ecosystems males and females tend to occupy partly different dietary niches. We propose that this occurs because terrestrial ecosystems have abundant and predictable carbohydrate resources while protein resources are more diffuse and less predictable. Cross-culturally, females devote more time to producing the more certain carbohydrate resources (e.g., Codding et al., 2011), and this may limit the time available for hunting and fishing by females, creating a context in which males and females more frequently eat apart (e.g., inside camp vs. outside camp). Thus, we expect that females living in environments dominated by terrestrial resources, on average, consume less protein or, rather, from lower trophic levels than males. Conversely, marine ecosystems have abundant prey species that are high in protein and fewer accessible species that are high in carbohydrates. As a result, in marine ecosystems, even when males and females target different aquatic habitats and species (e.g., fish vs. shell-fish), they only harvest and consume protein-rich resources from higher trophic levels.

The second strand of scholarship that informs our hypothesis recognizes that social–ecological structures change over time. The Mississippi River Valley case noted above illustrates this point. Population density in that region expanded over 3,000 years, and, coincident with this expansion, individuals shifted their consumption of resources toward more carbohydrates (e.g., Freeman et al., 2024c; Milner and Boldsen, 2023; Milner, 2004). As noted above, sex differences in protein consumption also become more evident with the consumption of more carbohydrates and population expansion during the Late Woodland Period.

In general, we propose that population expansion and the scaling-up of production in terrestrial ecosystems amplifies differences in the dietary niches of males and females and reinforces the similarities of dietary niches in marine ecosystems. This expectation follows from (1) a recent series of papers that develop and refine an Ideal Specialization Model (ISM) of population expansion (Freeman et al., 2024c,a,b, 2023, 2021) and (2) theory describing how and why scaling-up the production of resources should follow different strategies in terrestrial vs. marine ecosystems (Boone and Alsgaard, 2024).

(1) The ISM describes the long-term expansion of population as a consequence of a Malthus–Boserup Ratchet (MaB) that makes the following core assumptions:

- Humans use a network of infrastructures to generate flows of resources between ecosystems and social systems. All else equal, the network of infrastructures of technology, social organization, and norms of labor allocation set the limit on a human population in a fixed territory.
- Innovation—the generation of options on an infrastructure network—is frequent and inexpensive. As people live their lives, they generate latent sets of options, such as fall back foods, rare technologies, and experiments with landscape modifications. This latent set of options provides one source of material (and ideas) for changes in an infrastructure network.

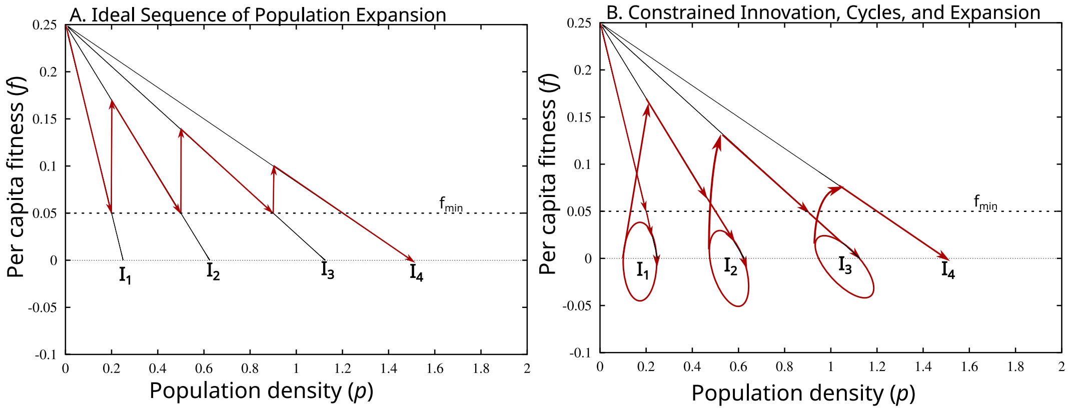

Fig. 1. A. The Ideal Specialization Model (ISM) of population expansion. B. Modified ISM with constraints on innovation and the emergence of population cycles. The red arrows in A and B illustrate the direction of population change over time generated by the assumptions of the ISM. In graph A, the population displays successive demographic transitions. In graph B, the population displays cycles and demographic transitions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

- Declines in fitness beyond a culturally defined threshold, f_m, stimulate individuals to search the latent sets of options on a network and recombine them in ways that, in the short-run, increase their *per capita* fitness and often increase the productivity of an environment in an emergent way.

Fig. 1 illustrates the dynamics that result from the above assumptions. The black curves describe the *per capita* fitness and maximum population densities of alternative infrastructure networks in a given region. The red curves with arrows describe an ideal sequence of population change over time. Note that the red curve begins on the I_1 *per capita* fitness-population density curve. As population density increases, *per capita* fitness declines until the threshold of 0.05 (f_m). At this point, a population searches and combines options in the latent innovation space to increase their individual *per capita* fitness. We call this intensification via the formation of new networks of infrastructure that, for a time, increase the yield of an environment per person and per unit area. Consequently, the population experiences a demographic transition in which population initially grows as *per capita* fitness increases and then the relationship switches and *per capita* fitness declines as population density increases (the red curve makes an inverse V/U shape). The switch point occurs when the costs of competition outweigh the initial gains in productivity generated by the new infrastructure network.

The above assumptions generate an ideal sequence of population expansion. In this ideal sequence, innovations in networks of infrastructure (tools, landscape modifications, transport, labor norms, etc.) with lower upfront fitness costs are adopted first. In turn, the new infrastructure system lowers the barriers of entry to more productive but more costly infrastructure networks as population density increases. For example, once a population grows maize in the floodplain of small-rivers (I_1), it is easier and more cost effective to build out irrigation systems in those floodplains (I_2). In turn, once populations improve the efficiency of small river irrigation, the entry costs of large river irrigation systems declines (I_3). Thus, an ideal sequence of network innovations (maize, small-scale irrigation, and large scale irrigation) that allow individuals to use less space and, in an emergent way, expand a population's limit, can occur in a Malthus–Boserup system.

(2) The ISM provides a heuristic model of the interrelationship between changes in networks of production and consumption (innovation) and population expansion. There is no reason to expect that the process will occur the same way across all ecosystems nor is the process progressive.[2] Over the last 10,000 years the consequences of constraints on innovation and differences in ecosystems should impact the options available for foragers to scale-up production. For example, Fig. 1B illustrates the consequences of relaxing the assumptions that innovations are frequent and inexpensive. In such situations, it is possible that innovation slows to the point that populations simply overshoot, decline, and then grow again, oscillating around a relatively constant mean population density in a Malthusian cycle. The red circles on Fig. 1B illustrate the dynamic. Such cycles may persist for thousands of years in the absence of innovations, or cycles might be interspersed by periods of Boserupian expansion (a sequence of cycle, inverse V/U transition, cycle on the graph) (Freeman et al., 2024a).

Importantly, Boone and Alsgaard (2024) argue that the common Malthus–Boserup population ratchet (whether it includes cycles or not) plays out differently in terrestrial vs. aquatic (especially marine) ecosystems. This argument has important implications for female vs. male dietary niches.

In coastal ecosystems, Boone and Alsgaard (2024) argue that forager households scale-up production (i.e., generate the inverse V/U shaped demographic transitions in an emergent way) via task specialization and the management of labor to mass harvest protein rich species. Foragers using marine ecosystems may increase their production and consumption along sex lines, as noted earlier, by females harvesting and eating more shell-fish and males more fish. Similarly, larger households can more easily mass harvest seasonally abundant species, such as eels and salmon, clean and smoke the species, and then store them (Boone and Alsgaard, 2024). In such situations, males and females may have very different roles in terms of labor and status, but everyone in the household eats high protein resources, whether shell-fish or smoked and dried eels.

Conversely, in terrestrial ecosystems, forager households scale-up production by integrating territory, and competition between households occurs for territorial units and the ability to extract tribute from the territory (Boone and Alsgaard, 2024). In such situations, it is female labor and their production of carbohydrates that underwrites surplus production and the integration of territorial units. The implication for dietary niches is a potential amplification of males' and females' allocation of labor to different resources, eating in different locations, and males controlling more limited protein resources.

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[2] The ratchet process could reverse, especially if innovations on an infrastructure network generate incentives to use more space. For example, the Pottery Neolithic in the Levant developed in the wake of the abandonment of "mega sites" and lasts for millennia. The whole period is marked by cyclical declines in population density as populations innovated new forms of production and consumption focused on crop production and mobile pastoralism (e.g., Watkins, 2023).

In summary, we expect that (1) more distinct female–male dietary niches occur among foragers exploiting terrestrial ecosystems but not among foragers exploiting marine ecosystems. (2) We expect that population expansion and the scaling-up of production amplify differences in the dietary niches of males and females in terrestrial ecosystems and reinforce the similarities of dietary niches in marine ecosystems.

The archaeological record of foragers in regions of Texas provides an opportunity to begin evaluating these expectations. Pre-contact foragers in Texas occupied interior terrestrial ecosystems, coastal ecosystems, and intermediate, riverine and terrestrial ecosystems. Previous research indicates that in Central Texas (terrestrial ecosystems) forager populations expanded, especially over the last 3500 years and, coincidentally, foragers increased their production and consumption of carbohydrates, especially root 'crops' from smaller territories (e.g., Freeman et al., 2024c,b; Thoms, 2009; Mauldin et al., 2003; Black and Creel, 1997). Similarly, on the Texas Coastal Plain, forager populations expanded and the production and consumption of estuary and marine resources increased on the coast and freshwater aquatic resources and terrestrial resources increased in riverine ecosystems (Freeman et al., 2024b; Hard and Katzenberg, 2011). On the Texas Coastal Plain, an increase in the frequency of burials and pronounced differences in diet suggest the emergence of restricted territories between riverine and coastal ecosystems between 3000 and 650 cal BP (e.g., Freeman et al., 2024b, 2019, 2017; Ricklis, 2012; Hard and Katzenberg, 2011; Perttula, 2001; Taylor, 1998; Hall, 1995; Huebner and Comuzzie, 1993; Hester, 1981, 1969). Thus, we should expect a gradient of differences in female–male diets, especially in protein consumption, from most pronounced among inland ecosystems, present but less pronounced in the riverine ecosystems, and absent from coastal ecosystems.

3. Data and methods

To evaluate the above expectations, we followed four steps. First, to collect data on the availability of marine resources, we recorded the spatial location of mortuary sites and labeled these locations as either inland, riverine-savanna, or coastal ecosystems (Fig. 2). Coastal ecosystems are defined by a 50 km wide strip that includes estuaries, bays, barrier islands, coast lines, and river mouths. These ecosystems contain mollusks and fish, especially redfish and black drum spawning in the shallow bays in the fall and late winter (Freeman et al., 2017; Hard and Katzenberg, 2011). Riverine-savanna ecosystems extend inland from the coastal ecosystems to an elevation of about 60 m above sea-level. Below 60 m in elevation, the rivers of the Texas Coastal Plain are sinuous with floodplains, oxbow lakes, and sloughs that contain both freshwater fish and shell-fish, as well as terrestrial resources like pecans and deer (Freeman et al., 2017; Hard and Katzenberg, 2011). Inland ecosystems occur mainly in Central Texas and, here, associate with the Edwards Plateau. These ecosystems contain small rivers and are dominated by terrestrial resources, such as deer, bison, and many species of plants, including species of geophytes, yucca, cactus, and grasses (Freeman et al., 2024b). Inland ecosystems in this study overlap with the distribution of Central Texas burned rock middens. These fire-cracked rock features resulted, in large part, from the repeated baking of wild plants high in carbohydrates, especially bulbs, corms, and roots (i.e., geophytes) (Freeman et al., 2024b; Black and Thorns, 2014; Freeman, 2007; Mauldin and Nickels, 2003; Black and Creel, 1997).

Second, we use a large sample of archaeological radiocarbon data to estimate changes in the relative population density of the Texas Coastal Plain over time (Freeman et al., 2024b; Bird et al., 2022). We construct kernel density estimates (KDEs) using the R package rcarbon (Crema and Bevan, 2021). To help minimize the impacts of bias due to site over-sampling and the non-linear radiocarbon calibration curve we constructed 200 simulated KDEs in rcarbon and used the h-function to cluster dates by site. We use an h-value of 100. After constructing the 200 KDEs, we calculated the mean KDE and summed the mean KDE into 30 year bins. These procedures smooth the KDEs and capture the long-term, shared trend of the simulated KDEs. Thus, our procedures de-emphasize intra-generational fluctuations over shorter time-scales induced by calibration and/or biases introduced by site over-sampling. We only estimate changes in population density on the Texas Coastal Plain because there are very few identifications of osteological sex in Central Texas, and studying changes in female–male diets over time in association with changes in estimated population density is limited. Further, we construct the KDEs from 12,000 to 200 cal BP and then trim the Texas Coastal Plain sequence to 5800 to 400 cal BP. This avoids edge effects (i.e., a lack of radiocarbon ages after 400 cal BP). Please see the Supporting Material for more details (e.g., on taphonomy).

We construct population density–*per capita* growth rate plots to detect demographic transitions and examine the relationship between cultural historical time periods and population expansion on the Texas Coastal Plain (see Supporting Material, Section 2). To construct this plot, we calculated the *per capita* growth rates of the mean KDE as: $\ln(MKDE_{t+1}/MKDE_t)$. That is, the natural log of the mean KDE at time t+1 divided by the mean KDE at time t.[3] Once we calculated the *per capita* growth of the mean KDE, we plotted the mean KDE against the *per capita* growth rate on the Texas Coastal Plain in order of time from the oldest 30 year bin to the youngest. This procedure creates empirical plots analogous to Fig. 1. This allows us to observe any inverse V/U shapes in these plots and document periods of population expansion to a higher carrying capacity (Supplementary Material, Section 2).

Third, reconstructing past diets in detail requires a knowledge of the resources in local ecosystems and the isotopic signatures of those resources (see Supporting Material, Section 1 for details on resources and Mauldin et al., 2024; Freeman et al., 2024b; Hard and Katzenberg, 2011). However, we are not interested in a detailed reconstruction, but rather with detecting differences in trophic position and protein consumption between the sexes. Thus, we focus our analysis primarily on δ^{15}N and, secondarily, on δ^{13}C collagen and whether these values are the same or different between males and females. We collected data from previously published studies in Texas (Mauldin et al., 2024; Freeman et al., 2024b; Mauldin et al., 2013; Hard and Katzenberg, 2011) that report osteological sex, and one or more of the following δ^{13}C collagen, δ^{13}C apatite, and δ^{15}N collagen stable isotope information.

The dataset contains 545 individuals from 21 archaeological sites (Freeman et al., 2025). Of these, in the riverine zone 135 individuals have osteologically identified sex estimations from four sites. The inland zone has 23 individuals with sex estimations from five sites, and the coast has 81 individuals with sex estimations from four sites. All sex estimations we made by researchers who studied the collections, and we did not reevaluate any of the osteological sex estimations. If researchers identified an individual as a probable male or female, we identified them as such for our analysis. Osteological sex estimations allow us to track potential sex differences in protein consumption via the analysis of δ^{15}N and δ^{13}C collagen.

The values of δ^{13}C collagen and δ^{15}N estimated from human bone are useful to make inferences about prehistoric diet and inferences about whether males and females occupied the same dietary niche. Variation in nitrogen (δ^{15}N) stable isotope values stems in part from trophic level enrichment within a food web (Bocherens and Drucker, 2003; Ambrose and DeNiro, 1986; DeNiro and Epstein, 1981). Atmospheric nitrogen (N_2, $\delta^{15}\mathrm{N} = 0$ ‰) is absorbed by plants either through the soil or, in the case of legumes, through the air (Mariotti, 1983). Plant δ^{15}N typically ranges between 1 to 6 ‰, with non-leguminous plants tending to hold to the higher end of that range (Ambrose, 1991;

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[3] The mean *per capita* growth rate is an estimate of *per capita* fitness. We use the term *per capita* growth rate to acknowledge that we cannot directly observe the fitness of an average individual in the archaeological record. Rather, the KDE contains a signal of changes in population, economic complexity, and noise (Freeman et al., 2018).

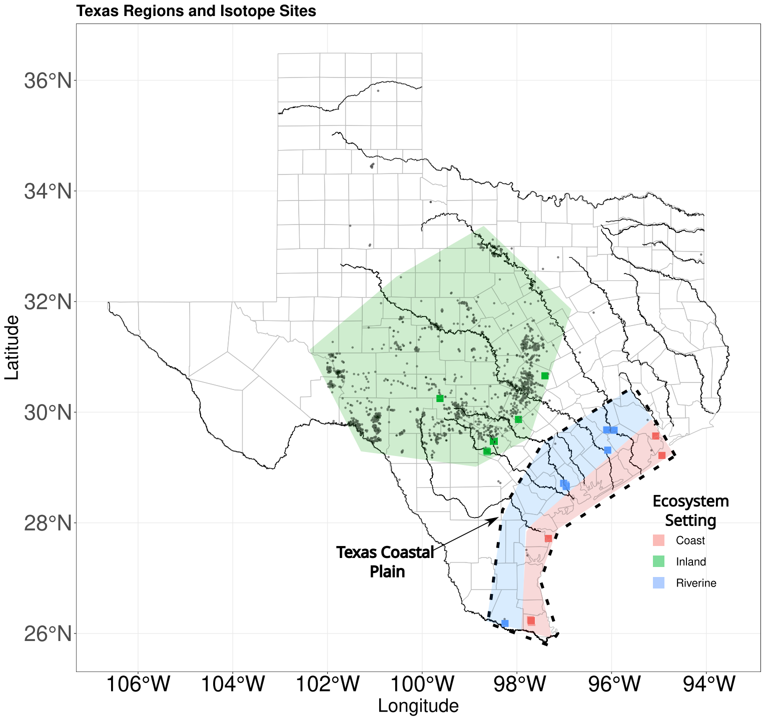

Fig. 2. Map of archaeological sites with human bone isotope and osteological sex data by ecosystem zones. Black dots indicate the distribution of burned rock middens on the Edwards Plateau. Colored points indicate mortuary sites. The red and blue shaded areas comprise the Texas Coastal Plain composed of coastal (red area) and riverine (blue area) ecosystems. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Shearer and Kohl, 1986). The δ^{15}N in herbivores feeding on plants is enriched above the values of the consumed plants, and carnivores have δ^{15}N values higher than herbivores. The degree of δ^{15}N enrichment in bone varies, but is estimated between 3 and 4 ‰ for each trophic level. As many aquatic food webs are complex ecosystems relative to terrestrial settings, the increase in δ^{15}N is especially apparent (see Oakley et al., 2014; Wissel and Fry, 2005; Fry, 1988; Minagawa and Wada, 1984; Chisholm et al., 1982). Thus, in a given environment, groups of individuals (in this case males vs. females) consuming from higher trophic levels should display higher δ^{15}N values. As noted above, because plant tissues generally have less protein and animal tissues are more dense in protein, eating at higher trophic levels for a greater percentage of one's food often associates with consuming more protein.

As humans consume resources, the δ^{13}C and δ^{15}N isotopic signatures present in those resources incorporate into flesh, organs, and bone, though with additional shifts depending on the tissue (Katzenberg, 2008; Ambrose and Norr, 1993a,b). While the relationship is complex in omnivores (Froehle et al., 2010; Kellner and Schoeninger, 2007), carbon routed to the organic component of bone (collagen) generally has values +5 ‰ higher than consumed plant values. Carbon routed to the mineral component of bone (apatite) increases by around +10 to +12 ‰ relative to the plant signature (Tykot, 2004; Lee-Thorp et al., 1989; DeNiro and Epstein, 1981; Sullivan and Krueger, 1981). Collagen contains both carbon and nitrogen isotopic signatures (Jim et al., 2006, 2004; Ambrose et al., 1997; Ambrose and Norr, 1993b; Tieszen and Fagre, 1993). The nitrogen signature in collagen is entirely derived from protein. The collagen carbon signature reflects both protein as well as carbohydrates and lipids, with protein contribution somewhere between 51% (Jim et al., 2006) and 75% (Fernandes et al., 2012) of the value.

Finally, once all the above data were integrated, we conducted an analysis of sex differences on δ^{15}N isotope values. To conduct this analysis, we divided individuals first by ecosystem zone and then by osteological sex identification (i.e., male, female). We then used two statistical approaches to compare the distributions of isotope values. We used a Bayesian *t*-test using the BayesFactor package in R (Morey and Rouder, 2023). The Bayesian *t*-test evaluates the confidence that we can have in the null hypothesis that the mean δ^{15}N values of males and females are the same in each ecosystem zone vs. the alternative hypothesis that the means are different. We use the default priors in the BayesFactor package, specifically the null and alternative are equally likely and that distributions are moderately dispersed. Rather than a p-value, the Bayesian *t*-test computes a Bayes factor (BF). The BF represents the odds, given the data, that the null is more consistent with the data or that the alternative is more consistent with the data (Rouder et al., 2009). In the BayesFactor package, as the Bayes factor (BF) approaches 0, the odds are higher that the null is more consistent with the data. BF scores greater than 1 indicate that the alternative is more consistent with the data (the larger the BF, the greater the odds), and a BF score equal to 1 indicates that both hypotheses are equally likely, given our priors and the data (Morey and Rouder, 2023).

We also use a complementary null hypothesis test method, the Mann–Whitney U test, to evaluate differences in female–male diets in each ecosystem zone. We use this method to help the reader judge the robustness of our results to changes in statistical test/approach. We use a p-value of less than 0.1 as sufficient evidence that we can reject the null hypothesis that males and females come from the same distributions of isotope values. The threshold of significance depends on a researcher's judgments about the consequences of erroneously rejecting the null when it should be accepted vs. erroneously accepting the null when it should be rejected (Clayton, 2021). All else equal, we argue that the analysis of archaeological data with low statistical power has a greater risk of erroneously accepting the null than erroneously rejecting the null.

On the Texas Coastal Plain, we divided the riverine-savanna and coastal ecosystems into five cultural historical phases: Early Middle Archaic (5800–4301 cal BP),[4] Late Middle Archaic (4300–2951 cal BP),

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[4] 15 Early Middle Archaic burials occur between 7400 and 5800 cal BP; however, none of the burials have sex identifications. Thus, the analysis begins at 5800 cal BP.

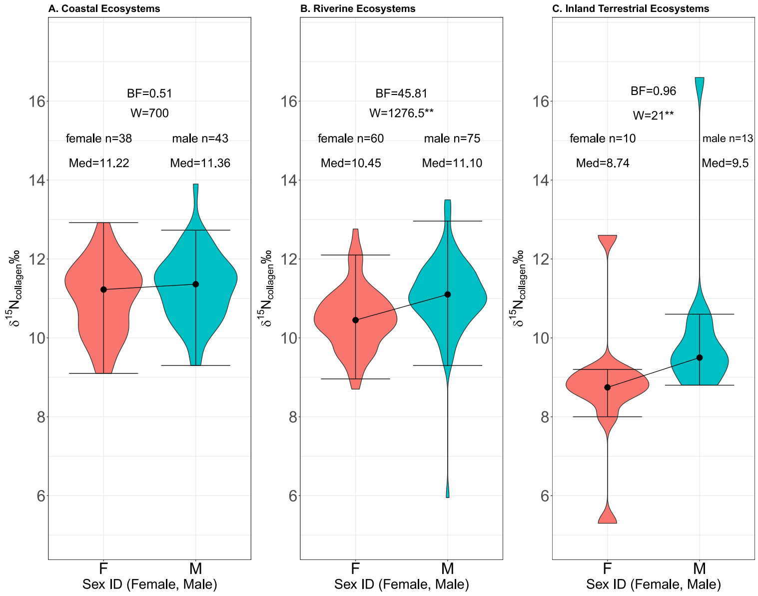

Fig. 3. Osteological sex differences in δ^{15}N by ecosystem setting. A-coastal ecosystems (females: n=38, median=11.22; males: n=43, median=11.36). B-Riverine ecosystems (females: n=60, median=10.45; males: n=75, median=11.10). C-Inland ecosystems (females: n=10, median=8.74; males: n=13, median=9.50). BF indicates the Bayes factor value, and W is the test statistic for a Mann–Whitney U test. ** indicates that the likelihood of observing differences in the distributions as extreme as those observed from random, independent samples is less than 0.05.

Early Late Archaic (2951–1351 cal BP), Late Late Archaic (1350–1151 cal BP), and Late Prehistoric (1150–400 cal BP). We only conducted this analysis on the Texas Coastal Plain because inland ecosystems do not have sufficient data to estimate changes in female–male diets over time. We tested for sex differences during each time period in each respective ecosystem zone and observed associations between population expansion and changes in differences in female–male diets over time. In all cases, we calculate the median values of male and female isotope values and observe the difference between these values over time to evaluate if sex differences increase or decrease with population expansion.

4. Results

The results of our analysis partly support expectations (1) and (2). We find that (1) osteologically identified sex differences in δ^{15}N occur in setting where hunter-gatherers consumed more terrestrial and riverine resources rather than marine resources. (2) We find that in the riverine ecosystems differences in female–male diets declined from 5800 to 2951 cal BP (pre evidence of territoriality). This decline in sex differences associates with population expansion and is evidence for an increased consumption of marine protein. From 2950 cal BP to 400 cal BP (post evidence of territoriality), population expansion associates with increasingly pronounced sex differences in δ^{15}N. In the coastal ecosystems, sex differences in δ^{15}N values do not associate with population expansion.

4.1. Ecosystem zones and sex differences

Fig. 3 illustrates violin plots of δ^{15}N values by sex in three different ecosystem settings: Coastal (A), riverine (B), and inland (C). Consistent with expectation (1), the δ^{15}N values of males and females overlap most in coastal ecosystems, where the medians of males and females are nearly identical. The Bayes factor of 0.51 in coastal ecosystems suggests that we should have more confidence in the null hypothesis that there are no observable differences in the mean δ^{15}N values of males and females. The δ^{15}N values of males and females overlap less in riverine and inland ecosystems. The Bayes factor of 45.81 in the riverine settings indicates that we should have more confidence in the alternative hypothesis that males and females display different mean δ^{15}N values. In the inland setting, although the differences in the distributions are visually clear, the Bayes factor of 0.96 indicates that we cannot have more confidence in either the null (no difference in the means) or the alternative hypothesis (differences in the means). In short, we have a strong hint that differences in female–male diets occurred in inland settings, but with small and dispersed samples of males (n=13) and females (n=10) from inland sites, we just do not have enough information to say more than this with a lot of confidence.

4.2. Population expansion and sex differences in riverine and coastal ecosystems

As noted above, the very small sample sizes of males and females precludes the study of differences in female–male diets in association with population expansion among inland ecosystems. However, there are sufficient data to study the association of sex differences and population expansion on the Texas Coastal Plain. The Texas Coastal Plain contains both coastal ecosystems, where foragers had access to marine resources, and riverine ecosystems, where foragers had access to terrestrial and freshwater resources. Thus, following expectation (2), population expansion should amplify sex differences in the riverine ecosystems and reinforce similarities in the coastal ecosystems. Recall that a major change in the archaeological record occurs on the Texas Coastal Plain around 2950 cal BP. Specifically, archaeologists observe multiple lines of evidence indicative of territoriality, small foraging ranges, and the extensive exchange of burial goods between ecosystem zones (Freeman et al., 2024b, 2019, 2017; Ricklis, 2012; Hard and Katzenberg, 2011; Perttula, 2001; Taylor, 1998; Hall, 1995; Huebner and Comuzzie, 1993; Hester, 1981, 1969).

Fig. 4 documents the association between population dynamics (A) on the Texas Coastal Plain and changes in δ^{15}N sex differences by cultural historical time periods in riverine ecosystems (B). Fig. 4A documents the change in estimated population density over time and cultural historical periods. Similar to Fig. 1B, population dynamics on the TCP display successive demographic transitions interspersed by cycles. The critical point: We observe ratchet–like population expansion interspersed by periods of population oscillation from period 1–2, 2–3, and then a third expansion during periods 4 and 5 (see Supporting Material, Section 2). Thus, we should expect each episode

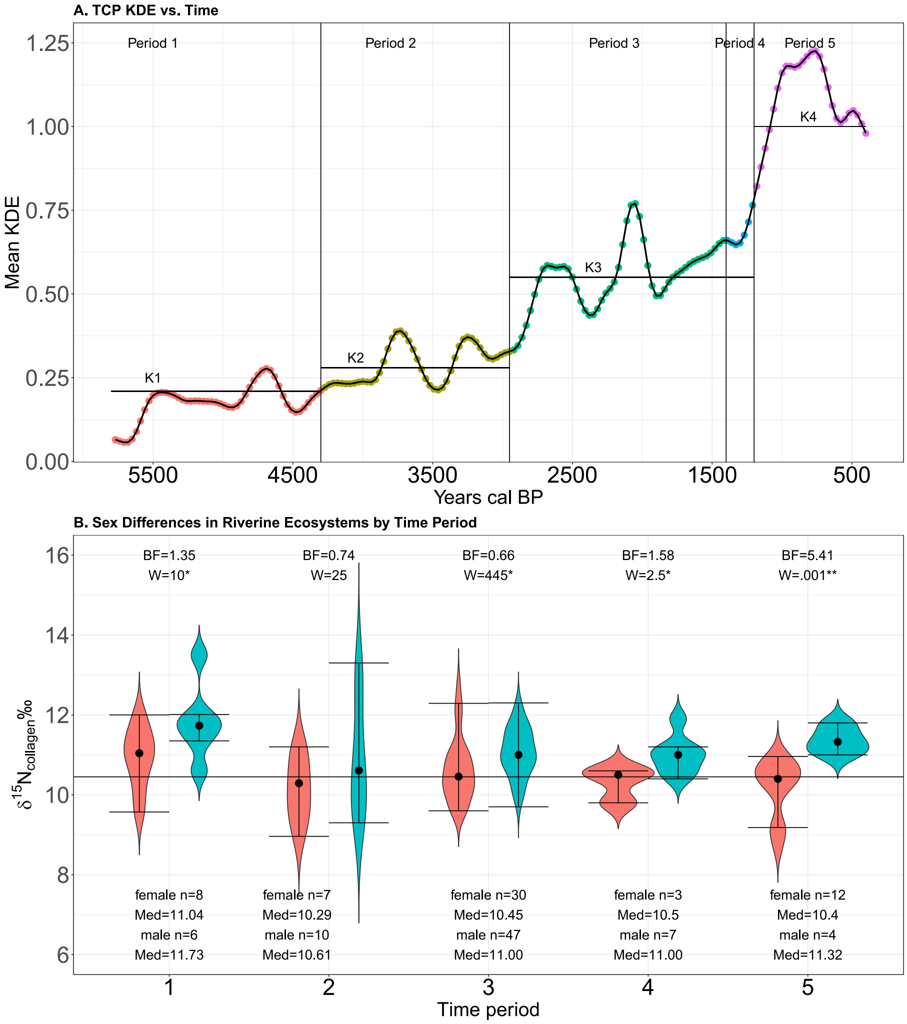

Fig. 4. Population dynamics on the Texas Coastal Plain and sex differences in δ^{15}N in the riverine ecosystems. A-Change in estimated population density over time. $K_1 - K_4$ indicate levels of carrying capacity. B-Change in δ^{15}N sex differences by time period. BF indicates the Bayes factor value, and W is the test statistic for a Mann–Whitney U test. ** indicates that the likelihood of observing differences in the distributions as extreme as those observed from random, independent samples is less than 0.05, and * indicates the likelihood is less than 0.1. Periods are defined as: Period 1=Early Middle Archaic, 2=Late Middle Archaic, 3=Early Late Archaic, 4=Late Late Archaic, and 5=Late Prehistoric.

of expansion to amplify differences in female–male diets from periods 1-to-2-to-3-to-4-to-5 in the riverine ecosystems.

Fig. 4B illustrates the changes in δ^{15}N sex differences with each successive turn of the population ratchet (shift from K_1 to K_4) during successive cultural historical periods. From period 1-to-2, sex differences decrease. From period 2-to-3, sex differences remain muted. However, from period 3-to-4-to-5, differences in female–male diets become more pronounced (larger differences between the medians of the male and female distributions), and our confidence in the alternative hypothesis that the means of the male and female distributions are different also increases. In simple terms: Prior to the emergence of increased territoriality (pre 2950 cal BP, Periods 1 and 2), as population expanded, foragers consumed more protein or aquatic resources and sex differences declined. However, after the emergence of territoriality (post 2950 cal BP, Periods 3–5), population expansion associates with amplifying sex differences in δ^{15}N, with males displaying higher values than females from periods 3–5. Interestingly, these patterns both support and contradict expectation (2).

For example, Fig. 5 documents changes in δ^{13}C collagen over time. Values of δ^{13}C collagen reflect, to a substantial degree, the protein component of foragers' diets, and higher values on the Texas Coastal Plain indicate the consumption of protein from estuaries and bays.[5] As population expands from period 1-to-2, the consumption of marine protein increases (Fig. 5A) and increases among both males and females (Fig. 5B). This suggests that the increase in population density did not amplify differences in female–male diets (contra expectation (2)). Rather the shift toward marine resources accompanied a decrease in sex differences in δ^{15}N (consistent with expectation (1)). Conversely, after the emergence of territoriality (periods 3-to-5), foragers focused their consumption on riverine and terrestrial protein resources. This is documented by the decline in δ^{13}C collagen values from period 2-to-3 and the slight decline in period 5. In short, evidence for the increased consumption of riverine and terrestrial protein sources associates with population expansion and amplifying sex differences in δ^{15}N values.

Finally, Fig. 6 documents the association between population dynamics (A) on the Texas Coastal Plain and changes in δ^{15}N sex differences over time in coastal ecosystems (B). As noted above, mortuary

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[5] The estuaries along the Texas coast are dominated by sea grass meadows with C_4 photosynthetic pathways (Hard and Katzenberg, 2011). Higher δ^{13}C may also result from the diffusion of carbon from the atmosphere directly into bodies of water, which increases δ^{13}C of bioavailable carbon within aquatic environments. The factors are not mutually exclusive and both should lead to increases in δ^{13}C collagen when individuals consume marine and estuary species.

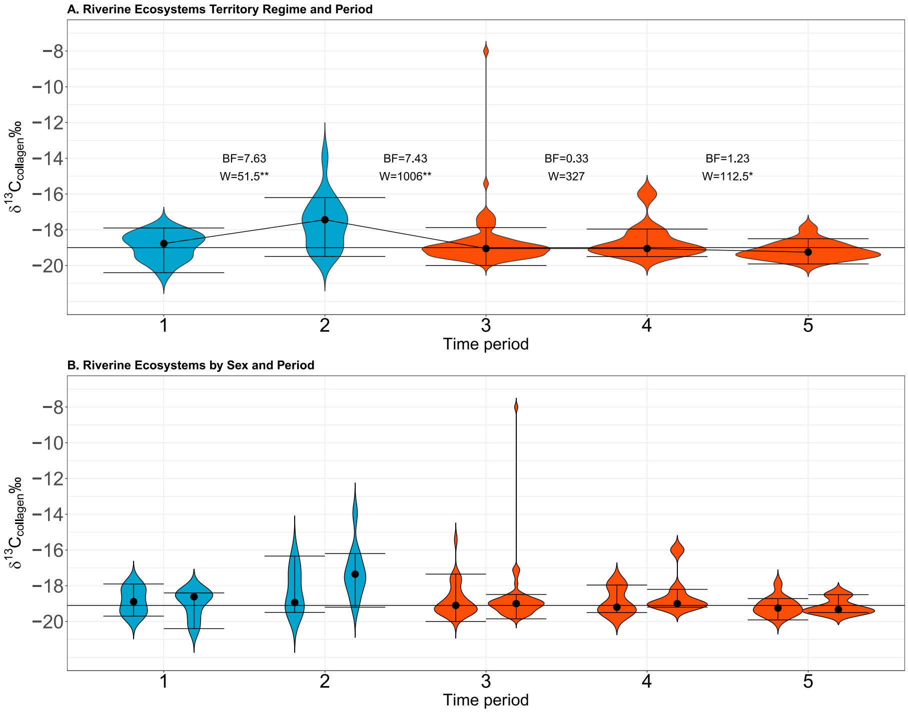

Fig. 5. A-Change in δ^{13}C over time for all individuals buried in riverine mortuary locations. BF indicates the Bayes factor value, and W is the test statistic for a Mann–Whitney U test. ** indicates that the likelihood of observing differences in the distributions as extreme as those observed from random, independent samples is less than 0.05, and * indicates the likelihood is less than 0.1. B-Change in δ^{13}C over time by sex. In both graphs periods are defined as: Period 1=Early Middle Archaic, 2=Late Middle Archaic, 3=Early Late Archaic, 4=Late Late Archaic, and 5=Late Prehistoric. The blue shading indicates time periods of less developed territoriality, and the orange shading indicates time periods of more developed territoriality. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

locations first emerge along the coast during period 3, and we have enough data to compare males and females in periods 4 and 5. In both periods, minimal differences in δ^{15}N values occur between males and females, and the Bayes factors indicate that we should have more confidence in the null hypothesis of no difference in the means of males and females. These patterns are consistent with expectation (2): Population expansion in coastal ecosystems reinforces similarities in protein consumption between males and females.

5. Discussion and conclusion

In this paper, we investigated the effects of resources and long-term population expansion on regional patterns of sex differences in protein consumption among hunter-gatherers. Previous research suggests that (1) male and female foragers in terrestrial environments are more likely to create partly distinct dietary niches. This may occur due to a couple of interacting processes: Males target more diffuse and uncertain resources than females and, thus, males and females spend more time consuming resources apart, and males may use this division of labor to control high value protein resources that increase their social standing. Conversely, where foragers target marine resources, male and female dietary niches overlap more. (2) Following the argument of Boone and Alsgaard (2024), we propose that population expansion amplifies sex differences in protein consumption in terrestrial ecosystems and reinforces similarities in coastal ecosystems. In coastal ecosystems population expansion associates with incentives for households to scale-up production via task specialization and the management of labor to overproduce patchy and seasonal aquatic resources. In such situations, males and females may have very different roles but everyone in the household eats resources from higher trophic positions. In terrestrial ecosystems, population expansion requires forager households to scale-up production by integrating territory and extracting tribute from territory. In such situations, the production of carbohydrates by females underwrites increases in production, potentially amplifying the tendency for males and females to eat in different locations and for males to begin controlling more limited protein resources to signal their prestige.

Our data are partly consistent with the above expectations. We observe osteological sex differences in δ^{15}N values among terrestrial and riverine ecosystems but not in the coastal ecosystems of Texas. However, the strong observed differences in the median values of δ^{15}N among inland ecosystems remain somewhat ambiguous due to the very small number of identified males and females in this setting. Further, we find that population expansion on the Texas Coastal Plain does not associate with sex differences in δ^{15}N values in coastal ecosystems, and population expansion correlates with differences in female–male diets in riverine ecosystems. Specifically, pre-territoriality, sex differences in δ^{15}N decline with population expansion (as foragers shifted to marine resources). Post-territoriality, sex differences in δ^{15}N amplify as population expands. These results provide an intriguing clue that different male–female dietary niches, especially in terms of protein consumption, emerge under general social–ecological conditions in which males and females have distinct economic roles.

We suspect that the general social–ecological conditions noted above relate strongly to the division of labor in specific resource environments rather than anything to do with foraging, farming, or pastoralism *per se*. For example, Lipan Apache and Comanche Indigenous peoples occupied much of the current study area in the 1700's and early 1800's CE. These peoples engaged in complex and sophisticated political and economic activities related to hunting, raiding, and trading horses, maize cultivation in the case of the Lipanes, and plant gathering (Hämäläinen, 2008; Minor, 2009). The horse trade, in particular, meant that young to middle-aged males conducted long, logistical forays to raid for horses, cattle, and trade (Hämäläinen, 2008; Minor, 2009). We would expect male and female dietary differences in these contexts because of the division of labor associated with the more

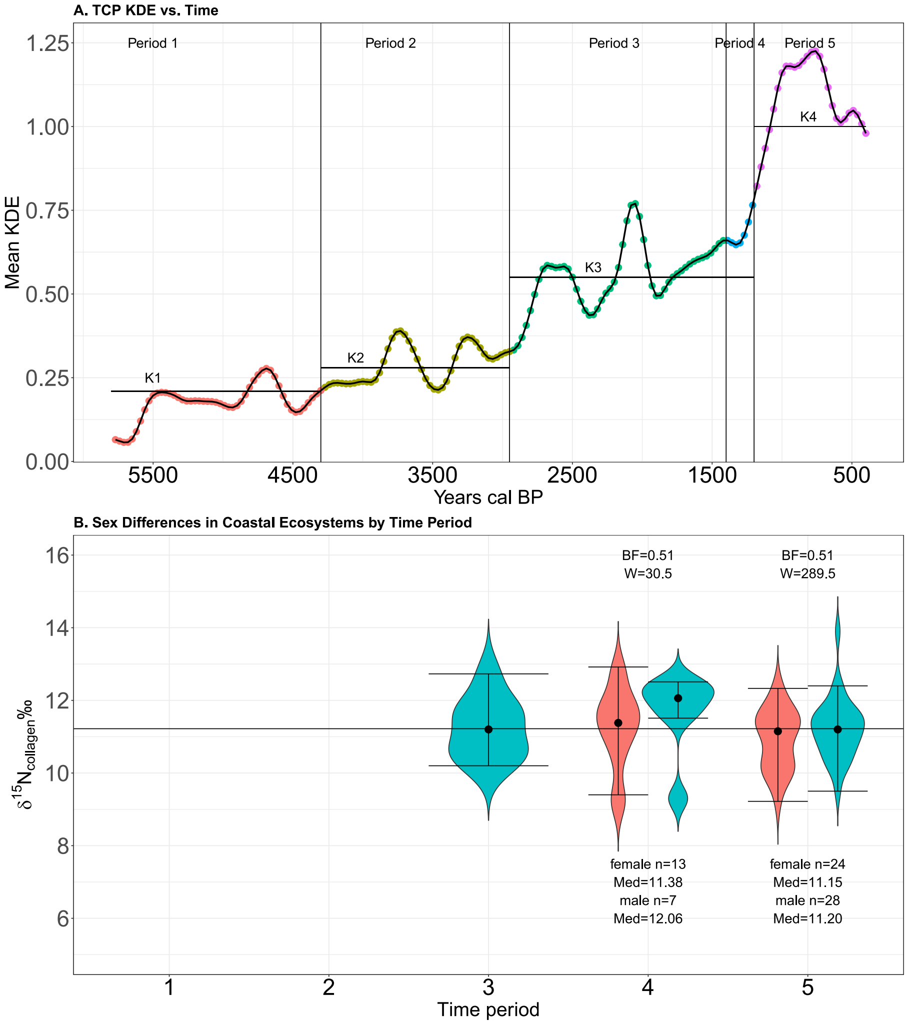

Fig. 6. Population dynamics on the Texas Coastal Plain and sex differences in δ^{15}N in the coastal ecosystems. A-Change in estimated population density over time. $K_1 - K_4$ indicate levels of carrying capacity. B-Change in δ^{15}N sex differences by time period. BF indicates the Bayes factor value, and W is the test statistic for a Mann–Whitney U test. ** indicates that the likelihood of observing differences in the distributions as extreme as those observed from random, independent samples is less than 0.05, and * indicates the likelihood is less than 0.1. Periods are defined as: Period 1=Early Middle Archaic, 2=Late Middle Archaic, 3=Early Late Archaic, 4=Late Late Archaic, and 5=Late Prehistoric.

certain activities of plant gathering/cultivating and more uncertain raiding activities led to males and females living in very different habitats for long portions of the year, presumably consuming different resource sets.

5.1. Limitations and future research

More work is needed to follow-up on our study. Three points stand out.

- Our study is based on small sample sizes from inland ecosystems and from some time periods on the Texas Coastal Plain. This situation is, in part, due to preservation and, in part, related to the reality that mobile foragers in Central Texas (inland ecosystems) did not create large mortuary sites. To continue to evaluate our main hypotheses, larger samples from inland contexts might create the ability to stratify these samples by time to evaluate associations between the differences in female–male diets and population expansion. Further, very few samples exist from early time periods in coastal and riverine ecosystems, which, again limits our ability to evaluate expectation (2). For example, larger samples of individuals with sex estimations from the Middle Archaic and from more sites in riverine ecosystems would allow researchers to make more confident judgments about changes in sex differences over time.
- More work is needed to interpret sex differences in nitrogen isotopes. Turnover rates in bone are complicated, vary with age, may vary with sex, and appear to vary with different bones in the body (Matsubayashi and Tayasu, 2019; Fahy et al., 2017; Hedges et al., 2007), though recent studies do not find significant differences between male–female remodeling rates (Quinn, 2024a,b). For example, among inland foragers, there may be no difference in protein consumption between males and females early in childhood. That is, isotopes incorporated into tissues are very similar during breast feeding, weaning, and pre-adolescent years (but see Khelouf et al., 2023). However, once individuals become adults, the generation of new bone that has the opportunity to express difference in diet slows considerably, regardless of sex. Thus, most of the divergence in isotopic signatures, as a reflection of resource consumption, may primarily occur during adolescence and early adulthood. This raises the possibility, for example, that older adults may have similar diets, but their isotope signatures express difference due to different dietary niches during early adulthood. Recent studies have begun to examine the relationship between isotope signatures and development (Eerkens et al., 2024; Eerkens, 2022; Eerkens et al., 2022). Eerkens et al. (2024), in particular, study teeth to obtain serial samples of bone growth, and they find evidence among agropastoralists that differences in

childhood training (pastoral herding vs. domestic work and gardening) associate with differences in δ^{15}N values. More work on sex differences in isotope values by age would improve our ability to investigate the biogeography of sex differences in protein consumption.
- Finally, future work could overcome some of the above limitations through meta analyses at a continental or global scale that include regions beyond Texas. This would potentially allow for site based analyses from a larger sample of sites and would improve the ability to evaluate expectations (1) and (2). For example, much of the increase in δ^{13}C in the riverine ecosystems during the first period of population expansion (Figs. 4 and 5) comes from the site of 41VT1. This site is closer to the coast than other riverine sites in the data set, and, thus, the increase may be related to site level options (lower transport costs and easier access to the coast) during the first period of population expansion. It makes sense that access to marine resources tracks the distance of sites to the coast, and we may find, in larger samples, that differences in female–male diets track distance to the coast in a more fine grained way. The key is the interaction of resource options indexed by distance to the coast and intensification, which relates to how people organize labor.

5.2. Conclusion

Consistent with Wood and Eagly (2002), our study suggest that sex differences in protein consumption emerge under regular sets of social–ecological conditions. It is important to test the generality of these conditions by expanding the study to include more regions and engage in a meta analysis of osteologically identified sex differences in protein consumption. Further, the data support the proposition that population expansion associates with changes in the social–ecological structures used to extract and consume resources on a landscape. Population expansion should interact with local histories and ecologies to either amplify differences in female–male diets or reinforce similarities in dietary niches.

CRediT authorship contribution statement

Jacob Freeman: Writing – original draft, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Alyssa Ahmann:** Writing – original draft, Methodology, Funding acquisition, Data curation, Conceptualization. **Robert J. Hard:** Writing – original draft, Data curation. **Raymond P. Mauldin:** Writing – original draft, Data curation.

Declaration of generative AI in scientific writing

The authors did not use generative AI in the preparation of the manuscript.

Declaration of competing interest

The authors have no competing interests to declare.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.jas.2025.106293.

Data availability

The data and code used in this study are published without restriction (Freeman et al., 2025). The Associate Editor for Reproducibility downloaded all materials and could reproduce the results presented by the authors.

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