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Cross-cultural variation in thirst perception in hot-humid and hot-arid environments: Evidence from two small-scale populations

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Abstract

Objectives: Thirst is an evolved central homeostatic feedback system that helps regulate body water for survival. Little research has examined how early development and exposure to extreme environments and water availability affect thirst perception, particularly outside Western settings. Therefore, we compared two indicators of perceived thirst (current thirst and pleasantness of drinking water) using visual scales among Tsimane' forager-horticulturalists in the hot-humid Bolivian Amazon and Daasanach agro-pastoralists in hot-arid Northern Kenya.

Methods: We examined how these measures of perceived thirst were associated with hydration status (urine specific gravity), ambient temperatures, birth season, age, and population-specific characteristics for 607 adults ($n = 378$ Tsimane', $n = 229$ Daasanach) aged 18+ using multi-level mixed-effect regressions.

Results: Tsimane' had higher perceived thirst than Daasanach. Across populations, hydration status was unrelated to both measures of thirst. There was a significant interaction between birth season and temperature on

pleasantness of drinking water, driven by Kenya data. Daasanach born in the wet season (in utero during less water availability) had blunted pleasantness of drinking water at higher temperatures compared to those born in the dry season (in utero during greater water availability).

Conclusions: Our findings suggest hydration status is not a reliable predictor of thirst perceptions in extreme-hot environments with ad libitum drinking. Rather, our findings, which require additional confirmation, point to the importance of water availability during gestation in affecting thirst sensitivity to heat and water feedback mechanisms, particularly in arid environments. Thirst regulation will be increasingly important to understand given climate change driven exposures to extreme heat and water insecurity.

1 | INTRODUCTION

Drinking to thirst is an oft-repeated guideline, as this recommendation suits the majority of healthy adults living in a temperate climate (Millard-Stafford et al., 2012). Thirst is a key central homeostatic feedback system that evolved to tightly regulate body fluid and ensure survival, yet there is a learned aspect to it as well, which may vary by environment (Kenney & Chiu, 2001). To date, the vast majority of studies have examined thirst in Western, educated, industrialized, rich, and democratic (WEIRD) countries and populations (Armstrong, Giersch, Colburn, et al., 2021; Brannigan et al., 2015; Carroll, 2020; Carroll et al., 2019; Kenney & Chiu, 2001; Martens & Westerterp-Plantenga, 2012; Millard-Stafford et al., 2012; Phillips, Rolls, Ledingham, Forsling, et al., 1984; Phillips, Rolls, Ledingham, & Morton, 1984; Rolls & Phillips, 1990; Rolls et al., 1982); therefore, much of our understanding is based on research with limited biological and cultural diversity (Gurven & Lieberman, 2020).

There are two types of thirst: homeostatic and non-homeostatic. Homeostatic thirst sensation generally occurs when plasma osmolality, which is a measure of the number of dissolved particles in the blood plasma and a strong driver of the body's electrolyte-water balance and a stimulus for thirst, increases 1%–2% due to a deficit of body water or to decreased plasma volume (Thornton, 2010; Zimmerman et al., 2017). Another homeostatic thirst response is anticipatory thirst, which occurs in relation to eating and consuming solutes (Zimmerman et al., 2016). The anticipatory thirst response is driven by neural circuitry as a way for the body to anticipate changes in body fluid and stimulate thirst to increase water intake to return to homeostasis (Gizowski & Bourque, 2018; Zimmerman, 2020).

The intrauterine environment may be a critical time for influencing the homeostatic thirst setpoint

(Rosinger, 2020). A developmental origins of health and disease (DOHaD) framework suggests that plasticity during development helps calibrate an individual to their future environment (Kuzawa & Quinn, 2009). Thus, differences in the intrauterine environment in terms of water availability and exposure to extreme heat may create variation in thirst setpoints. In fact, experimental animal studies have demonstrated that maternal dehydration in pregnant rats affects the development of thirst responses of offspring (Perillan et al., 2008). These studies demonstrated that thirst setpoints of offspring exposed to intrauterine water restriction were not activated until they reached relatively higher thresholds of dehydration compared to offspring not exposed to intrauterine water restriction. However, when the thirst setpoints were activated, they were experienced more strongly (Ross & Desai, 2005). Among humans, the intrauterine environment is critical for nephron development and later-life kidney health (Luyckx & Brenner, 2015; White et al., 2009). Kidney function and the baroreceptors detecting water deficits to stimulate thirst are thus also potentially modifiable (Thornton, 2010).

Yet, outside of extreme water loss, most drinking behavior is non-homeostatic and environmentally driven, often occurring around meal times (Rolls et al., 1982; Stevenson et al., 2015). Much of thirst may thus be habitual or contextual (Carroll, 2020). Thirst is also a type of interoceptive sensation or awareness of internal bodily state. This awareness is learned and also likely subject to environmental and cultural variation (Brannigan et al., 2015; Ma-Kellams, 2014; Stevenson et al., 2015). Drinking behaviors and cues for drinking are shaped as early as development and ontogeny (Rolls et al., 1982). In humans, as in all mammals who begin life by breastfeeding, suckling is not solely activated by a response to hydration state but rather as a response for feeding (Rolls et al., 1982). However, early feeding

practices have significant implications for plasma tonicity and the kidney as well as shaping preferences for dietary solutes and sodium chloride, especially since water is aversive to newborns (Desor et al., 1975). Breastfed compared to formula and solid food fed 1- to 3-month-old babies had significantly lower plasma osmolality, indicating better hydration status (Davies, 1973). Thus, early life experiences may be critical for thirst setpoint development as well as learned drinking behavior (Rosinger, 2020).

These early behaviors are shaped by cultural dietary and hydration customs. Every culture has specific hydration strategies which are learned. Among small-scale populations hydration strategies are often derived from the local ecology and environmental resources available, especially in places where market beverages, like sodas, are not regularly consumed (Rosinger & Tanner, 2015; Swanson & Pontzer, 2020). For example, in the Amazon, consuming chicha, a fermented yucca beverage, is a crucial way to stay hydrated (Bethancourt et al., 2021; Christopher et al., 2019; Rosinger & Bethancourt, 2020). Among pastoralists, drinking milk as well as coffee or tea represent major water sources (Galvin, 1992; Sagawa, 2006). Yet, other stimulants are also frequently used across populations to limit or quench thirst while providing energy and focus during work, like chewing on coca or tobacco leaves (Breithoff, 2017; Charlton, 2004). Thus, culturally specific customs may help explain how individuals within populations respond to increasing water needs and thirst.

It is unclear if thirst perception differs for populations living in water insecure environments with extreme temperatures. Extreme heat increases water needs (Sawka et al., 2005), yet differences in water availability in arid compared to humid environments may lead to variation in thirst responses as a way to adapt to the higher water needs. Since lifestyles and ambient environments lead to substantially different daily water turnover (Pontzer et al., 2021), we might expect to see differences in thirst across hot-humid and hot-dry environments. The hot-humid environment presents an additional physiological challenge in thermoregulation, such that sweat is harder to evaporate and stays on the skin longer (Best & Kamilar, 2018). Thus, there may be a greater awareness of body water loss in hot-humid environments than hot-dry environments, where body water evaporates much quicker and less noticeably (Kenney & Hodgson, 1987). In these hot environments, being aware of one's hydration status and thirst may be more important because of the potential for rapid water loss. Conversely, it may be possible that thirst perception is blunted due to water scarcity, which may lead to a decoupling of thirst from hydration status. However, little research has examined

how thirst perception and the desire to drink water is associated with these factors in diverse hot environments.

Therefore, to fill these gaps and examine thirst outside of WEIRD contexts, this study examined perceived thirst in two small-scale populations living in extreme thermal environments. We compared thirst perceptions among Tsimane' in the hot-humid Bolivian Amazon and Daasanach in the hot-arid Northern Kenya Lake Turkana region. First, we tested how these perceptions of thirst relate to physiological and environmental characteristics that are generally thought to influence thirst, including hydration status, ambient temperature and humidity, and age. Second, since early life environments may shape exposures to water availability, we tested if season of birth moderated the thirst response to ambient temperature across the dry and humid settings. Drawing on research in WEIRD settings and the animal literature, we hypothesized that thirst would increase with higher urine concentration (Armstrong, Giersch, Colburn, et al., 2021) and hotter temperatures (Kenney & Chiu, 2001), and decrease with age since thirst reportedly declines with age in Western populations (Kenney & Chiu, 2001; Rolls & Phillips, 1990). Furthermore, we hypothesized that season of birth would modify the relationship between the thirst response and ambient temperatures, such that those who experienced in utero water deficits would have less of a thirst response in relation to higher temperatures (used as a proxy of increasing water needs) (Perillan et al., 2008; Ross & Desai, 2005). Finally, we examined how population-specific cultural factors, like traditional hydration practices and stimulant use, were associated with thirst. We hypothesized that increased use of each beverage or stimulant would be associated with lower thirst.

2 | METHODS

2.1 | Ethics statement

The multisite Water Insecurity, Stress, and Hydration (WISH) study was conducted following the principles of the Declaration of Helsinki and was approved by the institutional review boards of Pennsylvania State University and the Kenya Medical Research Institute. Permission was obtained from the Gran Consejo Tsimane' in San Borja, Bolivia, the Director of Health in the county government of Marsabit, Kenya, and community leaders in each the five Tsimane' communities sampled in Bolivia and each of the seven Daasanach communities sampled in Kenya. All participants provided oral informed consent and Daasanach provided written informed consent.

2.2 | Fieldsites and data collection

The WISH study was an observational cross-sectional study among Tsimane' in lowland Bolivia and Daasanach in Northern Kenya in 2019 designed to examine how experiences surrounding water and thirst related to hydration and health in Lowland Bolivia and Northern Kenya (Figure 1). For the purposes of this study, we investigated the research questions among adults only as we had limited sample sizes of children with reliable thirst perception responses.

The fieldsites and comparative data collection procedures are described in detail elsewhere (Bethancourt et al., 2021). In brief, in both settings, data collection procedures were the same; and data was collected in the early part of the dry season in both sites for feasibility reasons and to have comparative seasonal data (April–May in Bolivia; June–July in Kenya). None of the sampled communities in either population had running water or electricity in their homes at the time of study. Both household heads were invited to participate, and each provided urine samples and then rated their thirst independently. Ambient temperature and humidity were recorded at this time. Participants then had their anthropometrics measured and participated in a household survey.

The data collection in the Bolivian fieldsite took place among Tsimane', an indigenous forager-horticulturalist population that live in the hot-humid Amazon. Approximately 16 000 Tsimane' live in ~100 villages, of which

five communities were sampled for this study (Leonard et al., 2015). We attempted exhaustive sampling in the five Tsimane' communities and had >90% participation rates.

Tsimane' have distinct hydration patterns as they consume traditional fermented beverages, like chicha as well as consume water from water-rich fruits (Rosinger & Bethancourt, 2020; Rosinger & Tanner, 2015). These hydration strategies translate into higher water intake than adults in the US, as one study found they consumed ~4.5 L of water on a given day (Rosinger & Tanner, 2015). Furthermore, prior work has found that approximately 50% of Tsimane' adults have concentrated urine and ambient temperature was strongly related to hydration status, indicating that it is hard to meet their water needs in this hot-humid environment (Bethancourt et al., 2021; Rosinger, 2015).

The data collection in the Kenyan fieldsite was also part of the Daasanach Human Biology Project. Approximately 19 000 Daasanach semi-nomadic pastoralists live in the hot-arid northern Kenya desert across 26 villages around the northeastern margin of Lake Turkana (Kenya National Bureau of Statistics [KNBS], 2019). Similar to many eastern African pastoralist groups, Daasanach rely on milk from cattle, goats, and other livestock as a major caloric and hydration source. Daasanach living in Kenya are distinctly more reliant on these traditional pastoral forms of subsistence than those who reside in the Omo River Basin of southern Ethiopia (Almagor, 1978), who have greater access to market and agricultural goods.

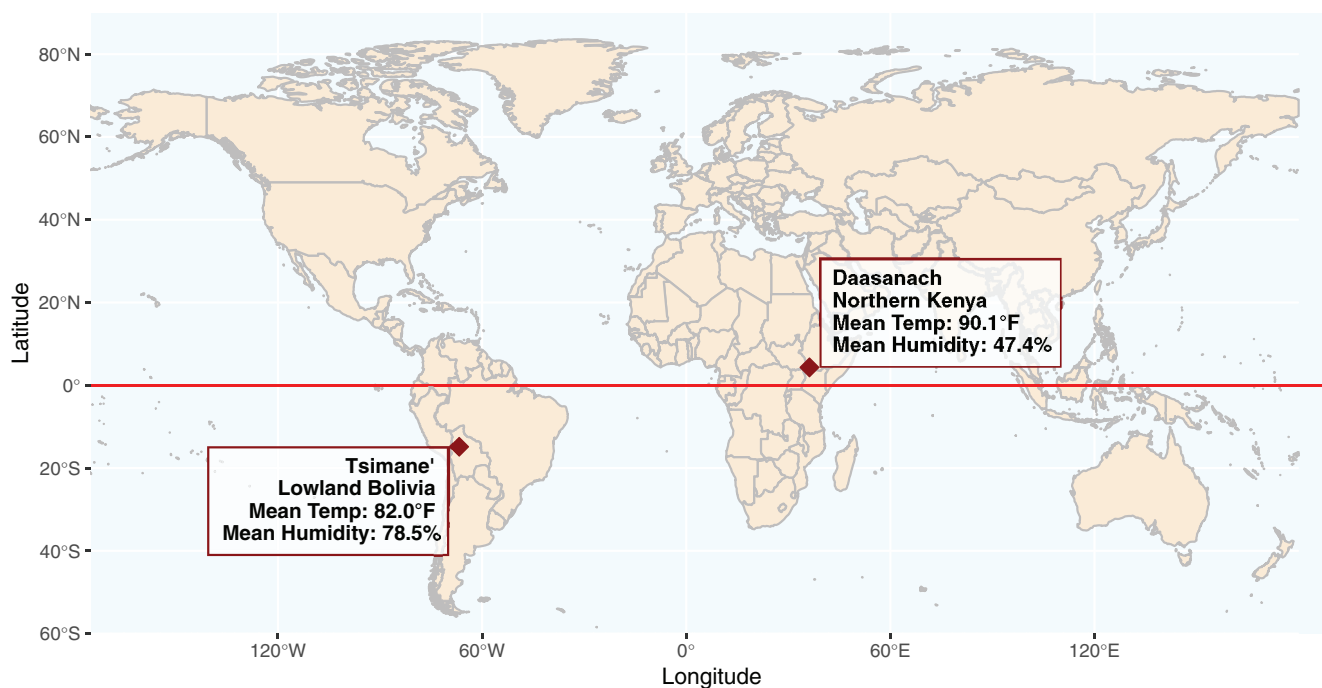


FIGURE 1 Fieldsite settings for the WISH study

Additionally, issues of food and water insecurity, which have previously been identified among Daasanach (Bethancourt et al., 2021; Rosinger et al., 2021), are worsened by increased climate variability in the region (MoALF, 2017). Furthermore, a tradition of drinking tea/coffee results in a regular consumption of these beverages at least twice per day, including in the morning (Bethancourt et al., 2021).

We sampled 7 Daasanach communities using a random sampling design of every third household, which resulted in sampling 12–28 households per community based on the pre-allocated amount of time the research team had in each location (Bethancourt et al., 2021; Rosinger et al., 2021). Exhaustive sampling in this site was not feasible due to time and resource constraints as several of the Daasanach study communities had >200 households, thus we chose a representative sampling approach.

2.3 | Outcome: Thirst perceptions

Foundational research demonstrated that thirst sensation is strongly associated with the pleasantness or desire to imbibe water, thus we asked questions using two visual analog categorical scales to measure perceived thirst (current thirst level and perceived pleasantness of drinking water) adapted from Rolls (Phillips, Rolls, Ledingham, Forsling, et al., 1984; Phillips, Rolls, Ledingham, & Morton, 1984; Rolls et al., 1982). On a laminated piece of paper, we showed participants hybrid visual analog scales with verbal anchors between 1 and 10 indicating increasing thirst or pleasantness of drinking water (Figure 2). We asked them to point to the ladder to indicate how thirsty they felt in the moment and separately how pleasant it would be to drink water in that moment.

Prior to data collection, we had extensive discussions with our translators and informants to translate these

concepts and words associated with thirst perception in both sites. Among Daasanach, thirst translated into the word *ba'are*, while the concept of pleasantness of drinking water translated to *bie imiyy midhanle*. Among *Tsimane'*, thirst translated to *jajriri'*, while pleasant to drink water was *jäm'dyi' coi' ojñi' tyeij*.

2.4 | Predictors

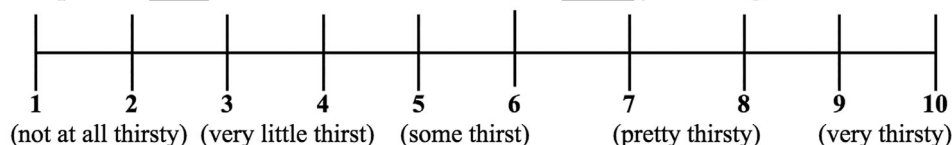
2.4.1 | Hydration status

Participants provided urine samples, which were covered and allowed to cool for ~10–30 min. Urine samples were then measured in triplicate with a Pen refractometer (Atago) for urine specific gravity (Usg) with the average used for analysis. Urine specific gravity is the ratio of urine to the density of water. Elevated Usg or concentrated urine, often categorized as hypohydrated was defined as values >1.020 (Armstrong et al., 2010). Participants were provided with the results of their urine concentration as well as hydration advice and water after they rated their thirst to prevent this from impacting their hydration status and thirst ratings.

2.4.2 | Current weather

Ambient temperature and relative humidity were measured in Bolivia with a mercury thermometer and a Fischer hair hygrometer, respectively. In Kenya, they were both measured using a digital Kestrel 3000 Pocket Weather Meter (Kestrel; Boothwyn, PA, USA). We used the ambient temperature (°F) as the primary predictor and adjusted for relative humidity, which can affect heat retention and perceived thirst (Raymond et al., 2020).

Perception of thirst: Please indicate on the line how thirsty you feel right now.



Perceived pleasantness of drinking water: Please indicate on the line how pleasant it would be to drink some water right now.

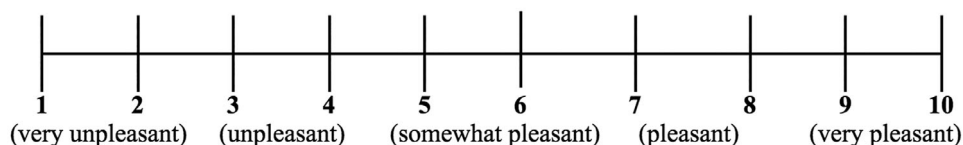


FIGURE 2 Adapted visual thirst scales

2.4.3 | Season of birth

As water availability during gestation and rainfall have been shown to affect birth outcomes in humans and thirst setpoints in animals (Godoy et al., 2008; Randell et al., 2020; Rosinger, 2020; Ross & Desai, 2005), we collected information on whether participants were born in the rainy or dry season, which is commonly known among participants. Being born in the wet season meant that the individual was in utero during the preceding dry season when water was less available to their mother; while being born in the dry season would mean that they were in utero during the rainy season when water was more abundant. In Kenya, Daasanach have a major wet season from March through May, when more than half of the annual precipitation falls and a second smaller rainy season in November. In Bolivia, the rainy season lasts from November through March. Using historical monthly rainfall totals, we simulated hypothetical births in the middle of the dry and rainy seasons by site to test our assumption of differential water availability by birth season (Table S1). Under this hypothetical situation, Daasanach born in the middle of the major wet season would have experienced ~47.5 mm (or 18.9%) less precipitation throughout gestation compared to being born in the dry season—which is consistent with our assumption. Furthermore, in this scenario, the biggest difference for Daasanach was the second trimester where being born in the rainy season might have been associated with 63 mm or 42.4% less rainfall compared to dry season birth. For Tsimane', we see a similar pattern consistent with our assumption, and the difference in this hypothetical scenario is 702 mm (or 35.7%), with the second trimester again being the biggest contributor. Thus, our assumption of differential water availability by birth season holds up if our simulation provides a reasonable approximation of rainfall in the years and seasons in which participants were born.

2.4.4 | Age

Since thirst reportedly declines with age in Western populations (Rolls & Phillips, 1990), we examined the association for age in years. Many Tsimane' and Daasanach adults do not know their exact age. Because of recent government efforts to provide identification cards, some adults have identification cards on which a birth date is given. For this study, age was estimated by either using the birth date provided on an identification card or by probing about when the participant was born in relation to locally known historical events.

2.5 | Population-specific predictors

Since both small-scale populations have specific culturally derived traditions for meeting their water needs and dealing with thirst, during surveys we asked adults about the frequency of their intake over the past week or 24 h depending on the item. For Tsimane', we inquired about chicha, fruit added to water, and coca leaf use over the past 7 days. Coca leaves are used throughout Bolivia, often as a way to abate thirst and hold off on eating or drinking during labor.

For Daasanach, who have a strong tea/coffee tradition and who rely on livestock and milk as part of their dietary and hydration strategies, we inquired about the number of times they consumed tea/coffee in the prior 24 h and the frequency of milk consumption in the prior week (categorized as 0, <1 time per day, and 1 or more times a day). Furthermore, we asked about the number of times in the prior week they chewed tobacco. This traditional behavior is a fairly common practice, which can also affect saliva production.

2.6 | Covariates

We adjusted for demographic and physiological variables that can influence thirst (Kenney & Chiu, 2001; Phillips, Rolls, Ledingham, & Morton, 1984; Rolls et al., 1982). During the survey, we collected information on sex (male/female). Time of day was recorded at the time of the urine sample/thirst measurement. For the analysis, the time was rounded to the hour. Finally, as fat and fat free mass have drastically different water composition and potential water reserve (Ritz et al., 2008), we adjusted for fat free mass as measured through a bioimpedance scale (Tanita).

2.7 | Statistical methods

Analysis was conducted in Stata V15.1 (College Station, TX). Statistical significance was set at alpha at 0.05 for a two-tailed test. We used *t*-tests to assess the association between bivariate season of birth and thirst outcomes as well as test differences in characteristics across the two populations. Linear fit and functional polynomial fit scatterplots were used to visualize the bivariate best-fit associations between variables of interest and dispersion of the data.

We used three-level mixed effect linear regression models with individuals nested within households within

communities to estimate how current hydration status ($U_{sg} > 1.020$), ambient temperature, season of birth, and age were associated with current thirst and perceived pleasantness of drinking water (Models 1.1–1.2). The models adjusted for the primary predictors, as well as fat free mass, humidity, time of day, and included fixed effects for population. Furthermore, we controlled for sex and estimated the regression models combined for men and women because there were no sex differences in thirst and there was no sex-specific effect modification with the main variables of interest. Also, neither pregnancy nor lactating status were associated with either thirst measure among women. We next tested for an interaction term between season of birth and ambient temperature (Models 1.3–1.4).

Second, we stratified the regression analyses by population to examine whether the results were consistent across both populations and to further adjust for population-specific factors. We re-estimated the fully adjusted models with the interaction term for both thirst outcomes, while additionally including amount of chicha, fruit-water, and coca use among Tsimane' and tea/coffee, milk, and chewing tobacco among Daasanach using two-level mixed-effects linear regression models with individuals nested within households (Models 2.1–2.4). We used marginal standardization of the fully adjusted models to estimate and visualize the interactions and examine the predicted thirst levels by season of birth across the range of ambient temperatures (Korn & Graubard, 1999; Williams, 2012).

TABLE 1 Descriptive characteristics of Daasanach and Tsimane' participants

Variable	Daasanach (<i>n</i> = 229) mean or % (SD)	Tsimane' (<i>n</i> = 378) mean or % (SD)	<i>p</i> Value ^a
Age (years)	39.6 (14.9)	37.3 (16.7)	.10
Sex (% men)	43.7%	49.1%	.20
Weight	51.1 (8.2)	59.2 (8.8)	<.001
Fat free mass (kg)	42.3 (6.4)	45.9 (7.2)	<.001
TBW (%)	56.9 (6.0)	55.1 (6.2)	<.001
Height (cm)	167.5 (7.6)	156.1 (7.4)	<.001
BMI (kg/m ²)	18.2 (2.8)	24.2 (3.0)	<.001
Current thirst perception (1–10)	5.5 (2.7)	6.0 (2.7)	.03
Perceived pleasantness of drinking water (1–10)	6.0 (1.9)	7.9 (2.3)	<.001
Birth season (% dry season)	31.0%	46.7%	<.001
Urine specific gravity (U_{sg})	1.011 (0.008)	1.020 (0.007)	<.001
% $U_{sg} > 1.020$	18.3%	55.4%	<.001
Ambient temperature (°F)	90.1 (4.9)	82.0 (5.9)	<.001
Humidity (%)	47.4 (12.4)	78.5 (9.1)	<.001
Tea/coffee consumption last 24 h (number of times)	2.1 (0.80)	–	–
Milk consumption last 7 days: 0 times per day (%)	42.8%	–	–
<1 time per day (%)	20.5%	–	–
1+ time per day (%)	36.7%	–	–
Chewing tobacco last 7 days	3.3 (3.5)	–	–
Chicha dulce consumption last 7 days (number of days)	–	1.3 (1.4)	–
Fruit water consumption last 7 days (number of days)	–	2.0 (2.1)	–
Chewing coca leaves last 7 days (number of days)	–	0.60 (1.5)	–

Abbreviations: BMI, body mass index; TBW, total body water.

^a2 sided *t*-test.

2.8 | Analytic sample

Our analytic sample included all adults aged 18 years and older with complete covariate data on the predictors of interest. 49 Tsimane' adults, all from one study community, were excluded because data on season of birth was not collected; this resulted in data being analyzed from 4 of the 5 Tsimane' study communities; however, those from the excluded study community had similar characteristics (age, sex, thirst ratings). Five Daasanach adults were excluded because of missing data on fat free mass and one due to an error in data entry. Furthermore, an additional 7 Tsimane' and 4 Daasanach were excluded because they reported that a doctor had told them they had diabetes, which can significantly increase thirst and confound associations. None of these exclusions (fat free mass or diabetes status) significantly differed in terms of their demographics. This left a total analytic sample of 607 adults: 378 Tsimane' and 229 Daasanach.

3 | RESULTS

The mean age and sex makeup were not different between the Tsimane and Daasanach samples (Table 1). However, fat free mass, total body water, BMI, % born in the wet season, and Usg were all significantly higher among Tsimane' than Daasanach. Specifically, 46% of Tsimane' reported that they were born during the rainy season, whereas 31% of Daasanach reported they were born during the rainy season. Daasanach were significantly taller and leaner. The ambient temperature was lower in Bolivia compared with Kenya ($82.0^{\circ}\text{F} \pm 5.9$ vs. $90.1^{\circ}\text{F} \pm 4.9$, $p < .001$), while the relative humidity was substantially higher in Bolivia ($78.5\% \pm 9.1$ vs. $47.4\% \pm 12.4$, $p < .001$).

3.1 | Bivariate analyses

In bivariate analyses, current perceived thirst was 0.5 pts higher ($t\text{-test} = 2.16$; $p = .031$) and the pleasantness of drinking water was 1.9 pts ($t\text{-test} = 10.5$; $p < .001$) higher among Tsimane' in the hot-humid environment than among Daasanach in the hot-arid environment (Table 1). Current perceived thirst and pleasantness of drinking water were significantly correlated ($r = .25$; $p < .0001$) when both populations were combined, with stronger correlation among Daasanach ($r = .35$; $p < .001$) than among Tsimane' ($r = .20$; $p < .001$) (Figure 3).

Both current thirst perception and perceived pleasantness of drinking water were not significantly different by season of birth in bivariate examination ($t\text{-tests } p = .89$).

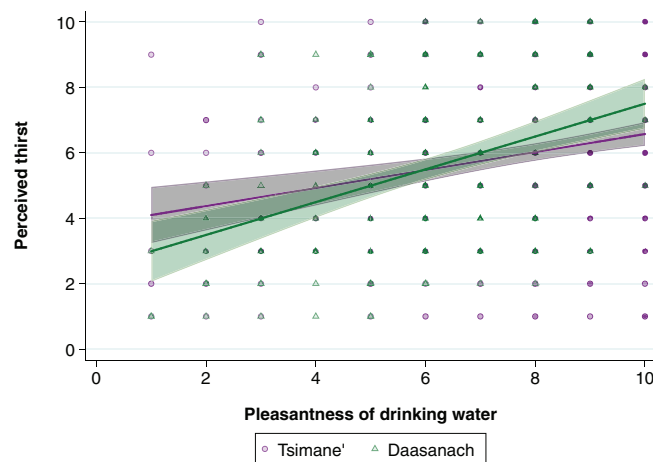


FIGURE 3 Perceived current thirst by perceived pleasantness of drinking water. Linear fit scatterplots with 95% confidence intervals

Among both Daasanach and Tsimane', Usg was not associated with perception of current thirst (Figure 4A) or perceived pleasantness of drinking water (Figure 4B). In fact, the relation between Usg with perceived thirst was fairly flat for both populations, and only mildly positive for perceived pleasantness of drinking water among Tsimane'.

Ambient temperature was positively associated with perceptions of thirst and pleasantness of drinking water among Daasanach ($r = .22$, $.24$, $p < .001$ for both) in the hot-dry environment; whereas there was no association ($r = -0.03$, 0.03 ; $p > .50$ for both) among Tsimane' in the hot-humid environment (Figure 5A,B).

Relative humidity was inversely associated with thirst perception among Daasanach and slightly positively associated or curvilinear with thirst among Tsimane' (Figure S1A,B). These associations with thirst are likely due to the inverse relationship between ambient temperature and relative humidity (Figure S2A); and the u-shape relations between temperature, humidity, and time of day (Figures S2B,C). Current thirst appeared to increase from the morning to 12-1 PM in both populations and then flatten (Figure S3A); whereas the pleasantness of drinking water did not have any association with time of day (Figure S3B).

Age was not consistently associated with either thirst perception or perceived pleasantness of drinking water (Figures S4A,B). Thirst did not appear to decrease markedly with age. Furthermore, when stratifying the sample by age bins (18–39, 40–59, and 60+), individuals 60+ years exhibited a thirst sensitivity to hotter temperatures indicating higher thirst responses among older adults similar to younger adults (Figure S5).

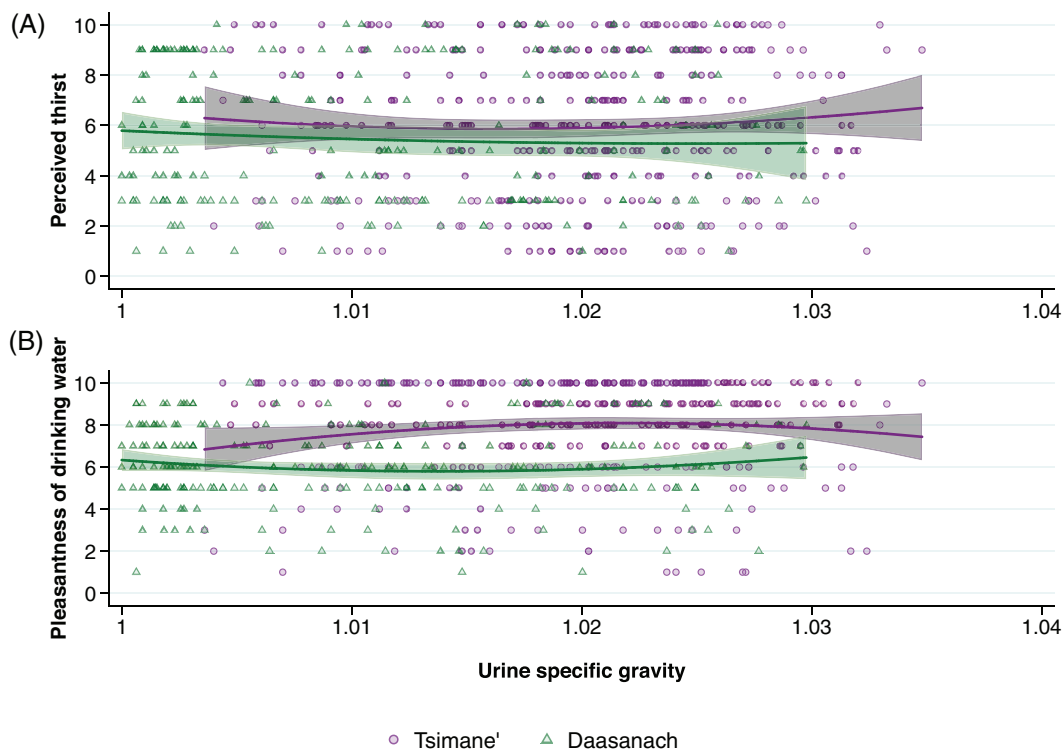
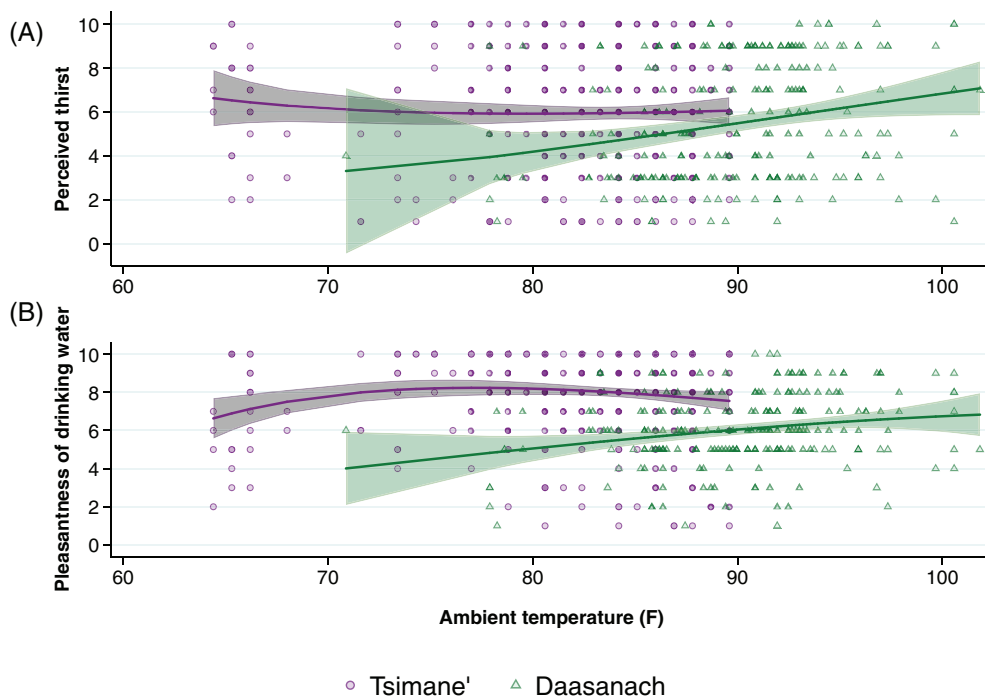


FIGURE 4 Urine specific gravity by (A) perceived thirst and (B) perceived pleasantness of drinking water. Local polynomial smooth plots with confidence intervals

FIGURE 5 Ambient temperature by (A) perceived thirst and (B) perceived pleasantness of drinking water. Local polynomial smooth plots with confidence intervals



3.2 | Regression analyses

Results of the 3-level mixed effects regression models indicated that none of the primary predictors or

covariates were associated with current thirst level (Table 2, Models 1.1). Having an elevated Usgr was not associated with either current thirst or perceived pleasantness of drinking water adjusted for covariates. Being

TABLE 2 Multi-level linear mixed effects regression models examining predictors of current thirst and perceived pleasantness of drinking water

Variables	Model 1.1	Model 1.2	Model 1.3	Model 1.4
	Current thirst	Perceived pleasantness	Current thirst	Perceived pleasantness
	Beta (SE)	Beta (SE)	Beta (SE)	Beta (SE)
Ambient temperature (per 10°F)	0.34 (0.36)	0.41 (0.27)	0.45 (0.39)	0.68** (0.30)
Birth season: Wet season (dry season reference)	0.06 (0.20)	-0.31* (0.17)	2.19 (2.52)	4.23** (2.11)
Wet season by temperature interaction			-0.25 (0.30)	-0.54** (0.25)
Usg > 1.020	0.24 (0.24)	0.12 (0.19)	0.23 (0.24)	0.10 (0.19)
Humidity (per 10%)	0.0001 (0.18)	0.02 (0.13)	0.01 (0.18)	0.04 (0.13)
Age (years)	0.01* (0.01)	-0.004 (0.01)	0.01* (0.01)	-0.01 (0.01)
Fat-free mass	0.001 (0.03)	-0.02 (0.02)	0.0003 (0.03)	-0.02 (0.02)
Male (female reference)	0.08 (0.35)	0.42 (0.29)	0.10 (0.35)	0.45 (0.29)
Time of day	0.02 (0.05)	-0.09** (0.04)	0.02 (0.05)	-0.09** (0.04)
Kenya (Bolivia reference)	-0.72 (0.62)	-2.29*** (0.46)	-0.72 (0.61)	-2.27*** (0.46)
Observations	607	607	607	607

Note: Standard errors in parentheses. *** $p < .01$, ** $p < .05$, * $p < .1$. 3-level mixed-effects model, with random effects (intercepts) for each participant nested 356 households and within a random effect for 11 communities of residence. Results for Models 1.1 and 1.2 indicate the association between current thirst and perceived pleasantness of drinking water in relation to ambient temperature, season of birth, hydration status, and controlling for covariates listed. Models 1.3 and 1.4 repeat the models along with an interaction between ambient temperature and birth season.

in the Daasanach sample (compared to the Tsimane' sample) ($B = -2.3$; $SE = 0.46$; $p < .001$) was associated with lower perceived pleasantness of drinking water. Being born in the wet season (compared to being born in the dry season) ($B = -0.31$; $SE = 0.17$; $p = .07$) and ambient temperature approached statistical significance ($B_{10^\circ F} = 0.41$, $SE = 0.27$, $p = .12$) (Model 1.2).

There was a significant interaction between season of birth and ambient temperature for perceived pleasantness of drinking water ($B = -0.54$, $SE = 0.25$, $p = .031$) but not current thirst (Table 2, Models 1.3–1.4). Adults born in the wet season, which indicates they were in utero during less water availability, had a reduced thirst response to higher ambient temperatures; in contrast, adults born in the dry season (in utero during greater water availability) had a more robust, linear thirst response to higher temperatures. In this model, the main

terms of temperature ($B_{10^\circ F} = 0.68$, $SE = 0.30$, $p = .021$) and birth season ($B = 4.2$; $SE = 2.1$; $p = .045$) were associated with increased pleasantness of drinking water.

3.3 | Population specific regression analyses

We re-estimated the full models with the interaction between season of birth and temperature stratified by population (Table 3). First, among Tsimane', none of the primary predictors nor the interaction between ambient temperature and season of birth were significantly related to measures of thirst (Models 2.1, 2.2). Having an elevated Usg (>1.020) and each 10 percentage points of humidity were positively but not significantly associated with both measures of thirst. Furthermore, the

TABLE 3 Multi-level linear mixed effects regression models examining predictors of current thirst and perceived pleasantness of drinking water among Tsimane' and Daasanach samples separately

Variables	Tsimane'		Daasanach	
	Model 2.1	Model 2.2	Model 2.3	Model 2.4
	Current thirst	Perceived pleasantness	Current thirst	Perceived pleasantness
	Beta (SE)	Beta (SE)	Beta (SE)	Beta (SE)
Ambient temperature (per 10°F)	−0.11 (0.45)	0.54 (0.38)	0.88 (0.87)	1.91*** (0.56)
Birth season: Wet Season (dry season reference)	−0.42 (3.60)	2.94 (3.07)	3.84 (6.42)	11.31** (5.08)
Wet season by temperature interaction	0.08 (0.44)	−0.40 (0.37)	−0.44 (0.71)	−1.29** (0.56)
Usg > 1.020	0.44 (0.29)	0.28 (0.25)	−0.08 (0.39)	−0.20 (0.32)
Humidity (per 10%)	0.22 (0.24)	0.21 (0.20)	−0.27 (0.28)	0.16 (0.17)
Age (years)	0.02 (0.01)	−0.003 (0.01)	0.01 (0.01)	−0.01 (0.01)
Chicha consumption (per 1 day)	−0.10 (0.11)	0.06 (0.09)	–	–
Fruit-water consumption (per 1 day)	0.05 (0.08)	0.01 (0.06)	–	–
Coca leaf use (per 1 day)	0.02 (0.09)	−0.06 (0.08)	–	–
Tea/coffee consumption (per 1 time)	–	–	−0.28 (0.23)	−0.32** (0.15)
Milk consumption (none: ref)	–	–	Ref	Ref
<1 time per day	–	–	−0.28 (0.51)	0.16 (0.33)
1+ times per day	–	–	−1.43*** (0.43)	0.22 (0.28)
Chewing tobacco leaf use consumption (per 1 time)	–	–	−0.05 (0.05)	−0.04 (0.04)
Observations	378	378	229	229
Number of household clusters	222	222	134	134

Note: Standard errors in parentheses. *** $p < .01$, ** $p < .05$, * $p < .1$. 2-level mixed-effects model, with random effects (intercepts) for each participant nested households. Results for Models 1.1 and 1.2 test the association between current thirst and perceived pleasantness of drinking water for Tsimane' in relation to ambient temperature, season of birth, with an interaction between ambient temperature and birth season, hydration status, culturally specific variables, and controlling for covariates listed as well as fat free mass, sex, and time of day. Models 1.3 and 1.4 repeat the models for Daasanach.

population-specific factors that may affect thirst, chicha, fruit-water, and coca leaf use were not associated with either measure of thirst.

Among Daasanach, the primary predictor results were consistent to the pooled models (Models 2.3, 2.4). However, milk consumption level was significantly

associated with current thirst perception, as those who consumed milk one or more times per day reported 1.4 pts (SE = 0.43; $p = .001$) lower current thirst than those who reported not consuming any milk per day (Model 2.3). Furthermore, each instance of tea/coffee consumption in the prior 24 h was associated with 0.32-pts

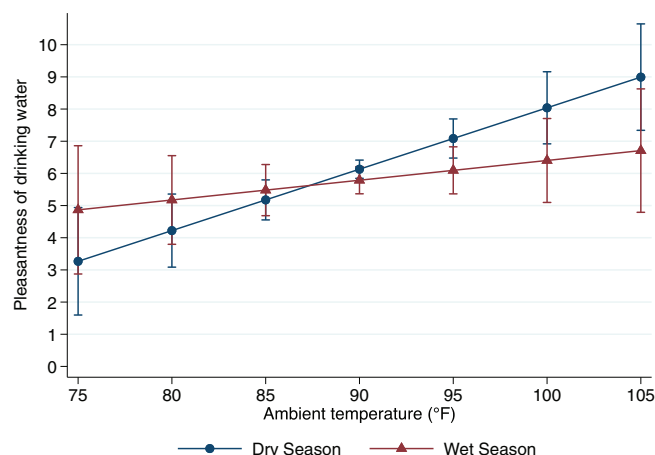


FIGURE 6 Season of birth interacts with ambient temperature in relation to predicted perceived pleasantness of drinking water among Daasanach. Plot generated using marginal standardization of OLS regression results presented in Table 3 model 2.4

(SE = 0.15; $p = .034$) lower pleasantness of drinking water. Chewing tobacco was not associated with either thirst measure. Ambient temperature and season of birth, as well as the interaction ($B = -1.3$; SE = 0.15; $p = .021$) between ambient temperature and season of birth were all statistically significant in the Daasanach-specific model for perceived pleasantness of drinking water (Table 3, Models 2.4). This interaction demonstrates significantly different slopes in the relation between ambient temperature and thirst by season of birth for Daasanach adults (Figure 6).

4 | DISCUSSION

This study aimed to compare perceptions of thirst in two extreme thermal environments—hot-dry compared to hot-humid—outside of the typically studied WEIRD settings. We examined how environmental, physiological, and culturally specific factors were associated with current thirst and perceived pleasantness of drinking water. We found that thirst ratings, particularly perceived pleasantness of drinking water, were higher among Tsimane' in the hot-humid Amazon than among Daasanach in hot-arid northern Kenya. Second, in contrast to our hypothesis of increasing thirst with greater Usg, our findings suggest that current hydration status is not a reliable predictor of thirst or perceived pleasantness of drinking water in non-WEIRD hot environments during times with free-access to water. Third, in partial support of our hypothesis that season of birth moderated the association between ambient temperature and thirst, there was a significant interaction between season of birth and ambient

temperature on the perceived pleasantness of drinking water, but not current thirst. This interaction was driven by the association among Daasanach in the hot-arid environment. In contrast to our hypothesis that thirst would decrease with age, we did not find that thirst consistently decreased with age; in fact, it increased among older adults in relation to hotter temperatures. Finally, in partial support of our hypothesis that culturally specific factors would reduce thirst, we found some evidence that tea/coffee and milk consumption were associated with lower thirst ratings among Daasanach.

The two measures of thirst, current thirst sensation and perceived pleasantness of drinking water, were significantly correlated ($r = .25$; $p < .001$) but not as strongly related (with the former explaining only 6% of the variation in the latter in adjusted models) as prior work has demonstrated (Phillips, Rolls, Ledingham, & Morton, 1984). This implies that in these non-WEIRD settings, they are potentially more independent constructs than previously assumed. As thirst is driven by homeostatic and non-homeostatic elements, it is possible that in these settings, these two questions were useful at capturing the two components of thirst, but future work is needed to assess this hypothesis. That the perceived pleasantness of drinking water was substantially higher (~2.4 points) among Tsimane' than Daasanach is important to explore.

Urine concentration, as well as humidity levels, were both significantly higher among Tsimane' than Daasanach, yet Usg and humidity were not associated with either measure of thirst among Tsimane' in either the pooled or the stratified models. Furthermore, it is unclear why Usg and humidity would be driving the higher perceived pleasantness of drinking water but not current thirst. We adjusted for culturally specific factors that may affect current thirst sensation and perceived pleasantness of drinking water in the population-specific models as a way to capture some of the cultural variation and behaviors that may modify thirst perception. We found no evidence that the number of days in the prior week of consuming chicha, fruit-water, or chewing coca leaves was associated with thirst among Tsimane'. However, we did find among Daasanach that daily milk consumption was associated with lower current thirst, while greater amount of tea/coffee consumption in the prior day was associated with lower pleasantness of drinking water (indicating less of a desire to consume water). Since the tea/coffee they drink is lower in caffeine than in Western settings as it is made with coffee husks, it would not reach the level needed to cause diuresis and serves as an important hydration source (Killer et al., 2014; Ruxton et al., 2015). These findings imply that those specific hydration strategies may be useful to lower thirst and the desire to imbibe water.

4.1 | Hydration, thirst, and interoception

None of the physiological factors, including hydration status, we examined were associated with thirst. Our finding that current hydration status as measured through Usg was not associated with thirst is surprising only when compared to experimental studies of induced dehydration. Normal plasma osmolality ranges between 275–295 mOsm/kg with values above 295 considered dehydrated, yet a meta-analysis found that thirst sensation is activated at a plasma osmolality mean of 285.2 mOsm/kg and that this threshold overlaps with increased secretion of arginine vasopressin (Hughes et al., 2018). One twin study found that thirst threshold, the plasma osmolality point at which the thirst sensation kicked in, was heritable; but that thirst sensitivity, the slope of the relation between osmolality and thirst, was not (Zerbe et al., 1991). Participants in experimental studies which induced water losses to a hypohydrated state consistently reported higher thirst ratings (Armstrong, Giersch, Colburn, et al., 2021; Carroll et al., 2019). Recent work demonstrated that thirst perceptions are significantly higher beginning prior to the 1%–2% body mass decrease from water restriction generally associated with the thirst response, and that changes in Usg and Posm during water restriction were associated with greater perceptual thirst and pleasantness of drinking water (Armstrong, Giersch, Colburn, et al., 2021). However, prior work has indicated that during free access to water, rather than in response to water challenges, body-fluid variables like plasma osmolality and angiotensin II concentrations did not relate to thirst perceptions but rather were influenced by anticipatory thirst as well as surrounding eating (Phillips, Rolls, Ledingham, & Morton, 1984). Recent experimental work has demonstrated that after rehydration following water restriction, Posm was dissociated with thirst ratings which suggests that thirst is more perceptual and not as directly tied to hydration status during ad libitum water drinking (Armstrong, Giersch, Dunn, et al., 2020). Those findings parallel our own that hydration as measured via Usg during an ad libitum state in extreme thermal environments were not associated with thirst perceptions.

Interestingly, our prior work in these populations indicated that current hydration status was associated with temperature and thus was sensitive to changes in the environment (Bethancourt et al., 2021). These results imply that Usg may not be physiologically coupled with thirst in ad libitum hot environments. This also demonstrates the importance of behavioral, cultural, and environmental cues surrounding drinking water and how thirst is a multi-faceted construct

driven by all of these cues. When water is not restricted, thirst may result from any number of these factors and mask our ability to detect the homeostatic thirst relationship.

Variation in interoceptive accuracy is another potential explanation for the finding that thirst and Usg were not associated in these extreme thermal environments. Interoception is one's awareness and ability to detect changes in internal bodily states, in this case thirst (Brannigan et al., 2015; Stevenson et al., 2015). The perception and sensitivity to the thirst sensation is what drives individuals to imbibe fluid. Evidence exists that learning and development within social groups and early life experiences can shape a wide range of behaviors, including interoception (Harshaw, 2008; Ma-Kellams, 2014).

While we could not find studies comparing thirst across WEIRD and non-WEIRD settings, prior work has found that Western and non-Western groups exhibit varying levels of interoceptive awareness and accuracy (Ma-Kellams, 2014). For example, Ma-Kellams' (2014) review of interoception found that both West-African and East-Asian groups had higher levels of somatic sensitivity and awareness than European-Americans. In those examples, the West-African sample studied placed greater emphasis on bodily cues, like heart rate and fatigue within their language and medicine—with more holistic explanations for emotions and bodily states. However, there is relatively scant literature comparing interoceptive accuracy (i.e., how well a person is able to detect changes in bodily states). In one of these studies, West-African groups showed lower interoceptive accuracy in identifying changes in heart rate than their European-American counterparts (Chentsova-Dutton & Dzokoto, 2014). This could be attributed to incorrectly identifying the cause of their bodily changes or that they are more aware of their bodies at all times and thus the greater awareness masks acute changes (Ma-Kellams, 2014). Thus, it is also possible that Tsimane' and Daasanach vary in both their interoceptive accuracy and awareness as it relates to thirst and their urinary markers of hydration status. Furthermore, there could be differences in expression across their languages that may affect the numerical score they provide. Yet, our use of the relative visual ladder and that the perceived thirst scores were more similar than pleasantness of drinking water scores help mitigate this potential limitation. Future work should measure thirst multiple times throughout a day alongside changes in environmental and hydration variables to better untangle how cultural understandings of thirst perception, including both interoceptive sensitivity and accuracy, changes in dynamic states.

4.2 | Developmental origins of thirst

To examine homeostatic thirst and whether there was a developmental driver of the thirst setpoint, we tested how thirst was associated with ambient temperature and humidity and whether season of birth modified this response. Ambient temperature, but not humidity, was associated with perceived pleasantness of drinking water. Furthermore, we found a significant interaction between season of birth and ambient temperature, which was driven by the hot-arid environment where water scarcity is a bigger problem. Daasanach born in the wet season (i.e., in utero during less water availability) reported a positive, yet blunted perceived pleasantness of drinking water with rising temperatures compared to those born in the dry season (in utero during greater water availability), translating to 1–2 points lower perceived pleasantness ratings at 95–105°F.

One potential reason why we may have found this interaction between birth season and ambient temperature on pleasantness of drinking water among Daasanach but not Tsimane' is that the Bolivian Amazon has substantially more water year-round even in the dry season than in Northern Kenya. In San Borja, Bolivia, the closest weather station, the mean annual rainfall of 2205 mm is nearly seven times higher than the likely overestimated 333 mm in Northern Kenya from a combination of the Lodwar weather station and historical local weather data from Turkana county, Kenya on the other side of Lake Turkana (Leslie & Fry, 1989) (Table S1). Therefore, among Tsimane', differences in season of birth may matter less and exert less of an effect in utero, that is, not be as significant a stressor as they are in an arid environment, on thirst responses to heat because of widespread water availability.

Our findings of a blunted thirst response to a situation of higher water needs (i.e., hotter temperatures) are similar to animal models (Perillan et al., 2008; Ross & Desai, 2005). Animal studies have demonstrated that maternal dehydration in rat dams affects the development of thirst responses of offspring, such that those exposed to in utero dehydration did not exhibit higher thirst responses in response to their own dehydration following birth (Perillan et al., 2008). This indicates that the adaptive thirst response may be blunted among those who experience water scarcity in utero.

Prior work examining developmental influences on nutrition and health, notably work in the developmental origins of health and disease (Kuzawa & Quinn, 2009), demonstrate how critical the maternal nutritional environment is to later life health (Thayer et al., 2020). The fetal environment and maternal exposure to heat and precipitation have been shown to affect birth outcomes

(Randell et al., 2020). For example, in Ethiopia, hotter temperatures throughout pregnancy, particularly in the first and third trimesters, were associated with greater odds of stunting, while *greater* rainfall in utero was associated with less stunting (Randell et al., 2020). Furthermore, the in utero environment, that is, water restriction particularly in the second trimester onward, is linked to changes in thirst setpoints and water intake behaviors of offspring (Ramirez et al., 2002; Rosinger, 2020; Ross & Desai, 2005; Xu et al., 2000). Animal studies have shown that this manifests in offspring through a lower plasma osmolality threshold at which arginine vasopressin is excreted to correct body water losses (Ross & Desai, 2005). The thirst setpoint and sensitivity to external environments is a likely mechanism driving the water intake behaviors. Our data suggest that broad categorization of water availability in utero, particularly in water scarce environments, may have critical implications for how thirst, and consequently, water drinking patterns develop in later life. However, our findings highlight the need for more careful studies which examine dosage effects, linkage of climate data to individual records, and examination of effects by trimester of exposure to further untangle the developmental origins of thirst and human water needs.

4.3 | Aging, thirst, and heat outside the Western context

In WEIRD settings, the sensation of thirst (Rolls & Phillips, 1990) and water drinking (Rosinger & Herrick, 2016) changes with age. Older adults exhibit reduced thresholds and sensitivity to somatic changes and drink less fluid compared to younger persons (Kenney & Chiu, 2001; Rolls & Phillips, 1990). We did not find that age was significantly associated with thirst ratings. However, among Daasanach, there was some evidence of a quadratic relationship with age—peaking around 30 years of age and then slowly declining, whereas, thirst was slightly positively associated with age among Tsimane' (Figure S4A,B). Kenney and Chiu (2001) demonstrated that osmoregulation is still present in older adults, but it just occurs later than younger adults due to a reduced ability to detect a volume deficit. In our study, as it was *ad libitum* and not under conditions of water restriction, the only test of water stress was to examine how thirst varied in response to ambient temperature. When the relation of ambient temperature to thirst and perceived pleasantness of drinking water was examined stratified by age group, adults aged 60+ years demonstrated increasing thirst with hotter temperatures (Figure S5). This indicated higher thirst responses among

older adults similar or even greater than among younger and middle-aged adults.

Prior work has shown that other physiological processes connected to thirst, like urine concentration (Rosinger et al., 2019) and blood pressure (Gurven et al., 2012; Raichlen et al., 2017), do not decline or increase, respectively, at the same rate in small-scale societies as in WEIRD settings due to more active lifestyles. It is possible that thirst sensitivity remains more tightly connected to ambient temperatures throughout the lifecourse in small-scale societies in comparison to WEIRD settings due to their non-industrial lifestyles and lack of reliance on climate control.

Given ongoing climate change and record-setting high temperatures, a greater understanding of thirst in extreme thermal conditions is critical, particularly among vulnerable groups like older adults whose thirst is more uncoupled from hydration status (Kenney et al., 2014). Extreme heat and rising temperatures will likely affect thirst and human water needs, and lead to higher risk of dehydration before thirst signals kick in. Prior work demonstrated the tight connection between hydration status and ambient temperatures among Tsimane', illustrating the challenge of keeping up with water needs as the day progressed and generally not rehydrating until the evening (Rosinger, 2015). Yet, hotter projected night-time temperatures will make this rehydration and cooling off even more challenging. Furthermore, problems with water availability (Konapala et al., 2020) and water insecurity may increase stress surrounding how one will meet their water needs and result in changes to thirst perception (Rosinger & Young, 2020). It will be important for future work to untangle the effects of extreme heat and water insecurity on thirst regulation patterns, especially in light of how extreme heat and dehydration contributes to kidney disease (Johnson et al., 2019).

4.4 | Limitations and future directions

As this is a cross-sectional, observational study, we cannot infer causality and all relationships should be viewed as associations. Water intake was ad libitum and we did not measure thirst in response to water deprivation or induced dehydration. While we did not induce water restriction, our sampling over a range of ambient temperatures allowed us to examine how thirst varied in relation to ambient environments as hotter temperatures increase water needs (Kenney & Hodgson, 1987). Furthermore, we do not have repeat measurements of thirst in different contexts among the same people, which limits our ability to infer how individuals' thirst within these populations respond to changing conditions. We also did not measure

an individual's physical activity levels over the prior 24 h, which is associated with water needs. Both small-scale populations are moderately active, and the study was conducted with ad libitum access to water and food—meaning that if participants were particularly active prior to our study, they would have had access to the water and food in their homes before coming to the interview site. Thus, there should not be systematic differences of increased physical activity associated with participating in our study by community or population. Nor did we measure their intake of liquids or hydrating foods in the previous 24 h. However, we do control for time of day when an individual was sampled, which adjusts for potential differences in time to the last meal as well as broad physical activity patterns. Future work in these settings should examine repeated assessments of thirst in relation to different ambient environments and control for physical activity and recent water intake.

While Usg is a reliable measure of hydration status, it may lag behind plasma osmolality by 30 min (Oppliger et al., 2005). This would matter more during periods of rapid water loss or gain rather than in ad libitum settings. Future work should examine other markers of hydration status like plasma osmolality, but if possible do so in more non-invasive ways than venous blood draws to minimize discomfort associated with the research.

Different dry and wet seasons vary in water availability, temperature, and duration over time. Thus our measure of birth season may be subject to some non-differential misclassification bias as we do not have the precise water availability or heat stress for each individual, nor in which trimesters of gestation they experienced the majority of conditions, which may bias our estimates toward the null (Szklo & Nieto, 2014). Future work in the DOHaD field should try to utilize natural experiments with higher resolution data of temperature and water availability during gestation and trimester and subsequent thirst perceptions. These relationships should also be explored among children and in longitudinal studies to examine how thirst changes throughout development.

Finally, it is hard to disentangle environmental effects (e.g., humidity) from culturally specific behaviors and norms of thirst, which may be specific to each population in explaining the population level differences between Tsimane' and Daasanach. For example, the morning tea drinking ritual among Daasanach, which is not present among Tsimane', was associated with lower thirst. Finally, water temperature has an impact on palatability of drinking water in terms of how much water volume is consumed (Rolls & Rolls, 1982), and may have unconsciously affected thirst perception scores if there were differences in envisioned water temperature across individuals or populations. However, as our scales were

validated as measures of thirst and hypothetical water intake, there is no mention of water volume or what the water temperature would be. Furthermore, since both settings are without refrigeration, water would be ambient temperature and thus this potential bias is unlikely to have influenced our findings. However, we can at least be sure that our measures of thirst are not driven by anticipatory thirst as participants did not eat food during the hour of data collection.

5 | CONCLUSIONS

This study presents some of the first research of thirst in non-WEIRD settings and contributes to an emerging framework in the human biology of water to better understand how water needs are shaped, vary, and met (Rosinger & Brewis, 2020). This study demonstrated that thirst varied cross-culturally and was greater in a hot-humid setting than a hot-arid environment among small-scale populations. In the hot-dry environment, we found that milk and tea/coffee consumption were associated with lower thirst. Our findings suggest that thirst sensation and the perceived pleasantness of drinking water are not coupled to current hydration status in ad-libitum conditions. Furthermore, we did not find that thirst decreased with age. Rather, thirst may be more responsive to current ambient environment depending on water availability and exposure to heat in utero which may affect sensitivity to heat and water feedback mechanisms throughout the lifecourse, particularly in arid environments, but more work is needed to confirm this. Thirst regulation will be increasingly important to understand given climate change driven exposures to extreme heat and water insecurity.

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AUTHOR CONTRIBUTIONS

Asher Y. Rosinger: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead);

project administration (equal); supervision (lead); writing-original draft (lead), writing-review & editing (lead). **Hilary, J Bethancourt:** Data curation (equal); investigation (supporting); methodology (supporting); project administration (supporting); writing – review and editing (supporting). **Zane S. Swanson:** Data curation (supporting); investigation (supporting); writing – review and editing (supporting). **Kaylee Lopez:** Writing – review and editing (supporting). **W. Larry Kenney:** Funding acquisition (supporting); writing – review and editing (supporting). **Tomas Huanca:** Investigation (supporting); project administration (supporting); writing – review and editing (supporting). **Esther Conde:** Data curation (supporting); investigation (supporting); methodology (supporting); project administration (supporting); writing – review and editing (supporting). **Rosemary Nzunza:** Funding acquisition (supporting); investigation (supporting); project administration (supporting); supervision (supporting); writing – review and editing (supporting). **Emmanuel Ndiema:** Funding acquisition (supporting); investigation (supporting); methodology (supporting); project administration (supporting); writing – review and editing (supporting). **David Braun:** Funding acquisition (supporting); project administration (supporting); supervision (supporting); writing – review and editing (supporting). **Herman Pontzer:** Conceptualization (supporting); investigation (equal); methodology (supporting); project administration (equal); supervision (equal); writing – review and editing (supporting).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available upon reasonable request due to privacy/ethical restrictions.

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