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The Human Ecology of Conflict: A Case Study from the Prehispanic Nasca Highlands of Peru

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Anthropology

by

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Dedicated to my dad, who was been a constant source of support and inspiration.

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ABSTRACT

The Human Ecology of Conflict: A Case Study from the Prehispanic Nasca Highlands of Peru

by

Weston Craig McCool

This dissertation research addresses two central questions: 1) what conditions promote warfare? 2) how do people cope with conflict? I seek to answer these questions by developing and employing osteological, stable isotope, and statistical methods, and using theoretical models from Human Behavioral Ecology (HBE).

The four dissertation chapters presented here articulate distinct but related aspects of warfare and concern casual forces, subsistence trade-offs, and well-being. The dissertation builds towards the third and fourth chapters, which evaluate the two primary questions of this research: 1) what variables explain the emergence and persistence of warfare? and 2) how do individuals manage the tradeoff between the risk of food shortages and the risk of wartime violence? Chapter three will focus on the climatological, demographic, and sociopolitical conditions that explain variability in warfare, and how these conditions may promote violence from an evolutionary perspective. Chapter four explores the ways in which the risk of interpersonal violence (RIV) structures the costs and benefits of alternative subsistence strategies and their attendant health impacts. Further, it investigates the factors that influence individual variability in risk-preference. Chapters one and two set the stage for the latter half of the dissertation by investigating 1) evidence for internecine warfare in the study region, and heterogeneity in the

risk of interpersonal violence, and 2) changes in pathology, mortality, and longevity by engaging with the osteological paradox using a multimethod approach.

These topics are explored using a case study population of agropastoralists from the Late Intermediate period (950 – 1450 C.E.; LIP) Nasca highlands of Peru. To accomplish dissertation goals, my research must demonstrate that 1) the LIP Nasca highland population experienced chronic, internecine warfare which produced high probabilities of interpersonal violence; 2) increasing pathological burden is the result of elevated biological stress rather than increasing longevity or robusticity; 3) variability in violent conflict can be explained by changes in socioecological and demographic variables, and 4) wartime changes in subsistence practices and dietary stress can be understood as optimal strategies that attempt to balance the risk of food insecurity with the risk of interpersonal violence.

Chapter one focuses on using osteological data and formal quantitative analyses to test various hypotheses concerning the character of conflict in the Nasca highlands region. This chapter develops and tests osteological expectations of what patterns should be observed if LIP violence is defined by intra-group violence, ritual conflict, intermittent raiding, or internecine warfare. This chapter will also highlight heterogeneity in violent mortality to assess whether certain subgroups were targeted for violence, or whether violence is best explained by the concept of social substitutability.

Chapter two assesses changes in morbidity, mortality, and longevity during the LIP. We leverage recent multimethod approaches to address the implications of the osteological paradox, which revealed profound equifinality in interpretations of health from skeletal samples. The goal of this chapter is to evaluate how conditions during the LIP impacted the general well-being of the population as well as variability in the risk of disease and death.

Chapter three investigates individual motivations for participating in warfare from an evolutionary perspective, and how they relate to the emergence and spread of conflict on large spatiotemporal scales. I derive and test hypotheses that predict how political transitions, climate change, dietary stress, and demographic pressure structure the payoffs for conflict and interact to promote warfare.

Chapter four develops and tests a risk sensitive HBE model that outlines how the local economy, while designed to reduce the risk of food shortages in the arid Andean environment, puts individuals at increased risk of violence during wartime. The model specifies resource returns and violence avoidance as an explicit tradeoff, whereby the probability of violence can be mitigated at the cost of food security and vice versa. This chapter seeks to develop a model that can explain how populations and individuals cope with subsistence needs during times of war, especially when local environmental conditions promote subsistence strategies that put individuals at a high risk of interpersonal violence.¹

¹ As a note on formatting, this dissertation is written as four standalone, article-length chapters rather than in the book format. As such, there is repetition between the chapters in certain sections and several figures are reproduced in multiple chapters.

ETHICS STATEMENT

All research was conducted with the formal permission of the Peruvian Ministry of Culture, with permits to collect, export, and analyze the skeletal and botanical materials (No.501-2018/DGPA/VMPCIC/MC; No.036-2019-VMPCIC-MC). Further, I felt it was equally important to obtain the full support of local communities prior to conducting fieldwork. To ensure my team fostered collaboration and mutual understanding we conducted a series of meetings with local officials and community members. We obtained written permission from the elected mayors from each of the districts where we conducted fieldwork, met and obtained consent from each of the community presidents and vice-presidents, and met with a number of secretaries of the local municipalities. We also conducted an ongoing series of conversations with local community members where we outlined our research goals and our curation plan to collect and conserve a sample of human skeletal remains from tombs that are in danger of looting and/or collapse. In all, we worked closely with the communities and obtained permission from all local levels of government as well as from the communities themselves.

During the course of project fieldwork, outreach activities included numerous talks with community members and K-12 students about archaeology. Discussion with teachers included topics of conservation, historical patrimony, and the inclusion of our research findings into local school syllabi so that children living in the area could understand more about the local archaeology. In addition to educational outreach, I found it appropriate to financially assist with several community-based development projects that were aimed at better facilitating transportation between communities and to and from the marketplace in the city of Nasca.

Communicating project results provides a unique opportunity to present the research at multiple levels. Myself along with my Peruvian Co-director are currently drafting a Spanish-language pamphlet that presents the results of our research as well as information on the local archaeology and the importance of cultural patrimony and preservation. This pamphlet will be distributed for free to all K-12 schools in the Nasca highland region with the full support of local government officials and school administrators. Future public consultation and outreach is planned for the summer of 2021 in order to continue our collaboration and present the results of our research to the local schools, administrators, and broader communities.

To facilitate the distribution of our data we will provide open access to our raw data files as well as our results on the tDAR web platform. This will allow other researchers to gain access to our data as well as view our analytical procedures.

Finally, on a philosophical note, it is important given the heady nature of the subject matter that we acknowledge the naturalistic fallacy, which states that because a phenomenon is natural does not mean that it is justifiable or ethically defensible. This dissertation treats warfare as a natural phenomenon not because it is morally permissible, but because it can and should be investigated through the natural and social sciences. I contend that in order to understand war, we must first understand its natural origins and evolution.

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I. The Character of Conflict: Using a multimethod osteological approach to determine the nature of conflict and heterogeneity in violent mortality

A. Introduction

The last several decades of anthropological research shows that interpersonal violence played and continues to play an important role in human evolution (Gat 2008; Glowacki and Wrangham 2013; Glowacki et al. 2017; Keeley 1996; Otterbein 1999; Pinker 2011; Walker 2001; Wrangham and Glowacki 2012; Wrangham et al. 2006). Violent conflict can dramatically affect population mortality, sociopolitical institutions, economic decision making, and all aspects of human behavior (Allen et al. 2016; Arkush and Tung 2013; Devakumar et al. 2014; Gat 2008; Glowacki et al. 2017; Gomez et al. 2016; Human Security Report 2005; Keeley 1996; Otterbein 1999; Pinker 2011; Walker 2001; Walker and Bailey 2013; Wrangham 1999; Wrangham et al. 2006). Despite the importance of interpersonal violence, our picture of conflict throughout the human career remains highly fragmented. In addition, it remains a substantial challenge to elucidate the basic character of prehistoric conflict. A lack of detailed information on multiregional patterns as well as the specific types of violence a population experienced limits our ability to develop and test hypotheses concerning its causes and consequences. This paper develops a means for establishing the character of conflict by generating and testing expectations regarding the distinct patterns of violence that result from differing forms of conflict.

The distinction between various forms of violence is important, and debates have erupted in numerous research areas regarding the nature of prehistoric conflict (e.g. Arkush 2008; Arkush and Stanish 2005; Bamforth 1994; Billman et al. 2000; Milner et al. 1991; Quilter 2002; Walker 2001). Interpersonal violence can take a number of different forms, all of which vary in their motivations, constellations of effects, and archaeological manifestations. Intra-group

violence can include domestic abuse, forced captivity, or punishment (Martin and Harrod 2010). Intergroup violence can include structured and ritualized conflict that is rule-bound and constrained to cohorts of willing combatants (Arkush and Stanish 2005; Keeley 1996; Meggitt 1977). Alternatively, intergroup conflict can manifest as internecine warfare that impacts all segments of society and the basic demographic structure of populations (Devakumar 2014; Keeley 1996; Walker 2001). If our goal as anthropologists is to understand the causes and consequences of violence, it is vital that we first elucidate the variable manifestations of conflict in specific contexts. Of course, various types of conflict can co-occur, but should be distinguished nonetheless. Human osteology can produce crucial information on the character of prehistoric conflict by assessing general mortality patterns as well as intragroup variability in the risk of violent mortality (Allen et al. 2016; Arkush and Tung 2013; Kellner 2002; Martin and Harrod 2014; Milner 1999; Milner et al. 1991; Tung 2007, 2012; Walker 1997, 2001).

The goal of this paper is to use a multimethod osteological approach and quantitative analyses to test various hypotheses concerning the character of conflict in Prehispanic Peru. The first “ritual conflict” hypothesis proposes violence was structured, predictable, and centered predominately on combatants. The second “intra-group violence” hypothesis proposes violence centered on particular subgroups, was primarily non-lethal, and involved patterned recidivism. The third “intermittent raiding” hypothesis proposes low levels of violence, primarily lethal, with little recidivism, and temporal lags between episodes of violence. The fourth “internecine warfare” hypothesis proposes conflict was frequent and unpredictable, with violence targeting both combatants and non-combatants alike, and high levels of lethal trauma and recidivism. We test these hypotheses using a sample of Middle Horizon (500 – 950 C.E., MH) agriculturalists

from lowland Nasca, Peru (Kellner 2002) and a population of Late Intermediate period (950 – 1450 C.E., LIP) agropastoralists from the Nasca highlands.

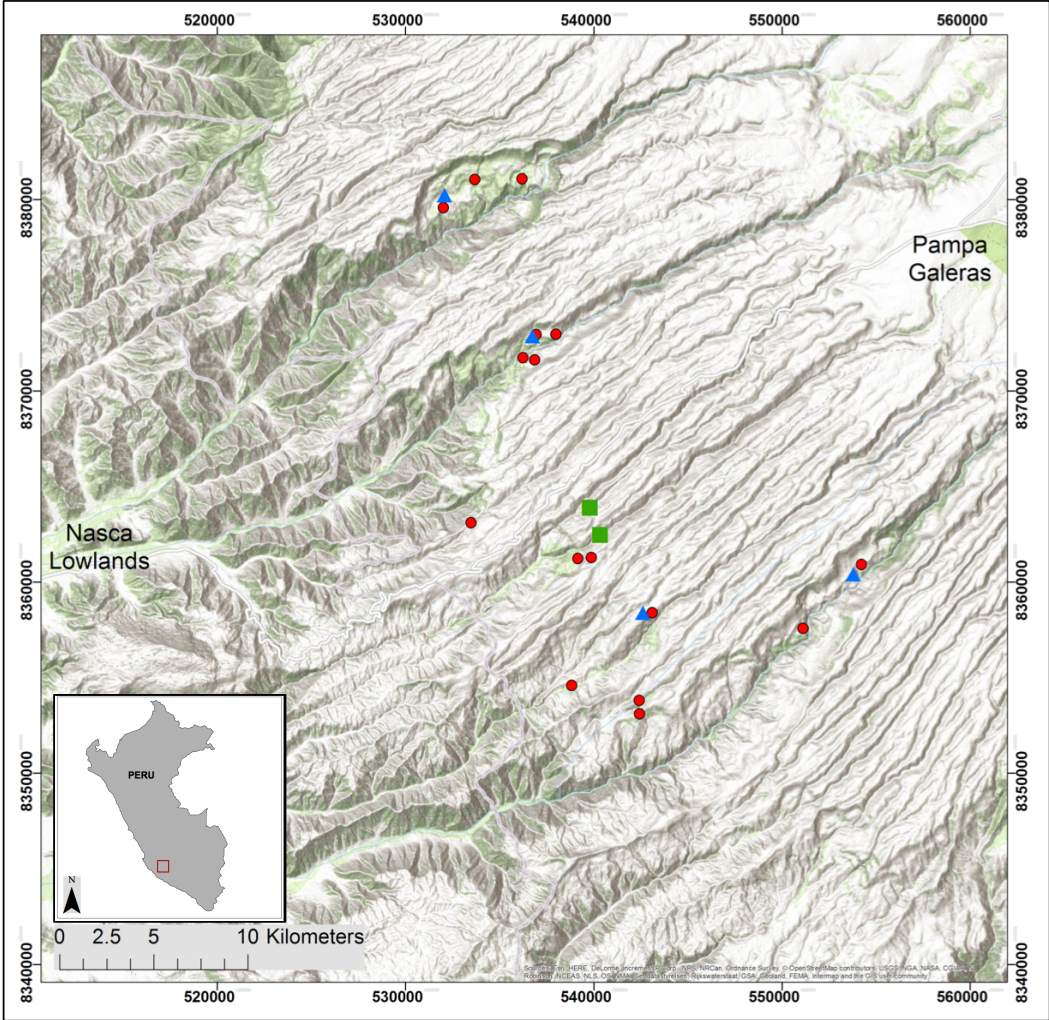


Figure 1.1. Map of the Nasca highlands. Points = LIP residential sites, triangles = *chullpa* cemeteries, squares = *machay* cavern tombs.

B. Materials and Methods

1. Case Study: The Nasca Region

The Nasca highlands is a remote, highly bounded region roughly 30km east and over 3,000 meters above of the modern city of Nasca, Peru (Figure 1.1). During the LIP the region contained a population of small-scale agropastoralist communities scattered throughout the

region's five river valleys. These valleys straddle the coastal and sierra ecologies, and are the definition of ecological circumscription, with each containing a fast-flowing river and a small, well-defined patch of open terrain with sufficiently flat topography to permit the construction of terraces and canals for agriculture (McCool 2017). All currently known LIP residential sites are located within, or immediately adjacent to, these arable patches. The surrounding "*Puna*" high grasslands are suitable for herding but cannot be intensively cultivated due to inadequate precipitation for dry farming or ground water for irrigation. As a result of these environmental characteristics the Nasca highland region is somewhat isolated. The region's valleys and residential sites are densely clustered, with nearest neighbors averaging only several kilometers from each other. Neighboring regional populations are however dozens of kilometers (or several days walk) in any direction, which manifests as a buffer zone between the Nasca highlands and neighboring population centers. Whether this buffer zone was intentionally maintained or is an artifact of environmental constraints is unknown.

The principal author recorded 19 LIP residential sites and associated cemeteries located throughout the region's five river valleys (McCool 2017). Each of the settlements was permanently occupied as evidenced by dense housing clusters and middens along with the total lack of households outside of hilltop residential centers. Residential sites are located on difficult to access hilltops and mesas or along steep ridgelines and exhibit multiple lines of robust fortification features (McCool 2017).

Either within or, more often, immediately adjacent to the hillforts are cemeteries consisting of several dozen to several hundred artificially constructed tombs known in Quechua as "*chullpas*" (Figure 1.2). Chullpa tombs are fairly uniform in size and consist of both conical and square construction styles. The tombs contain up to several dozen individuals along with

associated mortuary goods. Each interred individual was at one time a desiccated bundle wrapped in a cotton shroud and placed upright in tight clusters on the ground surface. Subsequent taphonomic processes and substantial looting have disarticulated and commingled these remains.

To assess patterns and variability in violence, we compare our LIP data with osteological analyses of 97 MH crania recovered from tombs in the Nasca lowlands to the west of the Nasca highlands (Kellner 2002). This comparative sample is used because it immediately predates the LIP, represents the only discernable residential population in the general Nasca region during the MH; due to the low levels of violence, this sample can serve as a baseline against which LIP data can be evaluated (Table 1.2).

2. Osteological Methods

During the fall of 2018 eleven LIP tombs in the Nasca highlands were excavated, producing a human skeletal sample of 325 (determined by the number of crania). Of the 325, all underwent sex determination, age-estimation, and an assessment of cribra orbitalia. Only 270 were sufficiently intact to fully assess biological profiles, trauma, and pathology (cribra orbitalia and porotic hyperostosis). The commingled nature of the LIP burial contexts prevents us from linking post-cranial remains to the crania. As such, we restricted our osteological analyses to the sample of crania.

The age-at-death for each individual was estimated using the standards protocols of assessing stages of cranial suture closure, dental formation/eruption and surface wear to estimate age (Bass 2005; Buikstra and Ubelaker 1994). Age-at-death estimations were completed for seven age cohorts: infant (0–4), child (4–12), adolescent (12–20), young adult (20–35), middle adult (35–50), and old adult (50+) (White and Folkens 2005). Sex was estimated using sexually

dimorphic cranial features as per the standards protocol (Bass 2005; Buikstra and Ubelaker 1994; Murphy et al. 2010; Vercellotti et al. 2014; White and Folkens 2005).

Rates of ante-mortem and peri-mortem trauma were recorded using evidence of bone healing indicating ante-mortem trauma (Lovell 1997; Sauer 1998; Tung 2007). Radiating fractures, discoloration in fracture lines, and bone hinging at fracture margins were used to determine peri-mortem trauma (Ortner 2004; Sauer 1998; Tung 2007). Postmortem damage was distinguished from peri-mortem trauma based on the coloration and shape of fracture margins and the presence of hinging bone and radiating fractures (Berryman and Haun 1996; Murphy et al. 2010; Ortner 2008; Sauer 1998; White and Folkens 2005). Observations of cranial trauma distinguished between sharp-force and blunt-force trauma (Kurin 2012; Lambert 1997; Lovell 1997; Tung 2007, 2012). In addition, “overkill” and “critical” trauma were measured for the LIP sample. Overkill trauma is that which goes beyond what is necessary to dispatch an individual (Kurin 2012; Simmons 2007; Šlaus et al. 2010). This involves multiple peri-mortem traumas that disarticulate and/or destroy a large portion of the cranium. Critical trauma is defined as any trauma, healed or unhealed, greater than 25 mm in diameter or over 2.5 mm in depth. Critical trauma is measured to capture injuries that are likely life-threatening and can be definitively attributed to interpersonal violence (Andrushko and Torres 2011). This is important, as ante-mortem traumas can range from accidents that result in hairline nasal fractures to catastrophic violent injuries. LIP weaponry consisted of maces, hand-axes, and slings, which often require direct cranial contact to inflict peri-mortem injuries. Previous research in the Andes and elsewhere has found cranial trauma analysis to be an effective means of establishing rates of violence (Kurin 2012, 2016; Martin and Harrod 2014; Torres-Rouff and Costa Junqueira 2005). In order to highlight heterogeneity in violence risk we evaluate the relationship between trauma

and 1) sex, 2) age-at-death, and 3) cranial modification, which has long been acknowledged to signal group affiliation (Kurin 2012; Torres-Rouff 2003).

To determine cranial modification, we followed Torres-Rouff (2003), who divided modified crania into two broad categories: tabular (fronto-occipital) and annular (circumferential). Annular crania can be further sub-classified into annular erect and annular oblique variants based on the posterior angle of the skull. Crania without evidence for intentional deformations are classified as non-modified. Our sample did not contain any crania with tabular modification. As a result, our sample was divided into three modification categories: annular erect, annular oblique, and non-modified. Non-modified individuals are those with the normative rounding of the cranium and no appearance of depressions or elongation. A cranium was classified as annular erect when compressions to the posterior cranium resulted in the superior elongation of the occipital and posterior parietal bones. Annular oblique modification was determined by the posterior trending elongation of the frontal bone, and occasionally the bregma, along with the postero-superior elongation of the occipital and posterior parietal bones. 249 crania were sufficiently intact to determine modification. Of the modified crania 5% are annular erect and 95% are annular oblique, while 20% of the sample crania are non-modified.

To evaluate diachronic trends in violence AMS radiocarbon dates were obtained for 124 crania distributed throughout the eleven tombs. Samples of cranial bone were taken from the vomer and nasal concha when possible or the nasals/styloid process when necessary. In several cases, none of these elements were available requiring the zygomatic arch to be sampled. Bone collagen for ^{14}C measurement and stable isotope chemistry was extracted and purified using the modified Longin method with ultrafiltration at Penn State University and the University of California, Irvine using protocols established by the UC Irvine Keck Carbon Cycle AMS facility

(UCI KCCAMS, 2007) where AMS ^{14}C measurement was conducted (see Chapter four for radio and stable isotope protocols). Results were calibrated using the rcarbon package in the R programming environment (Crema and Bevan 2019) with the SHCal13 calibration curve (Hogg et al. 2013). The resulting chronology spans the terminal MH and the entire LIP (Table 1.5), permitting an analysis of diachronic changes in violence throughout the entire study period.

The dated subsample of Nasca highland crania was divided into three temporal phases: Phase I (950 – 1200 C.E., PI) represents the transition into the LIP, Phase II (1200 – 1300 C.E., PII) represents the middle LIP, and Phase III (1300 – 1450 C.E., PIII) representing the final phase of the LIP. The variable duration of each phase is necessary to (1) maximize intra-period temporal resolution without decreasing sample sizes such that statistical tests are unreliable, and (2) align temporal phases with important environmental and demographic transitions to facilitate future research on the causes of conflict. Individuals whose calibrated C14 range overlaps multiple phases were binned into the phase containing the majority of the 1SD range. For example, a cranium with a calibrated C14 range of 1175 – 1300 C.E. was binned in PII (1200 – 1300, C.E.), as 100 years of the C14 range fall into the PII interval while only 25 years fall into PI. The resulting dated sub-sample exhibits trauma rates that are higher (though not significantly) than the parent sample of 270. This is because our sampling strategy intentionally included a large number of trauma victims for stable isotope chemistry. As such, the trauma rates in the diachronic section represent slightly high estimates.



Figure 1.2. An example of a typical *chullpa* tomb.

C. Evaluating Hypotheses on the Character of Conflict

1. Ritualized Conflict

In general, ritualized conflict takes the form of organized challenges and preplanned battles or a series of conflicts informally or formally arranged (Arkush and Stanish 2005; Keeley 1996; Larson 1987; Meggitt 1977; Tung 2007; Walker 1997, 2001). The resulting conflict is often game-like, low casualty, and combatant-focused (Keeley 1996). Rarely are non-combatants targeted for violence, and the conflicts are generally ended after a small number of combatants are injured or killed. Ritual conflict has been recorded among numerous small-scale societies including the Mae Enga (Meggitt 1977), Dani (Heider 1979; Larson 1987), Yanomamo (Chagnon 1968), Prehistoric Californian groups (Walker 2001), Andean groups (Arkush and Stanish 2005), and many more. Osteological patterns include:

- Primarily non-lethal trauma

- Violence directed at combatants (primarily young adult males, see below for justification)
- Violence directed at the front of body (facing your adversary)
- Combatants exhibit ante-mortem trauma recidivism
- Little to no evidence for overkill trauma
- Little evidence for body mistreatment

2. Intragroup Violence

Intragroup violence is typically manifested as domestic abuse, captive abuse, and punishment. Intragroup conflict takes many forms, but generally focuses on acts of non-lethal aggression towards certain subsets of society (Martin et al. 2010; Walker 1997). Intragroup violence exhibits predictable osteological patterns (Martin et al. 2010; Martin and Harrod 2014; Martin and Tegtmeyer 2017; Walker 1997), including:

- Victims typically non-combatants
- Ante-mortem trauma recidivism for non-combatants
- Little to no lethal or overkill trauma
- Population sub-groups exhibit preponderance of trauma
- Pathologies related to extreme workload
- Punishments utilize specific tools (e.g. whips) and repeatedly target certain regions of the body.

3. Intermittent raiding

This type of violence includes infrequent, resource focused raids (Allen et al. 2016; Keeley 1996). Often the intention is to avoid violent encounters, although confrontations are often lethal when they do occur. Patterns include:

- Low levels of trauma
- Trauma primarily lethal (little ante-mortem trauma)
- Low levels of trauma recidivism
- Victims across demographic spectrum
- Little to no overkill / body mistreatment
- Temporal lags between episodes of violence

4. Internecine warfare

Interneicine warfare is defined as frequent, intergroup lethal aggression. Combatants and non-combatants are targeted, many individuals killed are the victims of surprise raids and ambushes (Keeley 1996; Scaffidi and Tung 2020).

- High proportion of lethal trauma
- Combatants and non-combatants targeted
- Traumas center on posterior of cranium (not facing assailant)
- Multiple trauma / recidivism for combatants and non-combatants
- High proportion of overkill and critical trauma
- Mistreatment of bodies
- Consistently high rates of trauma through time

While important exceptions exist (e.g. Bengtson and Gorman 2017), much of the research on non-state warfare shows that combatants overwhelmingly tend to be adult males (Glowacki and Wrangham 2014; Heider 1979; Keeley 1996; Kelly 2000; Meggitt 1977). Females, subadults, and elderly males tend to take on the role of non-combatants (Glowacki and Wrangham 2014; Heider 1979; Meggitt 1977). This is not to say that non-combatants play an unimportant role in wartime strategy, logistics, and other aspects of the conflict process—they certainly do. Rather, we emphasize this dichotomy because combatants tend to perpetrate the majority of wartime killings and are typically the only victims of lethal and sub-lethal aggression when violence is regulated and ritualized. Non-combatants are only routinely targeted with intra-group violence (typically non-lethal) and warfare (often lethal). Of course, non-combatants attempt to avoid violent encounters when at all possible, suggesting that a high degree of non-combatant deaths is the result of the inability to predict when and where lethal violence will ensue. When a violent encounter between a combatant and non-combatant does occur, unarmed individuals will attempt to flee from their adversaries, often leading to violent trauma to the posterior regions of the body (Tung 2007).



Figure 1.3. Critical blunt-force ante-mortem trauma.



Figure 1.4. Critical blunt-force ante-mortem trauma.



Figure 1.5. Left parietal contains critical blunt force ante-mortem trauma. Right parietal and temporal contain multiple peri-mortem traumas.



Figure 1.6. Overkill trauma.



Figure 1.7. Overkill trauma.

D. Results

Descriptive and inferential statistical results are summarized in Tables 1.1 – 1.3. All tests were done in the R programming environment.

1. Population-level Trauma

Overall, 31% LIP human skeletal sample exhibits ante-mortem trauma and 13.1% (n = 267) exhibits peri-mortem trauma. 38% of individuals exhibit at least one peri-mortem and/or ante-mortem trauma. LIP trauma rates are significantly higher than the preceding Middle Horizon population (ante-mortem $p = 0.000$; peri-mortem $p = 0.000$). Of the sub-sample of individuals with peri-mortem trauma nearly half (49%) exhibit overkill trauma (6.4% of total

sample). In addition, 25% of the sample exhibits critical trauma, showing that a quarter of the population experienced a violent encounter that was very likely life-threatening. The average number of traumas per individual also significantly increases during the LIP ($p = 0.000$), from an average of 0.10 traumas per individual during the MH to 0.80 during the LIP. The average number of traumas per LIP individual for only those that exhibit trauma is 2.1.

Table 1.1. Trauma patterns comparing MH sample to LIP sample.

Trauma by Period	MH	LIP	Results	Test
Ante-mortem	9.3% (9 of 97)	31% (83 of 267)	$X^2 = 16.78, p = 0.000$	Chi-squared
Peri-mortem	0%	13.1% (35 of 267)	$X^2 = 12.6, p = 0.000$	Chi-squared
All trauma	9.3%	38% (102 of 267)	$X^2 = 26.139, p = 0.000$	Chi-squared
Peri-mortem distribution	NA	Anterior-Posterior	$X^2 = 13.164, p = 0.000$	Chi-squared
Ante-mortem distribution	NA	Anterior-Posterior	$X^2 = 0.666, p = 0.414$	Chi-squared
Overkill trauma	0%	6.4% (17 of 267)		
Critical trauma	0%	25.8% (69 of 267)		
Sum of traumas	0.1	0.8	$t = 7.593, p = 0.000$	t-test

2. The Distribution of Trauma

The distribution of peri-mortem traumas is highly patterned. In the LIP sample there is a significantly higher frequency of peri-mortem on the posterior of the skull ($p = 0.000$). Indeed, 47% of individuals with peri-mortem trauma do not exhibit any traumas on the anterior portions of the skull, while the majority of individuals with peri-mortem trauma on the front of the skull also exhibit posterior peri-mortem wounds. This pattern shows that the majority of lethal wounds were delivered from behind. The difference in the distribution of ante-mortem traumas was non-significant ($p = 0.414$), suggesting non-lethal wounds were equally as likely to be obtained facing an assailant as facing away.

3. Trauma and Age-at-death

The subadult aggregate cohort (ages 0 – 13) exhibits 6.9% peri-mortem trauma (3 out of 29) while the adult aggregate cohort (ages 13 – 50+) exhibits 13.9% peri-mortem trauma (33 out of 238), showing the probability of a lethal encounter increases during adulthood. Ante-mortem trauma is also higher among adults with 34.5% (n = 238) exhibiting ante-mortem wounds compared to 3.4% of subadults (n = 29). Overkill trauma follows the same pattern with 7.1% of adults and 0% of subadults exhibiting overkill. Finally, critical trauma is higher among adults (27.8%) compared to subadults (6.9%).

There is also a trend towards increasing number of traumas per individual with age (Figure 1.8). Indeed, when median age is compared against the number of traumas per individual using a General Additive Model (GAM) the results are significant ($p = 0.002$). Additionally, when median age is compared against the frequency of ante-mortem trauma using a binomial General Linear Model (GLM) a significant association is found ($p = 0.001$), which holds even when subadults are removed from the analysis. The results of both tests show that the average number of traumas per individual and the proportion of non-lethal trauma increase significantly with age.

When median age is compared to peri-mortem trauma using binomial GLM there is initially no significant relationship ($p = 0.324$). When subadults are excluded from the analysis a significant relationship emerges ($p = 0.031$), showing that the probability of a *lethal* violent encounter actually *decreases* with age. The converse results for ante-mortem and peri-mortem trauma are discussed in a later section.

While subadults have the lowest levels of trauma, 7% of the child cohort exhibits peri-mortem trauma, showing they were far from exempt from lethal killings (Figure 1.9b). Infants do

not exhibit any peri-mortem trauma, however the small sample size combined with the poor state of preservation renders general inferences tentative.

Table 1.2. Trauma by Age-cohort.

Trauma by Age	Ante-mortem	Peri-mortem	Median Age (M.A.) by Trauma	Test
Infant	0% (0 of 3)	0% (0 of 3)	M.A. by Ante-m	
Child	3.8% (1 of 26)	7.7% (2 of 26)	$p = 0.001$	GLM
Adolescent	15% (5 of 33)	21.2% (7 of 33)	M.A. by Peri-m	
Young Adult	30% (20 of 69)	18.8% (13 of 69)	$p = 0.031$	GLM
Middle Adult	42% (42 of 100)	9% (9 of 100)	M.A. by sum of trauma	
Old Adult	42% (15 of 36)	11.1% (4 of 36)	$p = 0.002$	GAM
Subadults	3.4% (1 of 29)	6.9% (2 of 29)		
Adults	35% (82 of 238)	14% (33 of 238)		

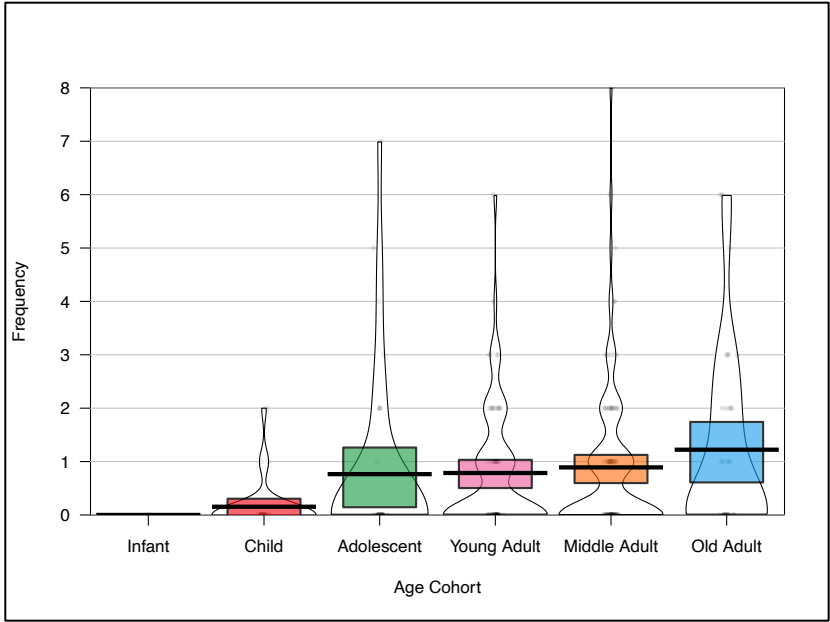


Figure 1.8. Number of traumas per crania by age-cohort.

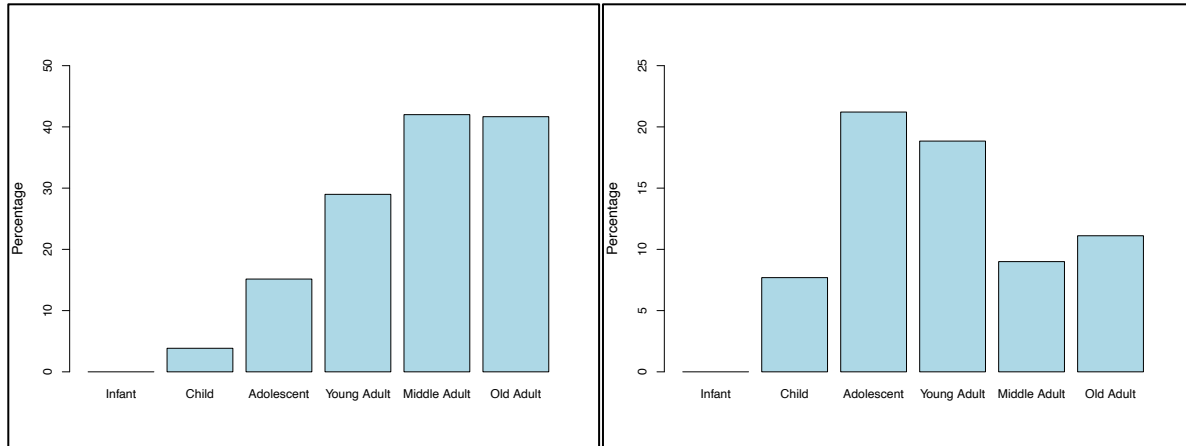


Figure 1.9a (left). Age-cohort by Ante-mortem trauma. **Figure 1.9b (right).** Age-cohort by Peri-mortem trauma.

4. Trauma and Sex

Trauma results by sex reveal interesting patterns. Males exhibit significantly more ante-mortem trauma compared to females ($p = 0.000$). The average number of traumas is also significantly higher among males ($p = 0.04$), as is the percentage of critical trauma ($p = 0.022$). Peri-mortem and overkill trauma do not vary significantly by sex (peri-mortem $p = 0.176$; overkill $p = 0.54$). Nevertheless, females exhibit a greater proportion of peri-mortem trauma than males (Figure 1.10)—in particular adolescent and young adult females.

Table 1.3. Trauma by Sex.

Trauma by Sex	Males	Females	Results	Test
Ante-mortem	44% (43 of 97)	29% (32 of 112)	$\chi^2 = 16.4, p = 0.000$	Chi-sq.
Peri-mortem	12% (12 of 97)	17% (19 of 112)	$\chi^2 = 3.5, p = 0.176$	Chi-sq.
Critical	38% (37 of 97)	25% (28 of 112)	$p = 0.022$	Fisher's Exact
Overkill trauma	7.2% (7 of 97)	8% (9 of 112)	$p = 0.54$	Fisher's Exact
Sum of traumas	1.2% (n = 97)	0.75% (n = 112)	$p = 0.04$	t-test

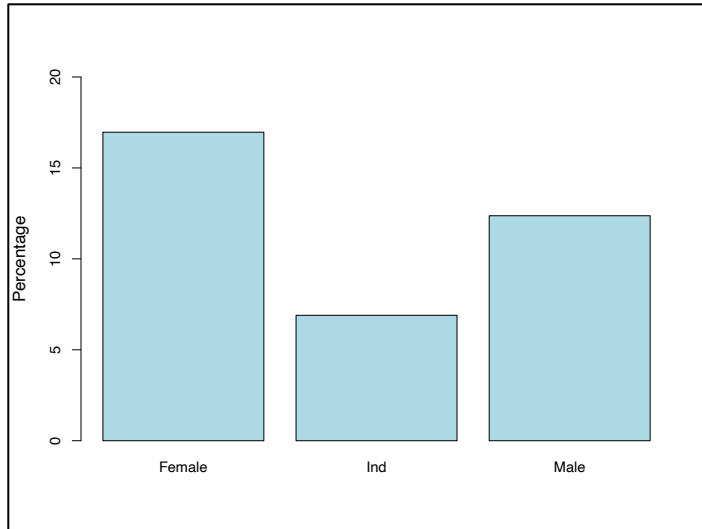


Figure 1.10. Peri-mortem trauma by Sex (Ind = Indeterminate, female n = 112, male n = 97).

5. Trauma and Cranial Modification

There are no significant relationships between cranial modification and violence. Individuals with and without modification do not have significantly different proportions of peri-mortem trauma ($p = 0.319$) or ante-mortem trauma ($p = 0.681$). Likewise, individuals with annular erect versus annular oblique do not significantly differ by peri-mortem trauma ($p = 0.627$) or ante-mortem trauma ($p = 0.336$).

6. Body Mistreatment

The sample shows possible evidence of body mistreatment (Figure 1.11), with 10–17% of the cranial sample showing evidence of burning on the ectocranial surface. Individuals with fire-altered bone are scattered throughout all 11 tombs and commingled with unburnt crania, which rules out natural fire episodes that would burn clusters of crania rather than isolated individuals. While it is difficult to discern whether the fire-alterations are due to body mistreatment, the high proportion and wide distribution of burnt crania suggests this pattern is the result of intentional human action.



Figure 1.11. Patchily distributed burns on the ectocranial surface of crania suggest possible evidence of body mistreatment.

7. Diachronic Patterns of Violence

All forms of trauma increase significantly from the MH to the LIP. Within the LIP peri-mortem trauma rises during Phase I then declines in Phase II, although the decrease is not significant ($p = 0.201$) likely due to small sample sizes restricting statistical power (Figure 1.12). Violence increases significantly to its highest-level during Phase III, when peri-mortem trauma climbs to 24% ($p = 0.05$). It is also noteworthy that overkill trauma remains low during the first two phases (4.8% and 3.7% respectively) then increases significantly during Phase III to 14% ($p = 0.049$; Figure 1.12). Interestingly, ante-mortem trauma varies little throughout the three phases, averaging 28.7% with a range of 26–31%. Critical trauma, a more reliable metric of violence, mirrors trends in peri-mortem trauma with an initial increase in Phase I, a decline in Phase II, and a significant rise in Phase III to 38% ($p = 0.002$; Figure 1.12). The average number of traumas per individual is significantly higher during Phase III (PI to PIII $p = 0.018$; PII to PIII $p = 0.002$), showing the intensity of violence and/or trauma recidivism increased during this time (Figure 1.12b).

These results show that warfare emerged during the onset of the LIP and persisted throughout, with a slight decrease in lethal violence during Phase II and a sharp increase circa

1300 C.E. until the arrival of the Inca around 1450 C.E. These results also show that warfare persisted throughout the LIP, while the intensity of violence sharply increased during the last 150 years, corresponding with chronic warfare and mass migrations in the Sierra regions east of the Nasca highlands (Arkush 2008; Kurin 2012).

Table 1.4. Trauma by LIP Phase.

Trauma by Phase	Phase I (PI)	Phase II (PII)	Phase III (PIII)	Test
Ante-mortem	29% (5 of 21)	25.9% (7 of 26)	31% (22 of 71)	
Results	PI~PII $p = 1$	PII~PIII $p = 0.211$	PI~PIII $p = 0.134$	Fisher's Exact
Critical trauma	23% (5 of 22)	7.4% (2 of 26)	38% (27 of 71)	
Results	$p = 0.119$	$p = 0.002$	$p = 0.174$	Fisher's Exact
Peri-mortem	19% (4 of 21)	7.4% (2 of 26)	24% (17 of 71)	
Results	$p = 0.201$	$p = 0.05$	$p = 0.485$	Fisher's Exact
Overkill trauma	4.8% (1 of 22)	3.7% (1 of 26)	14.1% (10 of 71)	
Results	$p = 0.688$	$p = 0.146$	$p = 0.228$	Fisher's Exact
Sum of traumas	mean = 0.57	0.41	1.1	
Results	$p = 0.398$	$p = 0.002$	$p = 0.007$	t-test

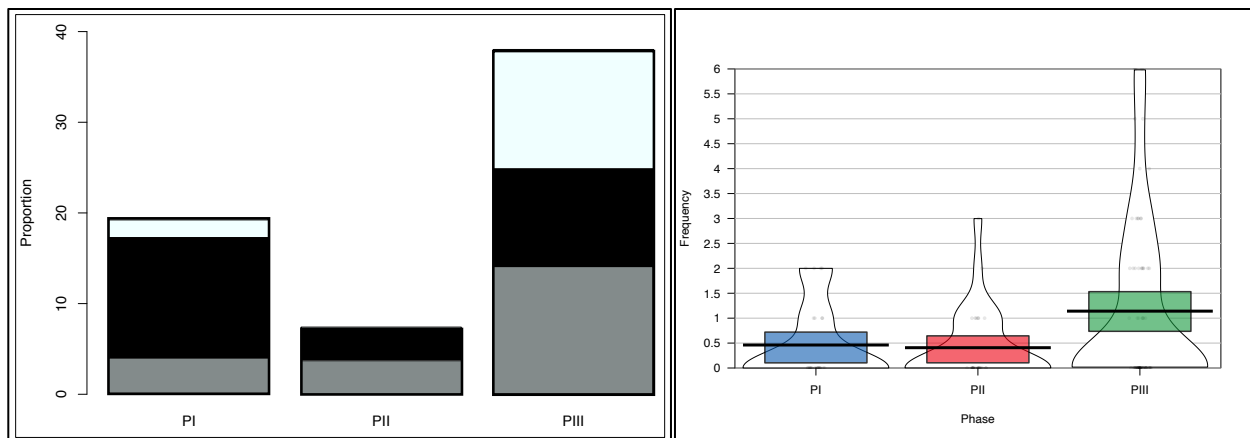


Figure 1.12a (left). LIP Phase by Trauma. Light blue = Critical, black = Peri-mortem, gray = **Figure 1.12b (right).** LIP Phase by number of traumas per crania.

E. Discussion and Conclusion

The result of these analyses clearly show evidence for internecine warfare in the Nasca highlands during the LIP. More than one-in-ten individuals could expect to die violently, while 25% experienced a life-threatening violent encounter. Thirty eight percent of the population sustained an injury that resulted in the fracture of cranial bone, which, even if well-healed has been shown to increase mortality risk throughout an individual's life (Boldsen et al. 2014). Females (especially adolescents and young adults), children, and older adults were routinely the victims of lethal violence. Indeed, rates of peri-mortem trauma are higher among traditional non-combatants compared to those who typically make up the combatant profile. The majority of lethal encounters resulted in peri-mortem traumas to the posterior of the skull, suggesting victims were either ambushed from behind or were attempting to flee an assailant. While the locations of healed traumas were more evenly distributed on the skull, nearly half of the sample of individuals with multiple ante-mortem traumas had injuries on the posterior of the skull, suggesting the many non-lethal violent encounters were perpetrated from behind. Half of the individuals with peri-mortem trauma were killed in such a way that much of the skull was largely destroyed (overkill trauma)—a pattern most typically observed with intense, intergroup warfare (Kurin 2012).

The lack of any relationship between cranial modification and trauma, along with the non-significant difference in peri-mortem trauma between the sexes suggests an absence of systemic lethal violence towards individuals based on personal identity or sex. Instead, the distribution of victims suggests a pattern of social substitutability (Kelly 2000), whereby any and all individuals belonging to an enemy group were viable targets for lethal violence (Durrant 2011; Kelly 2000). These results, along with the non-clustered distribution of ante-mortem

traumas reject the possibility that the observed patterns of violence are the result of intra-group violence.

Despite the absence of systematic violence towards sub-groups, results do reveal heterogeneity in the risk of violence. Adolescents and young adults exhibit excess mortality due to significantly higher levels of lethal trauma. This may be partially due to the participation of these age-groups in warfare, where the risk of immediate mortality can be high. Nonetheless, our measures of violence significantly positively co-vary with pathology, suggesting that those with pathological lesions were at greater risk of violent mortality. This is likely the result of 1) individuals experiencing food stress were more likely to participate in violent conflict (see, Chapter three), and 2) individuals experiencing dietary stress are more likely to conduct dangerous subsistence activities that put them at a high risk of violent mortality (see, Chapter four).

Ante-mortem and the average number of traumas per individual follow the opposite trend as peri-mortem trauma, increasing significantly with age. The trend towards greater proportions of ante-mortem trauma with age may simply be the result of the “law of averages,” whereby longer-lived individuals have a higher summed probability of violent encounters (Glencross 2003, 2011). During what phase in one’s life history these traumas were obtained however cannot be determined. The increase in the average number of traumas with age may suggest trauma recidivism, as individuals accumulate the traumatic scars of multiple violent events over one’s lifetime. Younger individuals exhibit less healed traumas and a reduced number of osseous wounds simply because their truncated lifespans did not allow for multiple violent events to be experienced.

Non-lethal violence shows sex-based heterogeneity in risk. Males were significantly more likely to be involved in non-lethal encounters and experience non-lethal recidivism, suggesting either a) organized forms of interpersonal violence that only rarely involved lethality (i.e. ritual conflict), and/or b) males were better able to survive the heinous blunt-force injuries that occurred so frequently due to lower rates of physiological stress (see, Chapter two). Indeed, where the proportion of healed to lethal trauma substantially deviate, as they do between the sexes in our sample, it is likely that this deviation is not the result of differences in violence with lethal intent, but rather a discrepancy in the ability of individuals to survive blunt force trauma long enough for healing to occur. If males were even slightly better able to survive critical trauma, the result would be a greater relative proportion of males in the ante-mortem category even if they eventually died as a result of injury-related complications.

The diachronic trends in violence presented here strongly indicate internecine warfare throughout the LIP, with even the lowest proportion of peri-mortem conflict remaining at 8%. Nevertheless, all forms of trauma change substantially throughout the three LIP Phases. Peri-mortem, critical, and overkill trauma all rise significantly from the preceding MH sample, which exhibits zero cases of each. During Phase II violence falls to its nadir. Nevertheless, each recorded case of critical trauma during this time was lethal, suggesting individuals who did receive life threatening violent injuries were not able to survive them long enough for the healing process to begin. During Phase III, all forms of violence reach their zenith, with critical trauma reaching nearly 40%. Finally, while it is tempting to infer causal connections at this time, testing the driving factors of warfare is beyond the scope of the current article and will be addressed in future research.

The recurrent targeting of non-combatants for lethal aggression along with the clear evidence that most victims were attempting to escape a violent confrontation matches closely with observed patterns of internecine warfare in small-scale societies (Arkush and Tung 2013; Keeley 1996; Milner et al. 1991; Tung 2007; Walker 2002). Indeed, small-scale warfare most often involves ambush and raids on unsuspecting individuals rather than organized battles and assaults on fortified centers (Arkush and Tung 2013; Burch 2007; Gat 2015; Keeley 1996; Kelly 2000, 2005; Heider 1979; Bishop and Lytwyn 2007; Milner 1999; Roscoe 1996; Walker and Bailey 2013; Wrangham and Galowacki 2012). The result is high casualty rates among non-combatants, and a majority of killings perpetrated against individuals conducting everyday activities rather than combatants seeking out a violent encounter. This kind of conflict is the most vicious and impactful, with the risk of violence interrupting everyday activities and often leading to profound changes in social, political, and economic strategies (Heider 1979; Meggitt 1977; Milner et al. 1991; VanDerwarker and Wilson 2016). These results show that observed patterns of violence more closely conform to the internecine warfare hypothesis rather than the ritual conflict, intra-group violence, or intermittent raiding hypotheses.

The result presented here parallel finding from neighboring regions during the LIP. Evidence for chronic warfare has emerged from the Ayacucho (Tung 2008; Tung et al. 2016), Andahuaylas (Kurin 2012), Apurimac (Lofaro et al. 2018), and Cajamarca (Toohey 2009) regions, the Lake Titicaca Basin (Arkush 2008, 2011), Colca valley (Kohut 2016; Valasco 2018) and the San Pedro Atacama Desert (Torres-Rouff and Costa Junqueira 2006). Thus, the results presented here add to a growing body of LIP conflict research and provides additional datapoints to a growing consensus that the Andean LIP was a period of widespread conflict and strife.

Developing and testing hypotheses regarding differing forms of violence can reveal salient insights into the character of prehistoric conflict and elucidate variability in mortality risk. Differentiating between the types of conflict a population experienced is a critical first step in the development and testing of models to evaluate causes and effects. Warfare, the topic in which bioarchaeologists are typically most interested, has predictable osteological patterns that differ from intra-group violence, intermittent raiding, and ritual conflict. This research highlights variability in violent outcomes, which can facilitate subsequent research regarding why certain groups may have been targeted for violence, or what factors may have driven individuals to conduct high-risk wartime activities. By carefully examining patterns of violence and conducting formal quantitative tests, bioarchaeologists gain the ability to discern the types prehistoric violence, with the goal of building more robust causal hypotheses and stronger explanations of heterogeneity in mortality risk.

Table 1.5. Information on the valley, associated residential site, *chullpa* tomb number, unique cranial ID, Radiocarbon age BP, C:N ratio, and calibrated chronological ranges for each individual in our sub-sample of 124.

Valley	Site	Tomb	Unique ID	Radiocarbon Age BP	C:N	Cal Range AD 1SD	Phase
Aja	Ayaorcco	C1	Cr1	805	3.2	1233 - 1278	PII
Aja	Ayaorcco	C1	Cr2	645	3.2	1321 - 1395	PIII
Aja	Ayaorcco	C1	Cr3	692	3.2	1268 - 1385	PIII
Aja	Ayaorcco	C1	Cr5	787	3.2	1211 - 1277	PII
Aja	Ayaorcco	C1	Cr8	775	3.2	1271 - 1288	PII
Aja	Ayaorcco	C1	Cr10	765	3.2	1275 - 1290	PII
Aja	Ayaorcco	C1	Cr11	645	3.2	1321 - 1394	PIII
Aja	Ayaorcco	C1	Cr14	805	3.2	1231 - 1278	PII
Aja	Ayaorcco	C1	Cr15	830	3.3	1229 - 1266	PII
Aja	Ayaorcco	C1	Cr16	690	3.2	1300 - 1384	PIII
Aja	Ayaorcco	C1	Cr17	670	3.2	1275 - 1390	PIII
Aja	Ayaorcco	C1	Cr19	735	3.2	1283 - 1373	PIII
Aja	Ayaorcco	C1	Cr22	745	3.2	1278 - 1371	PIII

Aja	Ayaorcco	C1	Cr29	595	3.2	1397 - 1410	PIII
Aja	Ayaorcco	C1	Cr30	670	3.2	1309 - 1390	PIII
Aja	Ayaorcco	C2	Cr31	610	3.3	1330 - 1408	PIII
Aja	Ayaorcco	C2	Cr32	595	3.3	1395 - 1414	PIII
Aja	Ayaorcco	C2	Cr33	605	3.2	1330 - 1412	PIII
Aja	Ayaorcco	C2	Cr34	660	3.2	1317 - 1391	PIII
Aja	Ayaorcco	C2	Cr35	650	3.3	1321 - 1392	PIII
Aja	Ayaorcco	C2	Cr36	715	3.2	1291 - 1378	PIII
Aja	Ayaorcco	C2	Cr37	464	3.2	1415 - 1454	PIII
Aja	Ayaorcco	C2	Cr40	655	3.2	1319 - 1392	PIII
Aja	Ayaorcco	C2	Cr41	620	3.1	1325 - 1403	PIII
Aja	Ayaorcco	C2	Cr44	655	3.3	1320 - 1391	PIII
Aja	Ayaorcco	C2	Cr45	825	3.2	1230 - 1271	PII
Aja	Ayaorcco	C3	Cr49	820	3.3	1230 - 1271	PII
Aja	Ayaorcco	C3	Cr50	880	3.3	1186 - 1222	PII
Aja	Ayaorcco	C3	Cr52	721	3.2	1258 - 1296	PII
Aja	Ayaorcco	C3	Cr54	855	3.3	1214 - 1264	PII
Aja	Ayaorcco	C3	Cr55	785	3.1	1238 - 1287	PII
Aja	Ayaorcco	C3	Cr58	830	3.3	1229 - 1266	PII
Aja	Ayaorcco	C3	Cr63	685	3.3	1302 - 1385	PIII
Aja	Ayaorcco	C3	Cr65	865	3.3	1203 - 1262	PII
Aja	Ayaorcco	C3	Cr68	865	3.1	1203 - 1262	PII
Aja	Ayaorcco	C3	Cr69	895	3.2	1182 - 1216	PI
Aja	Ayaorcco	C3	Cr71	820	3.3	1230 - 1271	PII
Aja	Ayaorcco	C3	Cr73	902	3.2	1040 - 1206	PI
Aja	Ayaorcco	C3	Cr74	815	3.3	1130 - 1273	PII
Aja	Ayaorcco	C3	Cr76	970	3.3	1047 - 1155	PI
Aja	Ayaorcco	C4	Cr77	635	3.2	1256 - 1294	PII
Aja	Ayaorcco	C4	Cr79	920	3.2	1158 - 1200	PI
Aja	Ayaorcco	C4	Cr80	730	3.3	1285 - 1375	PIII
Aja	Ayaorcco	C4	Cr81	860	3.3	1211 - 1261	PII
Aja	Ayaorcco	C4	Cr82	865	3.3	1203 - 1262	PII
Aja	Ayaorcco	C4	Cr83	695	3.2	1299 - 1382	PIII
Tierras Blancas	Ayapata	C1	Cr84	616	3.2	1295 - 1399	PIII
Tierras Blancas	Ayapata	C1	Cr85	670	3.2	1309 - 1390	PIII
Tierras Blancas	Ayapata	C1	Cr86	673	3.2	1272 - 1391	PIII
Tierras Blancas	Ayapata	C1	Cr88	670	3.2	1311 - 1390	PIII
Tierras Blancas	Ayapata	C1	Cr89	660	3.3	1317 - 1391	PIII
Tierras Blancas	Ayapata	C1	Cr90	675	3.2	1304 - 1389	PIII

Tierras Blancas	Ayapata	C1	Cr91	665	3.3	1315 - 1391	PIII
Tierras Blancas	Ayapata	C1	Cr92	700	3.3	1297 - 1381	PIII
Tierras Blancas	Ayapata	C1	Cr93	710	3.3	1293 - 1379	PIII
Tierras Blancas	Ayapata	C1	Cr97	665	3.3	1315 - 1391	PIII
Tierras Blancas	Ayapata	C1	Cr98	735	3.1	1282 - 1375	PIII
Tierras Blancas	Ayapata	C1	Cr99	720	3.3	1288 - 1377	PIII
Tierras Blancas	Ayapata	C1	Cr102	640	3.3	1323 - 1395	PIII
Tierras Blancas	Ayapata	C1	Cr104	780	3.3	1269 - 1288	PII
Tierras Blancas	Ayapata	C2	Cr105	689	3.2	1266 - 1387	PIII
Tierras Blancas	Ayapata	C2	Cr110	705	3.2	1296 - 1379	PIII
Tierras Blancas	Ayapata	C2	Cr115	700	3.2	1297 - 1381	PIII
Tierras Blancas	Ayapata	C2	Cr117	624	3.2	1291 - 1398	PIII
Tierras Blancas	Ayapata	C2	Cr121	885	3.3	1185 - 1219	PI
Tierras Blancas	Ayapata	C2	Cr128	725	3.3	1286 - 1377	PIII
Tierras Blancas	Ayapata	C2	Cr133	660	3.3	1318 - 1390	PIII
Tierras Blancas	Ayapata	C2	Cr139	680	3.3	1303 - 1387	PIII
Tierras Blancas	Ayapata	C2	Cr140	790	3.3	1240 - 1284	PII
Tierras Blancas	Ayapata	C2	Cr142	685	3.2	1301 - 1386	PIII
Tierras Blancas	Ayapata	C2	Cr144	640	3.1	1322 - 1396	PIII
Tierras Blancas	Ayapata	C2	Cr145	650	3.2	1320 - 1393	PIII
Tierras Blancas	Ayapata	C2	Cr151	685	3.1	1301 - 1386	PIII
Tierras Blancas	Ayapata	C2	Cr156	760	3.1	1276 - 1292	PII
Tierras Blancas	Ayapata	C2	158A	780	3.6	1289 - 1377	PIII
Tierras Blancas	Ayapata	C2	158D	785	3.2	1269 - 1284	PII
Tierras Blancas	Ayapata	C2	158H	545	3.4	1416 - 1433	PIII
Tierras Blancas	Ayapata	C2	158J	585	3.6	1400 - 1414	PIII
Tierras Blancas	Ayapata	C2	158N	765	3.4	1277 - 1288	PII
Tierras Blancas	Ayapata	C3	Cr159	600	3.4	1393 - 1414	PIII
Tierras Blancas	Ayapata	C3	Cr160	634	3.2	1285 - 1398	PIII
Tierras Blancas	Ayapata	C3	Cr161	708	3.2	1262 - 1381	PIII
Tierras Blancas	Ayapata	C3	Cr162	655	3.3	1320 - 1391	PIII
Tierras Blancas	Ayapata	C3	Cr166	651	3.2	1279 - 1394	PIII
Tierras Blancas	Ayapata	C3	Cr170	555	3.2	1411 - 1428	PIII
Tierras Blancas	Ayapata	C3	Cr175	610	3.3	1328 - 1409	PIII
Tierras Blancas	Ayapata	C3	Cr178	685	3.1	1301 - 1386	PIII
Tierras Blancas	Ayapata	C3	Cr179	645	3.2	1321 - 1394	PIII
Tierras Blancas	Ayapata	C3	Cr181	650	3.1	1320 - 1393	PIII
Tierras Blancas	Ayapata	C3	Cr184	650	3.2	1320 - 1393	PIII
Tierras Blancas	Ayapata	C3	Cr194	560	3.2	1409 - 1426	PIII

Tierras Blancas	Ayapata	C3	Cr195	605	3.2	1393 - 1409	PIII
Tierras Blancas	Ayapata	C4	Cr199	700	3.4	1297 - 1381	PIII
Tierras Blancas	Ayapata	C4	Cr200	685	3.3	1301 - 1386	PIII
Tierras Blancas	Ayapata	C4	Cr202	558	3.2	1307 - 1430	PIII
Tierras Blancas	Ayapata	C4	Cr207	607	3.2	1297 - 1404	PIII
Tierras Blancas	Ayapata	C4	Cr208	665	3.3	1315 - 1391	PIII
Tierras Blancas	Ayapata	C4	Cr209	650	3.3	1320 - 1393	PIII
Tierras Blancas	Ayapata	C4	Cr212	595	3.6	1397 - 1410	PIII
Tierras Blancas	Ayapata	C4	Cr215	595	3.2	1397 - 1410	PIII
Tierras Blancas	Ayapata	C4	Cr217	670	3.6	1311 - 1390	PIII
Las Trancas	C. Tribolpata	C1	Cr222	1163	3.2	895 - 976	TMH
Las Trancas	C. Tribolpata	C1	Cr223	1115	3.3	980 - 1015	PI
Las Trancas	C. Tribolpata	C1	Cr224	1090	3.3	994 - 1015	PI
Las Trancas	C. Tribolpata	C1	Cr225	1130	3.3	905 - 991	TMH
Las Trancas	C. Tribolpata	C1	Cr226	1210	3.3	798 - 961	TMH
Las Trancas	C. Tribolpata	C1	Cr227	910	3.3	1163 - 1209	PI
Las Trancas	C. Tribolpata	C1	Cr228	830	3.4	1229 - 1265	PII
Las Trancas	C. Tribolpata	C1	Cr229	1115	3.2	980 - 1015	PI
Las Trancas	C. Tribolpata	C1	Cr230	1220	3.3	780 - 946	TMH
Las Trancas	C. Tribolpata	C2	Cr232	1100	3.3	990 - 1015	PI
Las Trancas	C. Tribolpata	C2	Cr233	935	3.2	1024 - 1163	PI
Las Trancas	C. Tribolpata	C2	Cr234	910	3.3	1164 - 1208	PI
Las Trancas	C. Tribolpata	C2	Cr235	895	3.3	1182 - 1216	PI
Las Trancas	C. Tribolpata	C2	Cr236	1145	3.3	900 - 987	TMH
Las Trancas	C. Tribolpata	C2	Cr237	865	3.3	1203 - 1262	PII
Las Trancas	C. Tribolpata	C3	Cr239	884	3.2	1044 - 1218	PI
Las Trancas	C. Tribolpata	C3	Cr240	945	3.2	1053 - 1181	PI
Las Trancas	C. Tribolpata	C3	Cr241	900	3.3	1179 - 1214	PI
Las Trancas	C. Tribolpata	C3	Cr242	1005	3.3	1032 - 1136	PI
Las Trancas	C. Tribolpata	C3	Cr245	930	4.4	1153 - 1188	PI
Las Trancas	C. Tribolpata	C3	Cr246	975	3.5	1046 - 1152	PI
Las Trancas	C. Tribolpata	C3	Cr247	925	3.3	1155 - 1199	PI
Las Trancas	C. Tribolpata	C3	Cr251	899	3.3	1039 - 1211	PI

II. Navigating the Osteological Paradox using a Multimethod Approach: A case study from Late Intermediate period (950 - 1450 C.E.) Nasca, Peru

A. Introduction

It has been nearly 30 years since the publication of the groundbreaking paper “The Osteological Paradox: problems of inferring prehistoric health from skeletal samples” (Wood et al. 1992). Wood and colleagues provided compelling arguments and statistical models demonstrating profound problems with the use of human skeletal samples to understand patterns of ancient health and disease. Since the 1992 publication there has been a concerted effort in bioarchaeology to generate solutions to the interpretive equifinality inherent in the osteological paradox (Boldsen, 1997, 2005, 2007; DeWitte 2010; DeWitte and Wood 2008; DeWitte and Bekvalac 2010, 2011; DeWitte and Hughes-Morey 2012; DeWitte et al. 2013; DeWitte and Stojanowski 2015; DeWitte and Yaussy 2017; Redfern and DeWitte 2011; Usher 2000; Wilson 2010, 2014; Wright and Yoder 2003). Despite the development of viable solutions and the clear overarching ramifications of the osteological paradox (henceforth, O.P.), much subsequent bioarchaeological research has failed to explicitly address its implications. Indeed, DeWitte and Stojanowski’s 2015 literature review showed that the majority of articles with paleopathological data cite the O.P., but rarely engage with it in a meaningful way. DeWitte and Stojanowski (2015) go on to advocate for more direct engagement with the paradox, echoing Wood and colleague’s warning that without addressing the implications of the O.P. we cannot infer accurate or meaningful interpretations from skeletal data. Clearly, additional bioarchaeological research is needed that explicitly focuses on the issues of the O.P. in various prehistoric contexts.

To this end, we use recent advances in bioarchaeological methods to evaluate patterns of disease, mortality, and longevity in the Prehispanic Nasca highlands of Peru. Our goal is to

demonstrate how multiple analytical techniques can 1) reveal population-level morbidity and mortality patterns, 2) highlight salient heterogeneity in frailty, and 3) propose possible sources of heterogeneity. Our focus will be to use mixed methods to explicitly engage with the three main issues of the O.P., namely demographic non-stationarity, hidden heterogeneity in frailty, and selective mortality. Our multimethod approach will include: 1) leveraging archaeological and temporal context, 2) measuring the frequency and severity of pathologies, 3) survivor versus non-survivor analysis, 4) hazard models, and 5) stable isotope biochemistry. These methods have proven successful for navigating the O.P. in previous research (DeWitte and Bekvalac 2010, 2011; DeWitte and Hughes-Morey 2012; DeWitte et al. 2013; Wilson 2010, 2014; Wright and Yoder 2003) but are rarely used in-concert. Thus, the analysis presented here will be novel in its broad scope.

B. The Osteological Paradox

The osteological paradox has been discussed in-detail in multiple excellent publications (e.g. DeWitte and Stojanowski 2015; Milner et al. 2008; Wood et al. 1992; Wright and Yoder 2003). As the purpose of this article is to engage with the O.P. rather than rehash the arguments and counterarguments since its original publication, we will only provide a brief recitation of the O.P.'s three main issues: demographic nonstationarity, hidden heterogeneity in frailty, and selective mortality.

1. Demographic Non-stationarity

A population is non-stationary when it experiences growth or decline as a result of changes in mortality, fertility, or migration. Traditionally, bioarchaeologists have assumed that populations under study are demographically stationary (Milner et al. 2008). Stationary

populations are useful because life tables can be calculated using age-at-death profiles, which are assumed to reflect life tables calculated from contemporary populations. Life tables have long been the primary means by which demographers assess changes in a population's average life expectancy and age-specific mortality. Today we know that most populations are nonstationary, which can potentially undermine traditional interpretations drawn from life tables of skeletal samples (Milner et al. 2008). Most significantly, life expectancies can vary substantially with changes in total fertility rates (TFR), even when mortality remains constant (DeWitte and Stojanowski 2015; Milner et al. 2008; Paine 1989; Sattenspiel and Harpending 1983). Further, immigration events or pulses can alter population-level life expectancy, even when the original population does not experience changes in fertility, mortality, or morbidity. The result is a need to assess in-migration and changes in growth caused by fluctuations in TFR.

2. Hidden Heterogeneity in Frailty

A population is heterogeneous in fragility simply when susceptibilities to disease and death vary between individuals or subgroups within the population. Heterogeneity is "hidden" when inter-individual variation in the risk of death is not, or cannot, be determined (Wood et al. 1992). Thus, while a population may experience greater mortality, or a heavier disease load, not everyone will be equally vulnerable to sickness and death. Heterogeneity in frailty results from a mosaic of sources including phenotypic quality, differences in environmental productivity, social norms, structural inequality, and so forth (DeWitte and Stojanowski 2015). When aggregate markers of disease are calculated for a population the resulting data will potentially mask intra-population variability. If unaccounted for, bioarchaeologists will struggle to assess within group differences in health and disease or to compare different populations.

3. Selective Mortality

As an outgrowth of heterogeneity in frailty, mortality is selective. Frail individuals are, by definition, at a higher probability of dying than more robust members of their age-cohort. Individuals who die at a certain age are thus unlikely to be representative of the living population that was at *risk* of death during that life phase (Wood et al. 1992). As a result, cemetery age-cohorts contain only the frailest individuals in the osteological record and are not representative of experiences in the source population. In addition, most diseases do not result in skeletal changes, but even when experiencing stressors that result in skeletal indicators, the frailest members of a population may die before the body can mount an osseous response (Wood et al. 1992). Subsequently, individual skeletons without any obvious markers of disease may reflect a) the frailest members of the population, or b) the most robust members. Further, as population health increases members that would have previously died quickly from a stressor may now live long enough for an osseous response to occur. The result of extended longevity may be an increase in the proportion of the population with skeletal markers of disease—exactly the pattern traditionally used to infer *declining* population health.

Together, these three issues present substantial obstacles to the reconstruction of basic health and demographic data and require a multimethod approach to address each concern independently. In the following sections we present our strategy for coping with the concerns raised in the O.P. and show viable ways of navigating these important issues.

C. Materials and Methods

1. Case Study: The Nasca Highlands

The Nasca highlands is a remote, highly bounded region roughly 30km east and over 3,000 meters above of the modern city of Nasca, Peru (Figure 2.1). Straddling the coastal and

sierra environments, the Nasca highland region is the definition of ecological circumscription. The region contains five steep, fast flowing river valleys each with a well-defined area of open terrain with sufficiently flat topography to permit the construction of terraces and canals that are necessary for agriculture. All currently known Late Intermediate Period (LIP, 950 – 1450 C.E.) residential sites are located within, or immediately adjacent to, these arable patches. The surrounding “*Puna*” high grasslands are suitable for herding but cannot be intensively farmed due to inadequate precipitation and water for irrigation. McCool (2017) recorded 19 LIP settlements with associated cemeteries located throughout all five valleys. Each settlement was permanently occupied as evidenced by dense housing clusters and middens along with the total lack of households outside of settlement centers. Settlements are located on difficult to access hilltops, mesa-tops or along steep ridgelines, and exhibit multiple lines of fortification features (McCool 2017).

Either within or, more often, immediately adjacent to the hillforts are cemeteries consisting of several dozen to several hundred artificially constructed tombs known in Quechua as “*chullpas*.” These tombs vary substantially in terms of size and consist of both conical and square construction styles. The tombs contain up to several dozen individuals along with associated mortuary goods. Each interred individual was at one time placed as a desiccated bundle wrapped in a cotton death shroud and placed upright in tight clusters on the ground surface. Subsequent taphonomic processes and substantial looting have disarticulated and commingled these remains.

To establish baseline patterns and variability in morbidity and mortality, we compare LIP data with osteological analyses of 97 Middle Horizon (MH, 500 – 950 C.E.) crania recovered from tombs in the Nasca lowlands to the west of the Nasca highlands (Kellner 2002). This

comparative sample is used because it immediately predates the LIP and represents the only discernable residential population in the general Nasca region during the MH. Further, due to the low levels of pathology, exogenous stressors, and mortality factors (Kellner 2002) this sample can serve as a baseline against which LIP data can be evaluated (Table 2.1). Existing MH data also permit the generation of hazard models to compare mortality profiles to the LIP sample.

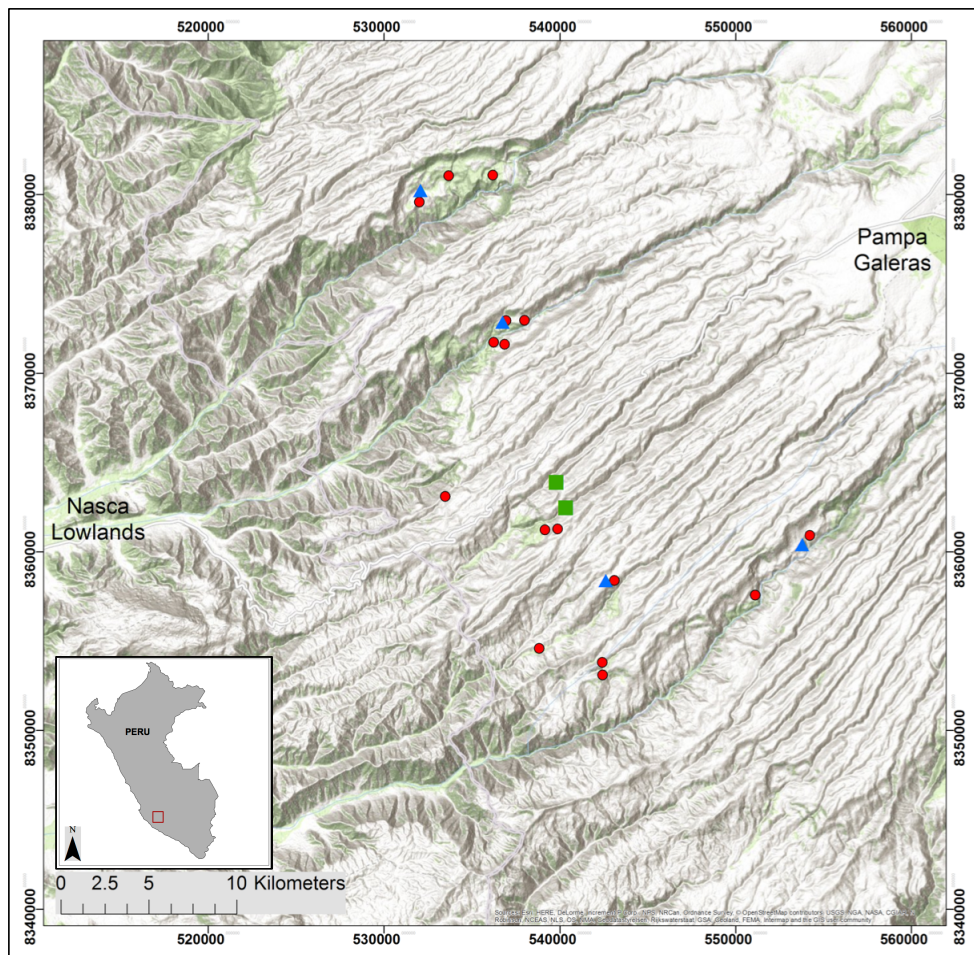


Figure 2.1. Map of the Nasca highlands. Points = LIP residential sites, triangles = *chullpa* cemeteries, squares = *machay* cavern tombs.

2. Human Skeletal Sample

Eleven tombs were completely excavated in the fall of 2018 for the purpose of obtaining a large human skeletal sample to test hypotheses concerning conflict and disease during the LIP.

The field project produced a sample of 325 individuals as determined by the number of crania. Of the 325 crania, all were evaluated for age-estimation and the presence and severity of cribra orbitalia. A subsample of 270 crania were sufficiently intact to permit the analysis of biological profiles, trauma, and pathology (cribra orbitalia and porotic hyperostosis). Due to the commingled nature of the skeletal assemblage, post-cranial elements could not be paired with cranial elements for osteological analyses. This kind of comingling is a common pattern in prehispanic Andean burials, and it has been shown that crania produce accurate information on patterns of violence and disease (e.g. Kurin 2012; Martin and Harrod 2014; Torres-Rouff and Costa Junqueira 2005).

The human skeletal sample was dated using associated ceramic and tombs styles and settlements patterns (McCool 2017) along with 124 radiocarbon dates obtained directly from the crania (discussed below).

3. Biological Profiles and Demography

Sex was estimated using sexually dimorphic nonmetric cranial features as per the standards protocols (Buikstra and Ubelaker 1994). Age-at-death estimations were based on established protocols (Buikstra and Ubelaker 1994) using stages of cranial suture closure, dental formation/eruption, and surface wear to estimate age (Bass 2005; Buikstra and Ubelaker 1994; Murphy et al. 2010; Vercellotti et al. 2014; White and Folkens 2005). Age cohorts were divided as per White and Folkens (2005) into infant (0 – 4), child (4 – 12), adolescent (12 – 20), young adult (20 – 35), middle adult (35 – 50), and old adult (50+). While more recent age-estimation methods, such as transition analysis (Baldsen et al. 2002), have proven to be more accurate and precise in estimating age-at-death, these methods require paired cranial and postcranial elements. Due to past mortuary practices, taphonomy, and looting the skeletal assemblage has commingled

to the point that pairing cranial and postcranial remains is not possible. While this context ensures less precise and accurate age-at-death estimations, it is nonetheless broadly representative of many of the available cemetery contexts in the Andes, and largely defines the typical cemetery for the LIP. Thus, in this case, the standards method (Buikstra and Ubelaker 1994) is the appropriate tool.

Figure 2.2 shows the demography of the sample. With the exception of low frequencies of infants, likely due to taphonomic processes, and the low proportion of old adults, the LIP sample exhibits a quasi-normal population distribution, with several interesting non-normative deviations (discussed below).

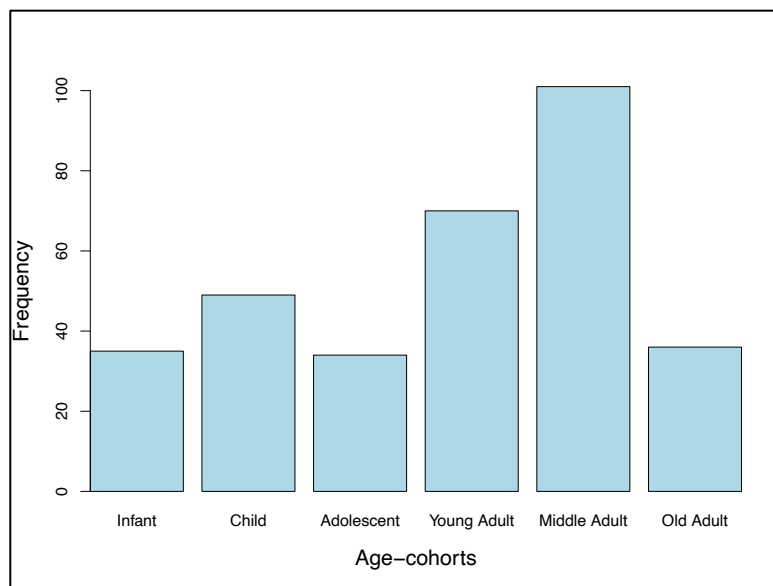


Figure 2.2. The demographic structure of the LIP human skeletal sample (n = 325).

4. Leveraging Archaeological Context

Wood et al. (1992) suggest that archaeological context may help navigate issues relating to the O.P. Specifically, they recommend that osteological analyses focus on small-scale, egalitarian societies. The rationale is that more complex societies have sociopolitical institutions that promote and maintain inequality, thereby exacerbating heterogeneity in frailty and risk of

death. Wood et al. suggest that small-scale societies are more likely to exhibit equality in health and disease susceptibility, thereby leveling the strength of selection. Further, Wood et al. and subsequent researchers have advocated for leveraging data on social, political, and environmental conditions that influence population health (DeWitte and Stojanowski 2015; Milner et al. 2008). Reconstructing the sociopolitical and ecological conditions a population experienced can reveal patterns of violence, dietary strategies, inequalities, and much more. Understanding these conditions can aid in the determination of population stress, living conditions, and attendant health benefits—all of which should figure into paleopathological interpretations.

5. Diachronic Evaluation

To evaluate diachronic trends in morbidity, mortality, and longevity AMS radiocarbon dates were obtained for 124 crania distributed throughout the eleven excavated tombs. Samples of cranial bone were taken from the vomer and nasal concha when possible or the nasals/styloid process when necessary. In several cases, none of these elements were available, requiring the zygomatic arch to be sampled. Bone collagen for ^{14}C measurement and stable isotope chemistry was extracted and purified using the modified Longin method with ultrafiltration at Pennsylvania State University and the University of California following protocols of the Pennsylvania State Carbon Cycle AMS Facility (Kennett et al. 2017) and run on the University of California, Irvine Keck Carbon Cycle AMS facility (UCI KCCAMS 2007) where the AMS ^{14}C measurement was conducted (isotope protocols are outlined in detail in Chapter Four). Results were calibrated using the rcarbon package in the R programming environment (Bevan and Crema 2019) with the SHCal13 calibration curve (Hogg et al. 2013). The resulting chronology spans the terminal MH

and the entire LIP (see, Chapter one), permitting an analysis of diachronic changes in morbidity and mortality throughout the entire study period.

Of the 124 individuals dated, 119 date to within the LIP and were used for the present study. The dated subsample of LIP crania was divided into three temporal phases. Phase I (950 – 1200 C.E., PI) represents the transition into the LIP. Phase II (1200 – 1300 C.E., PII) represents the middle LIP and a period of extreme drought (Schitteck et al. 2015). Phase III (1300 – 1450 C.E., PIII) represents the final phase of the LIP and a period of abundant and predictable rainfall and population increase (Chapter four). The variable duration of each phase is necessary to (1) maximize intra-period temporal resolution without decreasing sample sizes such that statistical tests are unreliable, and (2) align temporal phases with important environmental and demographic transitions to facilitate future research on the causes of conflict. Individuals whose calibrated ^{14}C range overlaps multiple phases were binned into the phase that contains the majority of the 1SD range. For example, a cranium with a calibrated ^{14}C range of 1175 – 1300 C.E. was binned in PII (1200 – 1300, C.E.), as 100 years of the ^{14}C range fall into the PII interval while only 25 years fall into PI.

6. Frequency and Severity of Skeletal Stress Indicators

Evidence of porous lesions in the orbits (cribra orbitalia) and cranial vault (porotic hyperostosis) were identified by direct macroscopic observation and examination under low magnification ($\times 10$). Cribra orbitalia and porotic hyperostosis were recorded using Buikstra and Ubelaker Standards (1994) in order to facilitate comparison of LIP lesion frequency to previously reported lesion frequency for Middle Horizon burials (Kellner 2002). Lesions were recorded as present even if unilateral, though side was noted in unilateral cases. Lesion activity status at time of death was determined based on criteria laid out by Mensforth et al. (1978), and

lesion expression was recorded using the Standards ordinal index (0 – 3). Each cranium was photo documented to facilitate independent validation of pathological findings by other researchers. We believe the frequency and severity data can complement each other in revealing salient information on individual and aggregate patterns of pathology.

7. Survivor versus non-Survivor Analysis

Wood et al. (1992) and more recent publications (DeWitte and Stojanowski 2015; Wright and Yoder 2003) note the ability of age-structured analysis to compare changes in lesion frequencies throughout aggregate life histories. Survivor versus non-survivor analysis compares individuals who survived their early life phases to those who died during childhood. By assessing rates of pathology between the frailest individuals who died during early childhood to those who survived to older ages we can reveal how the frequency and severity of pathological lesions varies by frailty. If lesions are highest among the non-survivor age-cohort and lowest among the older cohorts, it shows that the frequency of lesions positively co-varies with frailty, rather than longevity. If older cohorts exhibit higher lesion frequency it shows that porous cranial lesions reveal robusticity and resilience rather than susceptibility to illness.

8. Hazard Models

Hazard models can compare a broad suite of demographic phenomena on a population level. Hazard models that exclude subadults have been shown to effectively track both age-dependent and age-independent adult mortality within and between populations (Dewitte et al. 2013; Wilson 2010, 2014). Analyses that include subadults in the models can crudely track changes in fertility, as long as subadults are well represented in skeletal series (Buikstra et al. 1986; Milner et al. 2008; Paine 1989). Various researchers have incorporated hazard models into investigations that analyze health and demographic changes during key cultural transitions

(Wilson 2010), and to assess associations between stature, skeletal stress, mortality, and status within populations (Boldsen et al. 2015; DeWitte et al. 2013; Redfern and DeWitte 2011). To evaluate changes in mortality and longevity, hazard models were generated using the mortAAR package in the R environment (Müller-Scheeßel and Hinz 2017). The mortAAR package generates standard life tables using age-at-death estimation intervals that follow an equidivisional approach (called “proportional” by Boldsen 1988). Each year of an individual’s age interval is assigned the same value, essentially the same probability of being the true age. Following modern life table methods, the mortAAR package uses 5 year-classes, except for the youngest age-cohort of individuals <1 year. The mortAAR package also plots the relevant indices using five graphics: proportion of deaths, probability of death, survivorship, life expectancy, and population age structure. To create age-estimation intervals amenable to mortAAR hazard models we transformed our age-cohort intervals so that they do not have any overlapping members. Thus, age-intervals were re-classified to infant (1 – 4), child (5 – 12), adolescent (13 – 20), young adult (21 – 35), middle adult (36 – 50), and old adults (51 – 70), with 70 being the hypothetical cut off point specified in the model.

9. Stable Isotope Chemistry

Reconstructing past diet and population movement can reveal much about variability in nutritional intake, dietary diversity, mobility patterns, status, and migration (Finucane et al. 2006; Somerville et al. 2013). Stable $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope chemistry can reveal hidden heterogeneity by providing data on individual plant diet and protein intake. Populations with homogeneous diets may be less likely to exhibit heterogeneity in frailty than those with pronounced dietary differences. Individuals with stable carbon signatures that indicate a very monotonous plant diet may have poor nutritional health when compared to individuals who eat a

wider variety of plant foods. Those with depleted ^{15}N values may have had less access to meat or protein-rich plant foods relative to individuals with enriched nitrogen signatures.

Here, we assess stable $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in bone collagen and carbonates. We assess changes in diet from the MH to the LIP and within the three LIP Phases. We evaluate diet as it varies by sex, morbidity and mortality. Results will indicate whether average dietary patterns explain changes in population-level morbidity and mortality, as well as heterogeneity in frailty and the risk of death.

D. Results

When appropriate, descriptive and inferential statistical results are listed in tables below each paragraph. All statistics were conducted in the R environment.

1. Archaeological Context – Socioenvironmental Conditions

Archaeological context allows us to evaluate whether we should expect 1) heterogeneity in frailty as a result of social inequality, and 2) social and environmental conditions to have promoted good health or elevated stress. To assess archaeological markers of inequality, village sites, residential zones, and fortification features were mapped and assessed (McCool 2017). No discernable differences were apparent in the basic construction methods and quality between households. While household size varies, the difference is not substantial. There is little discernable variation in the basic layout, construction methods, or architectural quality both within and between sites. In addition, there is little difference in the mortuary treatment of bodies as they were all laid in a similar manner in tombs that display only subdued differences in the overall construction quality. Differential mortuary treatment in the form of grave goods however cannot be assessed due to the history of looting. These patterns may suggest a more egalitarian political

order in which hierarchies are either not maintained or lack obvious material signatures. Indeed, the LIP is largely characterized as a time of subdued or absent social hierarchies (Covey 2008; Parson and Hastings 1988; Toohey 2009). Thus, the most current research indicates that the LIP Nasca highland population was a small-scale society lacking pronounced manifestations of institutionalized inequalities.

The LIP Nasca highlands was also a context of chronic, internecine warfare (McCool 2017; Chapter one). Previous osteological research demonstrated a significant increase in ante-mortem and peri-mortem trauma as well trauma recidivism from the preceding Middle Horizon (Chapter one). Indeed, the peri-mortem trauma rates (13.1%) match the lethal violence rates of several ethnographically studied populations (Yanomamo 13%, and Mae Enga 15%; Keeley 1996) who were experiencing chronic warfare when casualty statistics were compiled. The LIP population itself was confined to inaccessible hilltop fortresses with multiple fortification features within which were dense clusters of houses (McCool 2017).

Paleoenvironmental research in the area has revealed patterns of pronounced climatic volatility. Palynological analysis of a Cerro Llamoca peatland core located approximately 30 km northeast of the Nasca highlands tracked the abundance of *Poaceae* pollen through time (Schitteck et al. 2015). The abundance of *Poaceae* is heavily influenced by the amount and variability of precipitation, and it thus an excellent climate proxy. These data show that *Poaceae* percentages fell to their lowest value at the onset of the LIP circa 950 C.E. revealing increasing stochasticity in precipitation regimes and an “extreme drought” event that persisted until 1225 C.E., at which time precipitation recovered (see, Chapter Three; Schitteck et al. 2015:207). These environmental perturbations reduced the flows of the rain-driven highland rivers, which are responsible for delivering the critical irrigation water to the terrace farm systems (McCool 2017;

Schittek et al. 2015; Sossna 2014). The pronounced drought conditions would have likely produced elevated population stress.

To summarize, the high rates of violence, increasing travel costs associated with inaccessible residential sites, unsanitary living conditions, and poor environmental productivity regimes are all likely to increase dietary stress and elevate general mortality. Further, the lack of obvious signs of hierarchy suggests subdued inequality, which may result in a lack of heterogeneity in frailty. Nevertheless, these data can solely provide expectations that must be empirically tested. The following sections will evaluate how well these predictions fit our bioarchaeological data.

2. Frequency and Severity of Skeletal Stress Indicators

The percentage of orbital lesions increases significantly from the MH to the LIP ($p = 0.008$), as does the prevalence of more extreme expressions of orbital lesions ($p = 0.034$). The percentage of vault lesions increases significantly from the MH to the LIP ($p = 0.000$), as does the severity of porous vault lesions ($p = 0.021$).

The frequency and severity of orbital and vault lesions also vary by sex, with females exhibiting a significantly higher frequency of cribra orbitalia ($p = 0.029$) and trending towards significantly higher severity ($p = 0.053$). The frequency of porotic hyperostosis does not differ significantly by sex ($p = 0.331$), although severity is significantly higher in *males* relative to females ($p = 0.039$). To further explore sex-based differences in morbidity we combined cribra orbitalia and porotic hyperostosis into a single “pathology” frequency measure that can assess general levels of morbidity. Results show greater sex-based parity with 33.9% of females and 31.5% of males exhibiting pathology, and a trending but non-significant difference in pathological frequency ($p = 0.123$).

It is important to note here that cribra orbitalia and porotic hyperostosis are pathogenic processes that occur during early development (Walker et al. 2009). As such, we will need to show that these pathologies have an impact on adult mortality if we are to connect exposure to stress during early development with downstream health conditions in adults. The link between childhood disease and adult health is evaluated in the hazard modeling section below.

Table 2.1. Statistical results for Morbidity by Period and Sex.

Morbidity over Time	MH (Freq.)	MH	LIP (Freq.)	LIP	Results
Cribra Orbitalia (Freq.)	8/92	8.20%	68/315	21.60%	$\chi^2 = 6.97, p = 0.008$
Cribra Orbitalia (Severity)		0.15		0.30	1-sided $t = -1.841, p = 0.034$
Porotic Hyperostosis (Freq.)	5/98	5.20%	55/257	21.30%	$\chi^2 = 11.987, p = 0.000$
Porotic Hyperostosis (Severity)		0.12		0.23	1-sided $t = -2.052, p = 0.021$
Morbidity by Sex	Male (Freq.)	Male	Female (Freq.)	Female	Results
Cribra Orbitalia (Freq.)	7/94	7.50%	21/111	18.90%	$\chi^2 = 4.749, p = 0.029$
Cribra Orbitalia (Severity)		0.30		0.10	1-sided $t = 1.859, p = 0.053$
Porotic Hyperostosis (Freq.)	23/92	25.00%	20/109	18.30%	$\chi^2 = 0.947, p = 0.3305$
Porotic Hyperostosis (Severity)		0.19		0.25	1-sided $t = 2.219, p = 0.039$
Pathology (Freq.)	28/89		37/109		$\chi^2 = 4.189, p = 0.123$

3. Survivors versus non-survivors

Non-survivors are those that died during infancy/childhood (0 – 12) and thus represent the frailest members of the skeletal sample. Survivors are those who survived this especially risky period and are characterized as all individuals 13 years and older. For the first analysis we are restricted to measures of orbital lesions, as the majority of infant crania in our sample were not sufficiently intact to measure vault lesions. We tested whether the frequency and severity of orbital lesions were significantly different between the two-aggregate age-cohorts. Results show that non-survivors exhibit a significantly higher proportion of orbital lesions ($p = 0.000$), and more severe orbital lesions ($p = 0.001$) compared to the survivor cohort. Further analysis shows that adolescents and young adults (13 – 35 years) when aggregated into a single age-cohort and compared against an aggregate age-cohort of middle and old adults (36 – 50+ years) have significantly higher proportions ($p = 0.000$) and greater severity ($p = 0.000$) of orbital lesions and

cranial vault lesions (freq. $p = 0.009$; severity $p = 0.005$). Lastly, an ANOVA and Tukey HSD pair-wise effect size test of the severity of orbital lesions among all age-cohorts shows a trending but non-significant difference ($p = 0.093$) between infants and children, suggesting that the frailest infants in this population died after experiencing a stressor before the development of skeletal lesions.

Table 2.2. Results of survivor vs. non-survivor analysis. The first two rows show the non-survivor aggregate cohort ages 0 – 12 compared to the survivor aggregate cohort ages 13 – 50+. The third through sixth rows show the non-survivor aggregate cohort of ages 13 – 35 compared to the survivor aggregate cohort ages 35 – 50+.

Morbidity by Frailty	Survivor (Freq.)	Survivor	Non-Survivor (Freq.)	Non-Survivor	Results
Cribra Orbitalia (Freq)	35/236	14.80%	33/79	41.80%	$\chi^2 = 23.813, p = 0.000$
Cribra Orbitalia (Severity)		0.22		0.51	1-sided $t = -3.366, p = 0.001$
Cribra Orbitalia (Freq)	11/131	8.40%	21/101	20.80%	$\chi^2 = 6.363, p = 0.012$
Cribra Orbitalia (Severity)		0.12		0.31	2-sided $t = 2.444, p = 0.016$
Porotic Hyperostosis (Freq)	20/131	15.30%	30/98	30.60%	$\chi^2 = 6.861, p = 0.009$
Porotic Hyperostosis (Severity)		0.15		0.33	2-sided $t = 2.865, p = 0.005$
		Infants		Children	
Cribra Orbitalia (Severity)		0.34		0.69	Tukey HSD $p = 0.093$

4. Hazard Models

Hazard models were generated for the LIP sample to assess differences in mortality over time and by sex and pathology. In order to generate accurate life tables for subadults, individuals with indeterminate sex >20 years old were removed from the sample before the models were run.

Several patterns are evident in the sex-based models (Figure 2.9). During the LIP the proportion of male deaths peaks at 40 years and exhibits the lowest values at old and young ages. The female sample peaks much earlier, around 15, with another smaller peak around 27 years. Subadults, unsurprisingly, peak very early around 5 years. The probability of death (q_x) is highest for subadults, with the surprising result that q_x is substantially higher for females throughout adult life history. This is also reflected in life expectancy at birth (e_0) which is 31 for females and 41 for males. Indeed, a Wilcoxon signed-rank test shows that the median age-at-

death is significantly earlier for females relative to males ($W = 719.5, p = 0.000$). Overall, these models show that survivorship and life expectancy at birth is significantly lower for females.

Comparison of MH and LIP samples yield several interesting patterns (Figure 2.10). The proportion of deaths have similar peaks between the two samples, however the largest MH peak is 30 years, while the LIP sample exhibits roughly proportional peaks in the subadult years and young adult years. The most interesting mortality pattern is the crossover that occurs in the probability of death and survivorship curves. The probability of death is higher in the LIP sample until 20 years, at which time the MH curve exceeds that of the LIP. Survivorship is substantially lower in the LIP until 35 years, at which time MH adult mortality becomes slightly higher. Average life expectancy is lower in the LIP at $e_0 = 26.8$ compared to $e_0 = 30.7$ for the MH. Combined these models suggest that the LIP population had high mortality when compared to the MH during the first few decades of life, and lower adult mortality during the last few decades, illustrating substantial heterogeneity in frailty and a strong selective sweep in the LIP population. Nevertheless, previous research has shown that the standards methods of age-at-death estimation (Buikstra and Ubelaker 1994) become less accurate with age (Milner and Boldsen 2012). As such, we suggest that mortality patterns after the age of 40 can only provide tentative interpretations.

Health practitioners have long debated whether acute or chronic stress experienced during early development has an impact on adult health (Gillman 2005; Wadhwa et al. 2009). Recent clinical and field research on the developmental origins of health and disease (DOHaD) hypothesis have produced evidence showing that exposure to disease during early life is associated with negative downstream health outcomes in adulthood (Almond and Currie 2011; Barker 1994; Kuzawa and Sweet 2009; Worthman and Kuzara 2005). The question for the LIP

population is whether health insults during early development lead to increased age-specific mortality in adulthood. To answer this question, we generated hazard models for 1) the frequency and severity of cribra orbitalia for all ages, and 2) porotic hyperostosis for individuals 15 and older to assess the impacts of developmental diseases on adult mortality. Results show that the presence of both cribra orbitalia and porotic hyperostosis increase mortality across all ages, with severity acting as positive feedback (Figures 2.11, 2.12), except in the case of cribra orbitalia, where individuals with a severity index of one exhibit higher mortality than indices of two or three. These results show that individuals who experienced biological stress during early development have higher mortality across the life history. In addition, mortality positively covaries with pathological severity in most cases.

5. Stable Isotope Chemistry

Cranial bone samples were collected from 119 individuals for stable isotope chemistry. Stable $\delta^{13}\text{C}$ from bone collagen and carbonate along with $\delta^{15}\text{N}$ from bone collagen were analyzed. The results reveal striking homogeneity in diet within the LIP population, when assessed by sex, and over time (Figure 2.7). The average $\delta^{15}\text{N}$ value for the sample is 13.2‰ with a standard deviation (SD) of 0.94 across the three LIP phases. The average $\delta^{13}\text{C}$ for bone collagen is -13.48‰ with a SD of 1.01, and the average $\delta^{13}\text{C}$ for bone carbonates is -8.01‰, SD = 1.15. Within period homogeneity stands in contrast to the major differences between the MH and LIP. Nitrogen in particular increases significantly during the LIP, with an average increase of 4.4‰. Chapter four explores the reasons behind this substantial enrichment and suggests dietary stress and possible anthropophagy as the driving mechanisms.

Table 2.3. Stable isotope values by Period.

Stable Isotope Values	MH	LIP	Results
	Mean, SD	Mean, SD	
$\delta^{15}\text{N}$	8.8‰, 1.4	13.2‰, 0.94	1-sided $t = 17.249$, $p = 0.000$
$\delta^{13}\text{C}$ (bone collagen)	-13.1‰, 2.1	-13.5‰, 1.01	1-sided $t = -2.0223$, $p = 0.051$
$\delta^{13}\text{C}$ (bone carbonate)	NA	-8.01‰, 1.15	NA

Within the LIP, small SDs show that inter-individual variability in isotopic values throughout the LIP was within a single trophic level, suggesting a strong consistency in diet within the population and through time. Significant temporal changes do however occur. Mean $\delta^{15}\text{N}$ values change significantly from Phase II to Phase III ($p = 0.032$), however these changes occur within a single trophic level. Average $\delta^{13}\text{C}$ for bone carbonate is significantly depleted during Phase III compared to Phase I ($p = 0.017$) and Phase II ($p = 0.011$). Likewise, these changes remain within a single trophic level. There are no significant temporal changes in $\delta^{13}\text{C}$ from bone collagen. To summarize, average isotopic values significantly change through time but only within a relatively standardized diet.

Table 2.4. Stable Isotope values by LIP Phase.

Measure	Phase			Result
Stable Isotope Values	PI	PII	PIII	
$\delta^{15}\text{N}$	13.1‰	13.46‰	12.97‰	PII~PIII: $t = 1.898$, $p = 0.032$
$\delta^{13}\text{C}$ (bone collagen)	-13.43‰	-13.33‰	-13.53‰	No significant relationships
$\delta^{13}\text{C}$ (bone carbonate)	-7.67‰	-7.58‰	-8.28‰	PI~PII $t = 2.452$, $p = 0.017$; PII~PIII $t = 2.636$, $p = 0.011$

Significant differences emerge when diet is compared between sexes. Males have significantly enriched average $\delta^{15}\text{N}$ values compared to females ($p = 0.001$). Males also have significantly enriched $\delta^{13}\text{C}$ bone collagen ($p = 0.013$). There is a trending albeit non-significant difference in $\delta^{13}\text{C}$ carbonate ($p = 0.094$). These significant and trending differences in average isotopic values are all within single trophic levels.

Table 2.5. Stable isotope results by Sex.

Stable Isotope Values	Female	Male	Results
	Mean	Mean	
$\delta^{15}\text{N}$	12.99‰	13.55‰	1-sided $t = -3.247, p = 0.001$
$\delta^{13}\text{C}$ (bone collagen)	-13.69‰	-13.26‰	1-sided $t = -2.263, p = 0.013$
$\delta^{13}\text{C}$ (bone carbonate)	-8.21‰	-7.83‰	1-sided $t = -1.690, p = 0.094$

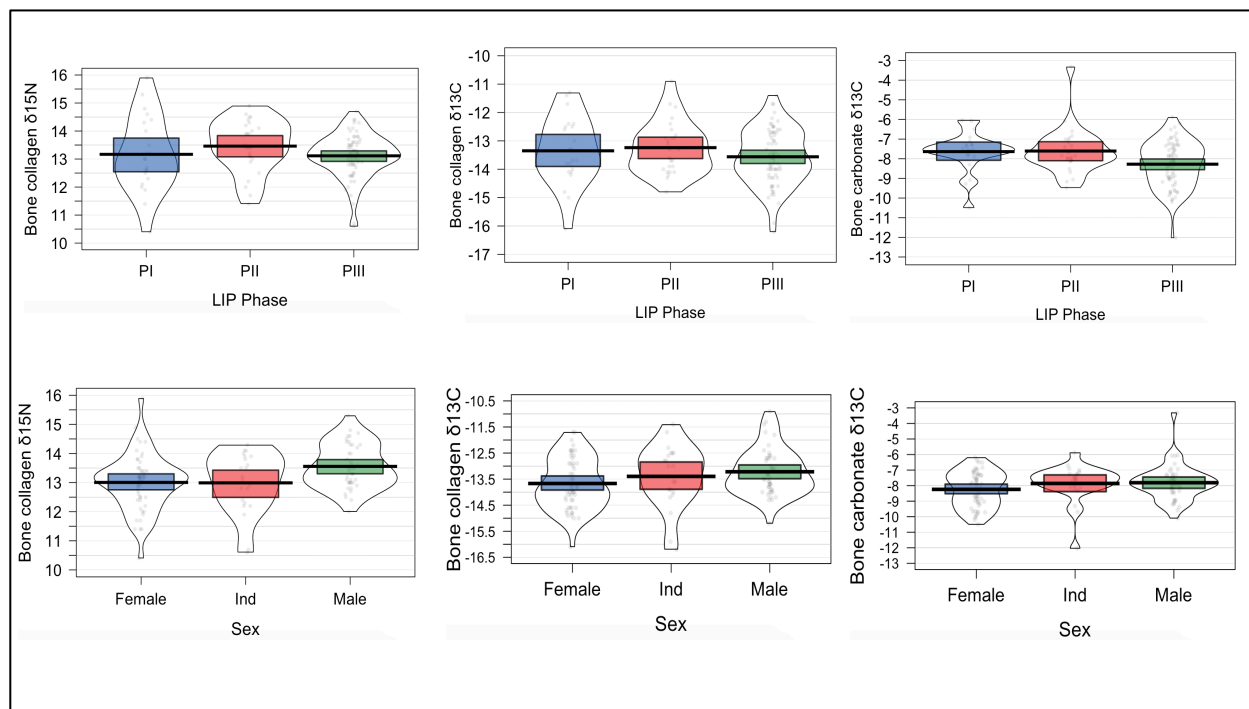


Figure 2.7. Stable isotope results show by sex and throughout the LIP temporal phases.

In order to measure the relationship between diet and morbidity, the pathology metric was used. Associations between stable isotope values and our pathology measure were determined using binomial General Linear Models (GLMs). There are no significant relationships between $\delta^{15}\text{N}$ and pathology ($p = 0.363$) or $\delta^{13}\text{C}$ bone collagen and pathology ($p = 0.212$). There is a trending, non-significant relationship between $\delta^{13}\text{C}$ carbonate and pathology ($p = 0.068$). Overall, results show a poor association between variability in diet and disease outcomes.

To assess the relationship between diet and frailty, we employ General Additive Models (GAMs) to test how stable isotope values vary with median age-at-death, with the expectation

that diets of frail individuals (early age-at-death) should differ from more robust members of the population. Results show that $\delta^{15}\text{N}$ values become significantly enriched with age ($F = 4.921, p = 0.03$, Figure 8). There is a non-significant relationship between $\delta^{13}\text{C}$ collagen ($F = 1.83, p = 0.115$) and carbonate ($F = 1.021, p = 0.405$), and median age-at-death, suggesting these isotopic measures do not reveal salient insights into changes in frailty and health during the life history.

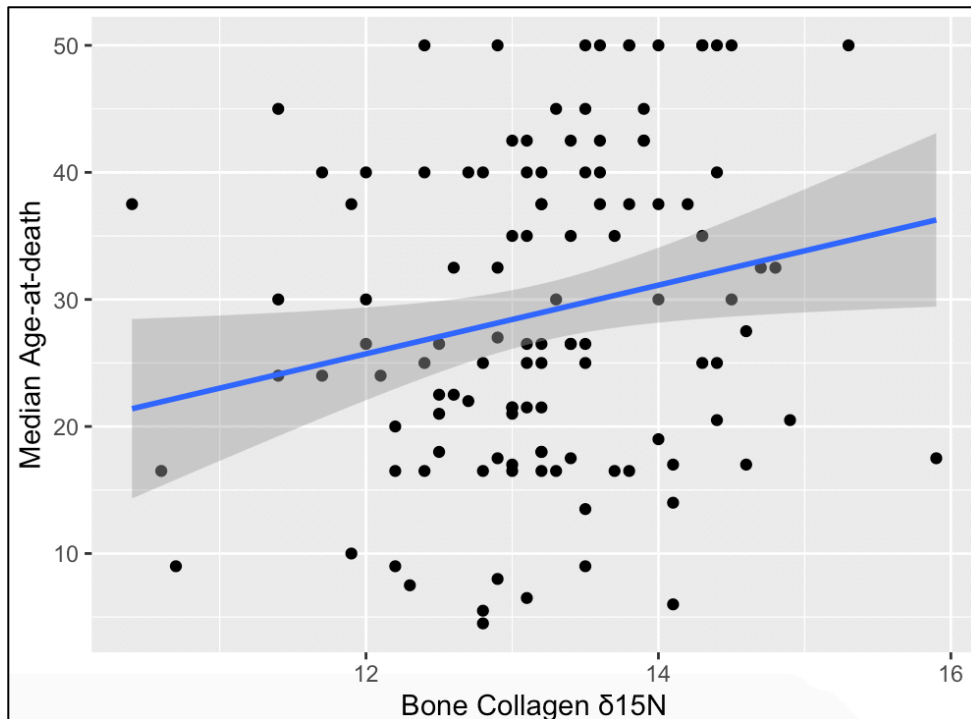


Figure 2.8. General Additive Model (GAM) comparing the $\delta^{15}\text{N}$ from bone collagen with median age-at-death. The model shows that higher $\delta^{15}\text{N}$ values predict later ages-at-death.

6. Diachronic Changes

Results show significant changes in morbidity and mortality. Cribra orbitalia increases to 10% at the onset of the LIP during Phase I, declines during Phase II to 3.8%, and significantly increases during Phase III to 22% ($p = 0.028$). Porotic hyperostosis rises to 22% in Phase I, increases to 25% in Phase II and reaches its peak in Phase III at 30%, although these changes are not significant. Severity patterns parallel frequency results, with cribra severity low in Phase II and higher in Phases I and III, and porotic severity increasing linearly through time.

Table 2.6. Morbidity by LIP Phase.

Morbidity	PI	PII	PIII	Results
Cribriform Orbitalia (Freq)	10%	3.80%	22%	PII~PIII Fisher's exact $p = 0.028$
Cribriform Orbitalia (Severity)	0.2	0.04	0.32	PII~PIII $t = -3.2, p = 0.002$
Porotic Hyperostosis (Freq)	22.20%	25%	30%	No significant differences
Porotic Hyperostosis (Severity)	0.22	0.25	0.31	No significant differences

Hazard models show adult survivorship trends that match pathology and trauma patterns (Figure 9). Life expectancy at birth is 34.2 in Phase I, 34.44 in Phase II, and 31.68 during Phase III. Survivorship is lowest during Phase III throughout the adult life history. During Phase I, the probability of (PoD) death spikes in the 20s and mid-30s, while in Phase II the PoD peaks in the mid-30s and remains high into the mid-40s (Figure 2.13). Phase III is closer to linear, with a consistent increase in the PoD until 40, when the curve sharply declines, indicating a strong selective sweep of frail individuals.

E. Discussion and Conclusion

Archaeological data show that the LIP population meets the standard of a small-scale, relatively egalitarian society. Paleoenvironmental data show that the first half of the LIP was a time of pronounced drought and unpredictability. Previous research has shown chronic, internecine warfare as well as likely unsanitary living conditions in the remote and inaccessible hillfort sites (McCool 2017; see, Chapter one). These data combine to suggest the LIP was a time of subdued hierarchies, high stress, and increased violent mortality. Nonetheless, the formal evaluations of morbidity and mortality presented here reveal much about population-level health and heterogeneity in frailty and the risk of death.

1. Population-level Morbidity and Mortality

During the LIP the frequency and severity of cribriform orbitalia and porotic hyperostosis increase significantly compared to the preceding MH. The highland's high elevation location,

extreme aridity, and pronounced drought conditions make it most likely that the observed pathologies are the result of malnutrition and/or malabsorption rather than parasitic infection. The specific etiology of the pathologies however cannot be determined, as previous research has shown that cranial porosities can be caused by anemia, scurvy, rickets, as well as hemorrhagic or inflammatory processes (Walker et al. 2009). It is clear however that the LIP population experienced a rise in physiological stress. In addition, females have slightly higher proportions of disease relative to males, suggesting females may have experienced greater childhood stress.

Survivor/non-survivor results demonstrate that the frequency and severity of pathology is associated with frailty rather than robusticity. These results show that the “paradoxical” interpretation that pathologies demonstrate increasing health and longevity does not apply in this context. However, the higher frequency and severity of pathologies in the child cohort relative to the infant cohort suggests that the infant cohort contains an especially frail subgroup that died after experiencing a stressor before the development of skeletal lesions. The significant increase in disease along with the negative co-variance between age and pathology frequency and severity provides compelling evidence that the LIP population experienced increased biological (likely dietary) stress on a population level. This argument is augmented by the unusually high stable nitrogen values, which suggest stress-induced catabolism and possible anthropophagy (see, Chapter four)

Hazard models corroborate our findings, showing that mortality increased during the LIP while life expectancy from birth decreased. These combined results indicate that population-level stress increased while survivorship and life expectancy declined.

Diachronic results show that morbidity and mortality increased significantly at the onset of the LIP and remained consistently high throughout the nearly 600-year period. Pathology and

mortality do nonetheless vary during the LIP, reaching their zenith in Phase III when violence and population densities were highest (see, Chapters one and three).

At first glance, stable isotope results do not appear to explain increased morbidity and mortality during the LIP. $\delta^{15}\text{N}$ changes significantly from the preceding MH population, revealing enriched $\delta^{15}\text{N}$ values, which have been traditionally interpreted as enhanced access to meat protein and thus reduced protein deficiency—although high $\delta^{15}\text{N}$ values can be the product of increased access to marine or freshwater resources (Knudsen and Frink 2011; Slovak and Paytan 2011). However, the uniquely high nitrogen values may be the result of catabolism or possible anthropophagy rather increased protein consumption (see, Chapter four), although further testing is required to understand these values. $\delta^{13}\text{C}$ values are in-line with previous MH signatures, suggesting continuity in plant diet over time with a slight increase in C_3 plant foods during the LIP.

As discussed earlier, hazard models are susceptible to changes in Total Fertility Rate (TFR) even when mortality remains constant. To what degree is it possible that the observed decrease in survivorship is the result of increased fertility rather than mortality? In other words, might the average reproductive success of the population be increasing such that the average age-at-death decreases, even if mortality remains constant? We find it extremely unlikely that TFR can account for patterns revealed by the hazard models. The LIP Nasca highlands is defined by resource scarcity, chronic warfare, drought, dense population aggregation, and marginal agricultural productivity regimes, all of which will tend to decrease average reproductive success. It is far more likely that observed changes in survivorship are the result of increasing mortality, due to the processes outlined in above. While population reconstructions do show increasing population density through time (see, Chapter three) we hypothesize this is most

likely the result of in-migration from Sierra regions to the east rather than an in-situ increase in TFR.

As outlined in the archaeological context section, the observed increases in population-level morbidity and mortality are not surprising as the LIP population experienced significant increases in warfare-based violence, population packing, drought, unsanitary living conditions, and additional factors that consistently promote dietary stress and elevated mortality. However, these general conditions do not explain the pronounced variability in frailty and the risk of death.

2. Heterogeneity in Frailty

Statistical results show important heterogeneity in frailty among certain subgroups and by sex. The results of the hazards models show that the force of mortality is strongest for the first half of life for the LIP population, with violence and disease selecting out the frailest individuals. Those who survive to older ages appear to be quite robust, even when compared to the MH population, which has far fewer factors affecting mortality. Nevertheless, individuals who experienced early developmental nutritional insults have higher age-specific mortality across the life history. This shows that: 1) in certain cases developmental diseases may be used to assess adult health and mortality risk as per the DOHaD hypothesis, and 2) even the most robust individuals who survived developmental diseases well into their later years had higher mortality at all ages compared to those lacking pathology. Females bore the brunt of increasing mortality as shown by their significantly lower age-specific survivorship and life expectancy at birth. High mortality among females is in part the result of higher relative rates of lethal trauma (see, Chapter one), however this difference is not significant. Sex-based differences in morbidity are subdued and cannot account for the marked differences in mortality. These factors suggest that sex-biased heterogeneity in mortality was driven by factors other than violence and disease.

Diachronic evaluation reveals significant differences in morbidity and mortality through time. Cribra orbitalia peaks during Phase I and Phase III and drops to its lowest levels during Phase II. Porotic hyperostosis does not change significantly, but peaks during Phase III. Population mortality parallels morbidity, with peaks in Phase I and Phase III and a decline in Phase II. Life expectancy at birth is lowest in Phase III and similar in Phases I and II. These results show that morbidity and mortality reached their zenith during Phase III and fell to their lowest levels during Phase II. Thus, it appears that those living during the last 150 years of the LIP were at the greatest risk of morbidity and age-specific mortality relative to those living at earlier times.

To summarize, the LIP population, while appearing to be generally egalitarian, varies considerably in frailty and risk. The increasing mortality and morbidity are concentrated on a subgroup of especially frail individuals and biased by sex, with more robust cohorts and males surviving far longer and exhibiting less pathology. Further, those living in the last 150 years of the LIP suffered higher rates of disease and decreased longevity.

3. Sources of Heterogeneity

This section explores the possible reasons for the observed heterogeneity in frailty and risk of death. We consider the following sources: violence, fertility and reproductive strategies, diet, inequality, migration, and genetics.

Violence

The advent and perpetuation of chronic warfare during the LIP is partially responsible for elevated population mortality. Indeed, the probability of peri-mortem trauma significantly decreases with age (see, Chapter one), suggesting the high mortality among young age-cohorts was partially due to interpersonal violence rather than poor health or disease. Warfare may also

be responsible for increasing dietary stress, as people were prevented from accomplishing quotidian subsistence activities due to the risk of violence (see, Chapter four). As stated earlier, peri-mortem trauma is not significantly associated with sex, which limits its influence on sex-based heterogeneity in frailty and risk of death. To what degree may changes in fertility and life history account for observed differences in frailty and mortality?

Fertility and Reproductive Strategies

Socioecological context plays an important role in fertility and reproductive decision making (Kaplan and Lancaster 2003). Changes in socioecological and economic conditions can prompt a reduction or increase in overall parental investment or skew the allocation of resources towards sons or daughters (Mathews and Sear 2008). Indeed, previous research has shown that some populations exhibit a strong preference for sons and allocate a greater proportion of resources to male children, especially in poor, rural areas (Chavada and A. Bhagyalaxmi 2009; Puri et al. 2011). The motivations for son preference are complicated and diverse and are beyond our current scope. Nonetheless, decreased female survivorship among the Nasca highland population may be partially the result of preferential treatment of sons during early development. Future research will test this offspring investment hypothesis as discussed below.

Sex-based differences in survivorship may also be due to changes in fertility and reproductive strategies. High adult mortality consistently promotes an earlier start to female's reproductive career and reduced inter-birth intervals (Mathews and Sear 2008). While this strategy, on average, increases fitness by confining reproduction to fecund life history phases when mortality is lowest, it also tends to further reduce female longevity and the phenotypic quality of offspring (Mathews and Sear 2008). A shift to earlier and faster fertility may partially explain the observed sex-biased survivorship patterns and may also contribute to the increasing

population mortality. Future research will test this hypothesis by serial sampling the dentition of a large number of LIP individuals to reconstruct weaning investment and timing via stable isotope chemistry. Serial sampling of first molars for stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ will assess whether reproductive aged females biased offspring investment towards one sex by extending or truncating the length of the breastfeeding period (Eerkens et al. 2017; Greenwald et al. 2016; Mathews and Sear 2008). Isotope data will also be used to evaluate the average duration of breastfeeding to assess whether earlier weaning, presumably to terminate lactational amenohera and recommence ovulation, may indicate decreasing inter-birth intervals.

Diet

Within the LIP diet varies little over time and space, by morbidity, or between the sexes. Despite inter-individual differences, the total amount of dietary diversity is minimal, with nearly all individuals exhibiting similar dietary patterns as indicated by the stable isotope results. The striking homogeneity in diet supports the idea that 1) the population was relatively egalitarian in terms of diet, and 2) intra-population dietary diversity cannot explain the majority of heterogeneity in frailty or risk of death.

Inequality

Institutionalized inequality does not appear to be present to the degree that it would explain the observed heterogeneity in frailty. As discussed earlier, the archaeology and diet of the Nasca highland population exhibit patterns in-line with non-hierarchical groups. While achieved inequalities could certainly have existed, we do not see evidence for subgroups of particularly robust individuals with distinct dietary patterns or burial statuses. However, additional research will be required to determine levels of inequality that exist beyond diet, architectural homogeneity, and burial practices.

Genotypic Diversity

Genotypic variability producing heterogeneity in robusticity and resilience (i.e. phenotypic quality) may play a large role, however we cannot evaluate this possibility at this time.

Migration

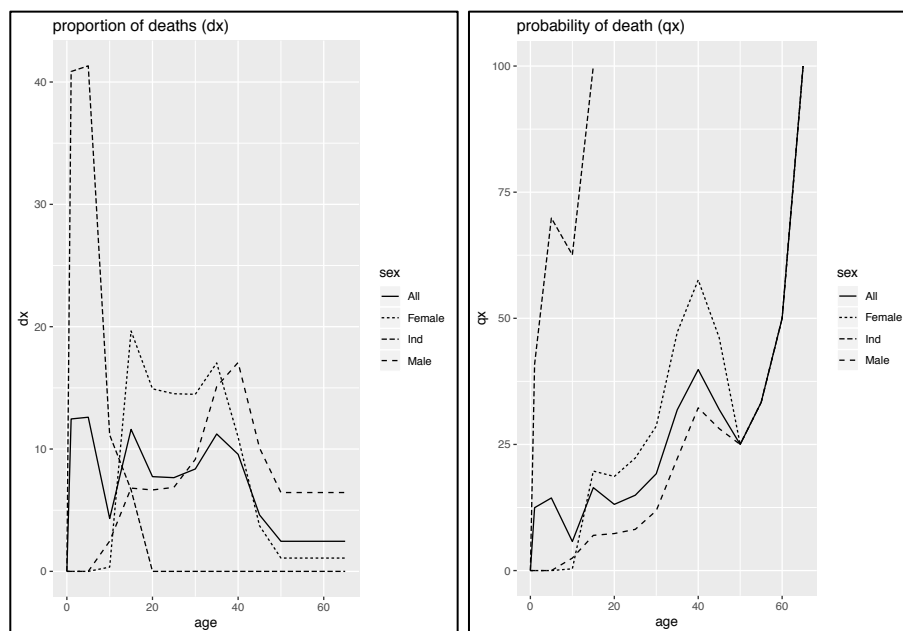
Migration is a potential interpretive issue, as increases in morbidity may be due to an immigration of individuals with a high disease load. Further, the heterogeneity in frailty may be a result of non-local groups in poor health moving into the region rather than pronounced differences in well-being among the source population. Future research will analyze the strontium values of a subsample of individuals with pathology to assess whether these individuals are migrants.

4. Conclusion

The results presented here provide compelling evidence of increasing physiological stress and mortality in the Nasca highlands of Peru during the Late Intermediate period. While the population as a whole experienced greater stress and reduced survivorship, we highlight substantial variability in frailty and the risk of death. The frailest members of society experienced a heavier disease burden and higher mortality compared to their more robust contemporaries. Females exhibit significantly lower life expectancies at birth and higher age-specific adult mortality. Elevated levels of disease and lethal trauma among females account for some of the differences in survivorship but cannot explain the large degree of sex-based divergence in mortality and life expectancy. We hypothesize that parental investment biases towards sons and/or changes in female reproductive strategies that led to earlier age at first birth and reduced inter-birth intervals may explain these differences. The sources of differential frailty

are complex and not immediately apparent. Stable isotope chemistry shows little dietary diversity throughout the LIP, with all individuals varying within single trophic levels. Diachronic analysis reveals that pathology and mortality peak during the first and final century of the LIP, with a century long drop in morbidity and mortality circa 1200 – 1300 C.E. This result suggests some heterogeneity in frailty and risk of death is temporal, although it does not explain why population health declined during Phase III of the LIP (see, Chapter Three).

This article has shown that a multimethod approach to the osteological paradox can aid in the navigation of “paradoxical” interpretations and provide detailed and compelling explanations of disease and mortality in past populations. While this research opens up as many questions as it answers, the approach taken here provides a roadmap to guide future research, with the ultimate goal of providing more complete information on health and disease in the prehistoric world.



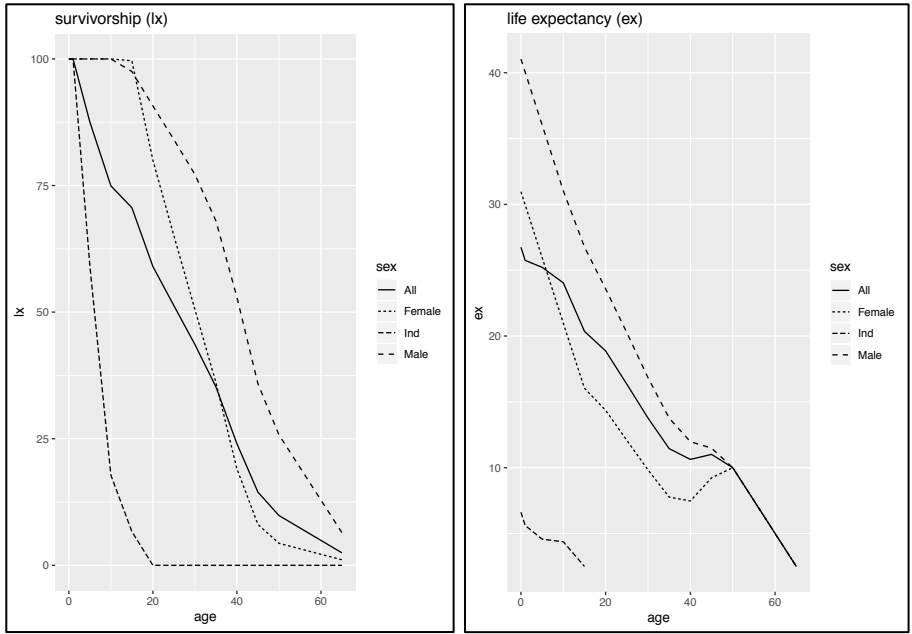
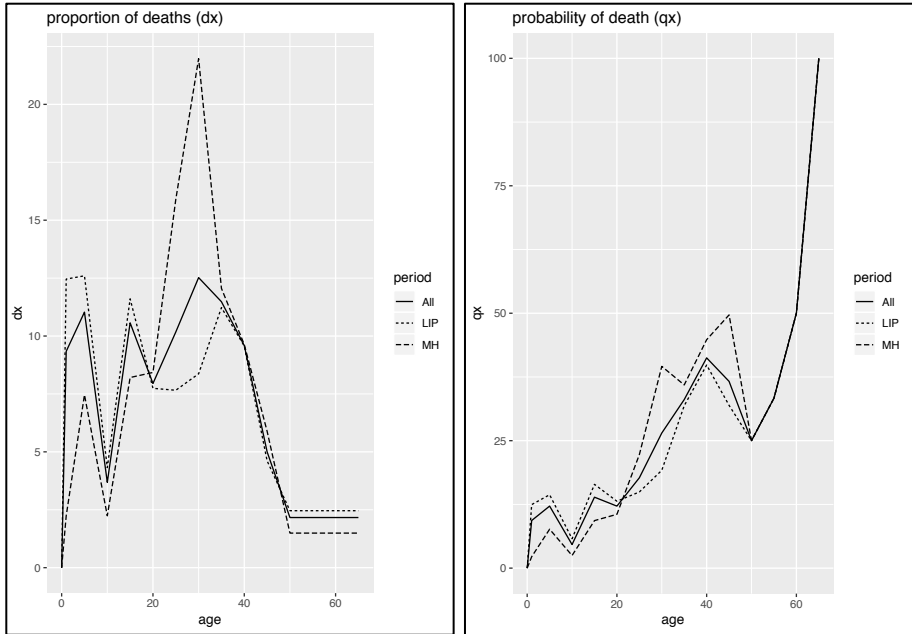


Figure 2.9. Hazard models for the LIP sample showing sex-based differences.



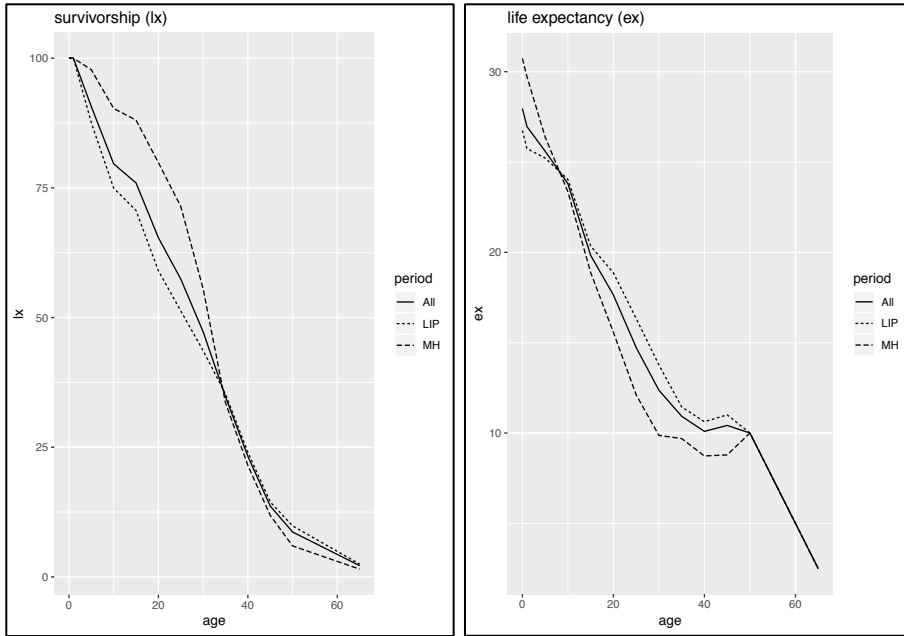


Figure 2.10. Hazard models comparing the Middle Horizon and Late Intermediate period samples.

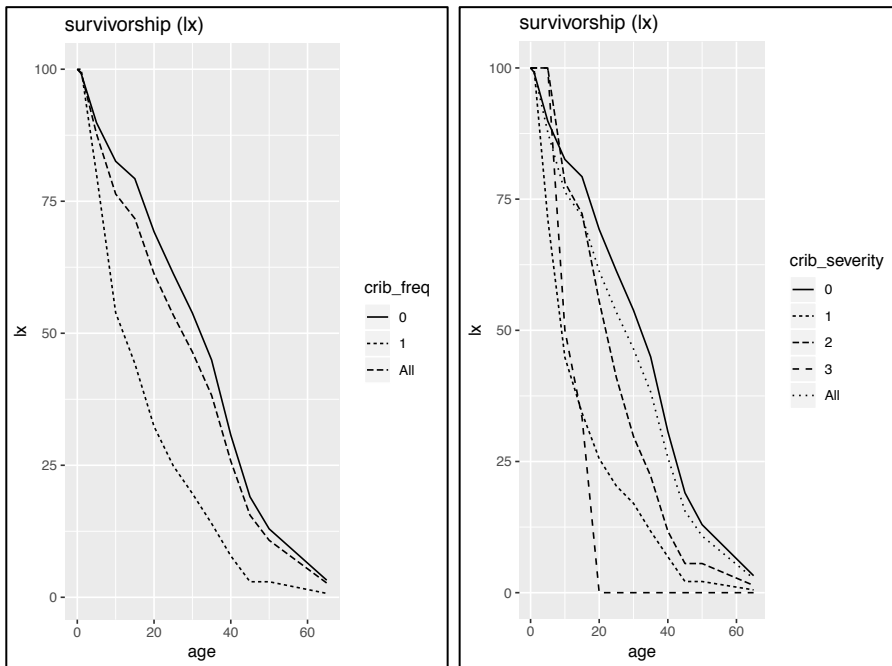


Figure 2.11. Survivorship curves for the frequency and severity of orbital lesions (cribra orbitalia) for subadults and adult.

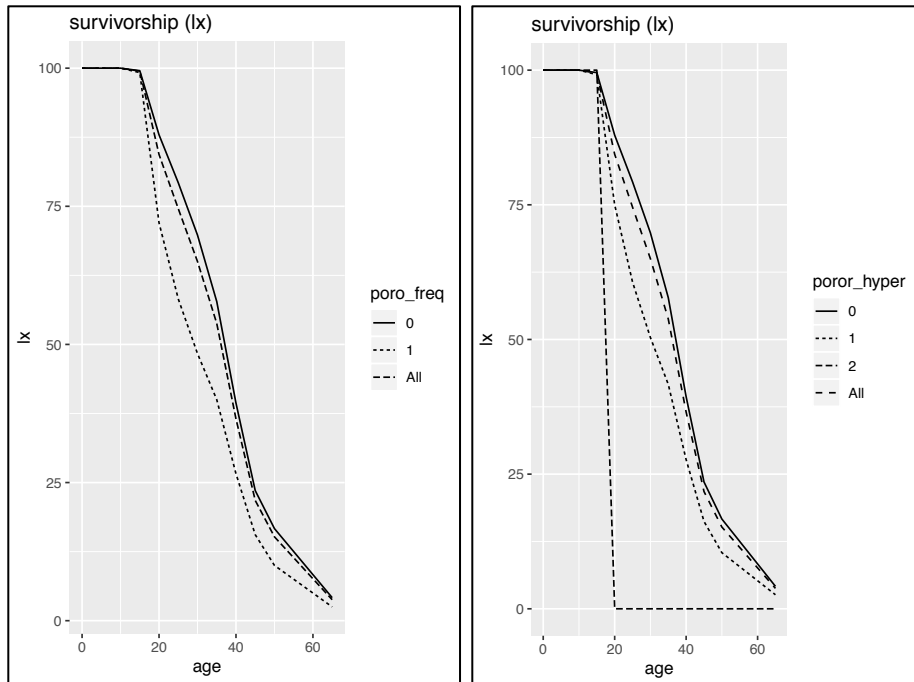
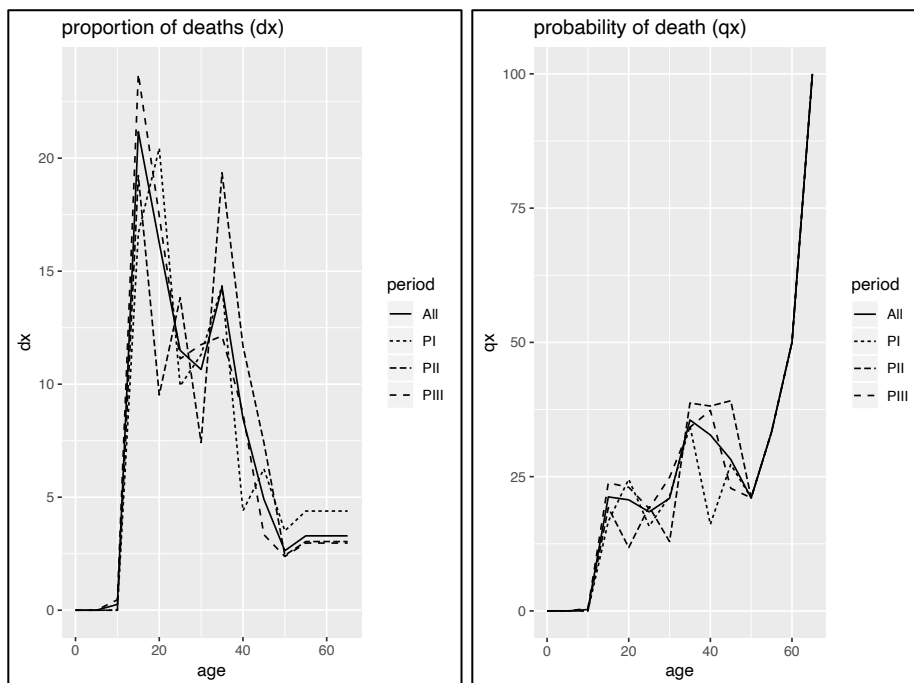


Figure 2.12. Survivorship curves for the frequency and severity of cranial vault lesions (porotic hyperostosis) for adults only.



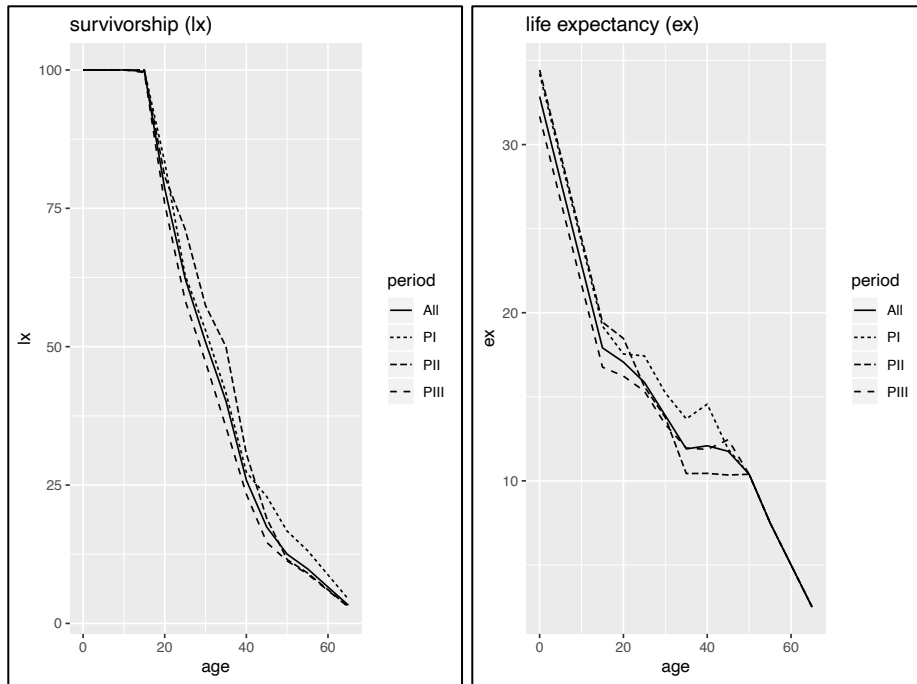


Figure 2.13. Hazard models evaluating diachronic changes.

III. Evaluating the Climatological, Political, and Demographic Drivers of Warfare: a case study from the Prehispanic Andean highlands

A. Introduction

Despite sustained efforts by modern democratic institutions, individuals and nations all too often engage in violent conflict. Generating a stable peace process requires that we understand what conditions lead to such behavior. Indeed, understanding the causes of warfare has been a major research initiative in the social, economic, and behavioral sciences for decades (Burke et al. 2015; Gleick 2014; Hsiang et al. 2013; Huntington 1917; Gat 2008, 2010; Keely 1996; Kelly 2000; Nordås and Gleditsch 2007; Scheffren et al. 2012; Zhang et al. 2007a, 2007b). This article contributes to this growing body of research by developing and testing models that predict how climate change, political transition, and demographic pressure relate to individual payoffs for warfare and explain large-scale patterns.

Recent research in biological anthropology has advanced our understanding of what motivates individuals to engage in coalitionary violence by evaluating associations between participation in conflict and individual material and status benefits (Chagnon 1988; Gat 2008; Glowacki and Wrangham 2013; Glowacki and Wrangham 2015; Glowacki et al. 2017; Macfarlan et al. 2014; Wrangham and Glowacki 2012). Further progress in the archaeological, geographical, and historical sciences has begun to generate coarse-grained estimates of conflict across space and time (Allen et al. 2016; Arkush and Tung 2013; Lambert 2002; O'Sullivan 2014; Tol and Wagner 2010; Zhang et al. 2007a), as well as some of the basic conditions that correlate with periods of conflict (e.g. Kohler et al. 2014; Zhang et al. 2007b). Yet, our picture of warfare throughout the human career remains highly fragmented, and scholars struggle to understand how individual motivations for violence relate to the emergence and spread of

conflict over large spatial and temporal scales (Allen et al. 2016). This article helps to address these issues by (1) generating a large novel dataset on prehistoric warfare, (2) developing general models that bridge individual motivations with macro-scale patterns to evaluate the factors that drive variation in warfare, and (3) testing model predictions using an archaeological case study from the Peruvian Andes.

Archaeological case studies provide a number of advantages to the investigation of warfare, perhaps most importantly allowing for the evaluation of changes in conflict over vast time scales not represented by modern or historic datasets. This article provides particular advantages because it includes: (1) a large archaeological dataset that spans diverse climatological, political, and demographic contexts; (2) an investigation of a Prehispanic population in an arid region of South America with considerable descriptive evidence for conflict (McCool 2017) but a paucity of explanatory research; and (3) an advance over monocausal explanations by testing the explanatory power of multiple predictor variables as well as their interactions.

This article consists of a case study from the Prehispanic South American Andes, where past conflict has been recorded and debated for several decades (Arkush 2011; Arkush and Stanish 2005; Arkush and Tung 2013; Murphy et al. 2010; Topic and Topic 1987; Tung 2007, 2012). This case study is particularly salient because the study period (950 – 1450 C.E.) represents an era of volatile climate change, political collapse, and increasing demographic pressure in a region of the world that will likely experience similar socioenvironmental upheavals in the near future.

1. Explanatory Conflict Research

Prior to the 1990s, archaeologists typically ignored evidence for prehistoric warfare or dismissed it as “primitive,” ineffectual, and unimportant (see Keeley 1996 for summary; Turney-High 1949). More recent archaeological research acknowledges that warfare, defined here as *potentially lethal intergroup aggression* (Arkush and Tung 2013; Beckerman 1991), is a frequent and significant, albeit variable, aspect of prehistoric life. The first research to explore prehistoric warfare focused on documenting the existence and patterns of violence, rather than its causes or consequences (e.g. Haas and Creamer 1997; Lambert 1994; Milner et al. 1991; Moss and Erlandson 1992; Turner 1983; Vencl 1984; Wilcox and Haas 1994). Rarely did these studies attempt to explain why one set of conditions might promote conflict over cooperation. Instead, much of the early literature on prehistoric warfare makes the assumption that any environmental or political perturbation that co-occurs with conflict must be the cause, without explaining the driving mechanisms.

More recently, multidisciplinary studies of conflict have begun to develop hypotheses that formally test competing explanations (e.g. Arkush 2008; Baysan et al. 2014; Burke et al. 2015; Gat 2009; Hsiang et al. 2013; Kennett et al. 2016; Kohler et al. 2014; LeBlanc 2007). Further, there is an increasing recognition that conflict studies require theory that predicts how individuals use conflict to achieve desired outcomes (Allen et al. 2016; Gat 2010; Glowacki and Wrangham 2013). This research examines warfare through an explicit cost/benefit framework, predicting that violence will arise when the anticipated costs are low, and the expected benefits are high (Allen et al. 2016; Glowacki et al. 2017). Applying predictive models that evaluate the conditions under which conflict yields high payoffs will help to disentangle the complex web of causal pathways that lead to intergroup violence.

B. Hypotheses

1. The Conditions that Promote Warfare

The proposed research adopts the central evolutionary tenet that participation in warfare should be primarily motivated by high fitness payoffs to the individual (Allen et al. 2016; Glowacki and Wrangham 2013; Glowacki and Wrangham 2015; Glowacki et al. 2017; Macfarlan et al. 2014; Wrangham and Glowacki 2012). The benefits of participation in warfare must be quite compelling, as the costs include the risk of immediate mortality, long-term retaliations, as well as economic and opportunity costs (Allen et al. 2016; Glowacki and Wrangham 2015; Glowacki et al. 2017). What conditions might predictably increase the benefits of participation, or the costs of non-participation, such that the payoffs for conflict outweigh those of positive-sum intergroup interactions?

2. Resource Scarcity

The abundance and distribution of resources affect the costs and benefits of conflict. Payoffs are most likely to outweigh the costs when resources are scarce, the costs of resource-loss due to theft are high, and the benefits of increased intergroup cooperation are limited (Allen et al. 2016; Ember 1982; Ember and Ember 1992; Ember et al. 2013; Gat 2009; Kelly 2000; Kohler et al. 2014; Vayda 1967, 1976). These conditions are most likely to arise in areas of low environmental productivity, where resource returns most frequently fall below minimum subsistence requirements (Allen et al. 2016; Ember and Ember 1992; Ember et al. 2013). In addition, economic and human behavioral ecology research has shown that environmental productivity is a significant predictor of economic risk-preference (Kuznar 2001; Winterhalder et al. 1999; Winterhalder et al. 2015). In areas of low environmental productivity individuals prefer risk-prone economic “gambles” because the expected payoff is, on average, worth the potential

risk of loss (Kuznar 2001; Winterhalder et al. 1999). However, like all economic gambling, risk-prone strategies occasionally fail. Thus, those living in marginal environments are under a double threat of resource scarcity, driven by low baseline productivity and high-risk economic strategies. When resources become scarce spatial autocorrelation may ensure limited benefits to increased cooperation with neighboring groups, who will likely be experiencing similar shortfalls. These factors render areas of low productivity especially vulnerable to resource scarcity, with episodes of low or volatile precipitation potentially acting as positive feedback that increase the likelihood and severity of food shortages (Kennett and Marwan 2015; Kennett et al. 2012). These conditions increase the payoffs for conflict as a resource procurement strategy.

Hypothesis 1 (Resource Scarcity). We expect that the intensity (i.e., rates of violence) of warfare should positively co-vary with resource scarcity. We may also expect violence to increase during periods of low and/or volatile precipitation.

3. Territorial Defense

The advantages of warfare may outweigh the disadvantages when there are high costs associated with being forcibly removed from a territory by a competing group (Coddington et al. 2017; Kennett and Winterhalder 2009; McCool and Yaworsky 2017). These costs increase considerably when an environment is circumscribed to the degree that the loss of a resource patch or territory may lead to starvation. Thus, we expect individuals to participate in violent actions when the costs related to participation are less than the anticipated costs of resource or territory loss to competitors. This behavior may be manifested in continual territorial defense against neighbors or short-term defense against an intruding group.

Hypothesis 2 (Territorial Defense). We expect that the intensity of warfare will be low and consistent until the invasion of a competing group, then rise to their highest levels and

remain high if territorial defense continues or it will disappear if the territorial dispute is resolved.

4. Collapse of Complexity

Scholars have suggested that the collapse of complex societies may be a key cause of conflict (e.g. Kurin 2012; Tainter 1988; Tung 2008; Yoffee 2005). Collapse events lead to warfare via (1) the dissolution of economic redistribution systems that can ameliorate local food shortages (i.e. create resource scarcity) (Halstead and O'Shea 1982; Pham 2011; Service 1975), and (2) competition for newly emergent positions of political power that may enhance the status and thus fitness of participating members (Allen 2016; Earle 1997; Glowacki and Wrangham 2013; Mabon et al. 2016).

Hypothesis 3 (Collapse). We expect that the intensity of warfare will be low and consistent until a collapse event, rise to their highest levels, then gradually decrease.

5. Demographic Pressure

The size and distribution of human populations have long been argued to influence rates of violence (Carneiro 1970; Ember 1982; Malthus 1798; Turchin and Korotayev 2006; Wood 1998). Previous research shows that resource abundance is density-dependent, meaning the efficiency of resource returns will diminish as the number of individuals exploiting them increases (Kennett and Winterhalder 2009; Kennett et al. 2009). Nevertheless, allee effects on agriculturalists (Coddington et al. 2017) may result in a temporal, but not necessarily spatial, lag whereby conflict emerges *after* population numbers begin to peak (Kohler et al. 2014). As resource abundance decreases and population densities rise, competition for resources may incentivize conflict. Indeed, previous research has shown that conflict and territoriality often

arise when populations are densely packed into circumscribed areas (Kennett 2005; Kennett et al. 2006; LeBlanc 1999; Malthus 1798; Wood 1998).

Hypothesis 4 (Demography). Variability in conflict tracks variability in both population densities and the economic trade-offs between resource sharing and resource competition.

Predictions specific to the case study are listed in Table 1 below the following section.

C. Case Study

1. Prehistoric Agropastoralists of the Nasca Highlands

The Nasca highland region is a remote, highly bounded area roughly 30 km east and over 3,000 m above of the modern city of Nasca, Peru (Figure 3.1). The region was occupied by the Wari empire sometime in the sixth century C.E. as evidenced by numerous Wari administrative sites scattered throughout both the highlands and lowlands (Edwards 2010). The Wari empire, which expanded from its base in Ayacucho to conquer much of the Peruvian Andes (Schreiber 1992), went into decline in the tenth century C.E. and collapsed circa 1000 C.E.

During the subsequent Late Intermediate period (LIP; 950 – 1450 C.E.), the Nasca highlands were home to a population of small-scale agropastoralist communities located throughout the region's five river valleys. All currently known LIP residential sites are located on arable patches of land located within or adjacent to the river valleys (Figure 3.1). The principal author (McCool 2017) recorded 19 LIP residential settlements with associated cemeteries located throughout the five valleys. Each settlement was permanently occupied as evidenced by dense housing clusters and midden areas, along with the total lack of households outside of fortified centers. Residential sites are located on difficult to access hilltops, mesa-tops or along steep ridgelines, and they exhibit multiple lines of fortification features (McCool 2017).

Either within or, more often, immediately adjacent to the hillforts are cemeteries consisting of several dozen to several hundred artificially constructed tombs known in Quechua as “chullpas”. Chullpa tombs are fairly uniform in size and consist of both conical and square construction styles. The tombs contain up to several dozen individuals of all age groups along with associated mortuary goods. Each interred individual was at one time placed as a desiccated bundle wrapped in a cotton death shroud and placed upright in tight clusters on the ground surface. Subsequent taphonomic processes and substantial looting have disarticulated and commingled these remains.

The LIP concluded with the invasion of the Inca empire circa 1450 C.E., when the Nasca region and surrounding areas were successfully conquered and brought under Inca imperial hegemony (Conlee 2015). Thus, the LIP is confined to an interregnum period in-between the collapse of the Wari empire circa 950 C.E. and the invasion of the Inca 500 years later.

Table 3.1. Case Study Predictions

Case Study Predictions	
<i>Prediction one (Resource Scarcity)</i>	We expect rates of violent trauma to positively co-vary with dietary stress and negatively co-vary with precipitation.
<i>Prediction two (Territorial Defense)</i>	We expect rates of violent trauma to remain low and consistent until the arrival of the Inca army circa 1450 C.E., significantly rise during that time, then significantly decrease after the successful Inca invasion shortly thereafter.
<i>Prediction three (Collapse)</i>	We expect the collapse of the Wari empire circa 1000 C.E. to correlate with significantly higher rates of violence trauma, with trauma decreasing through time.
<i>Prediction four (Demography)</i>	We expect that rates of violent trauma will positively co-vary with population density.

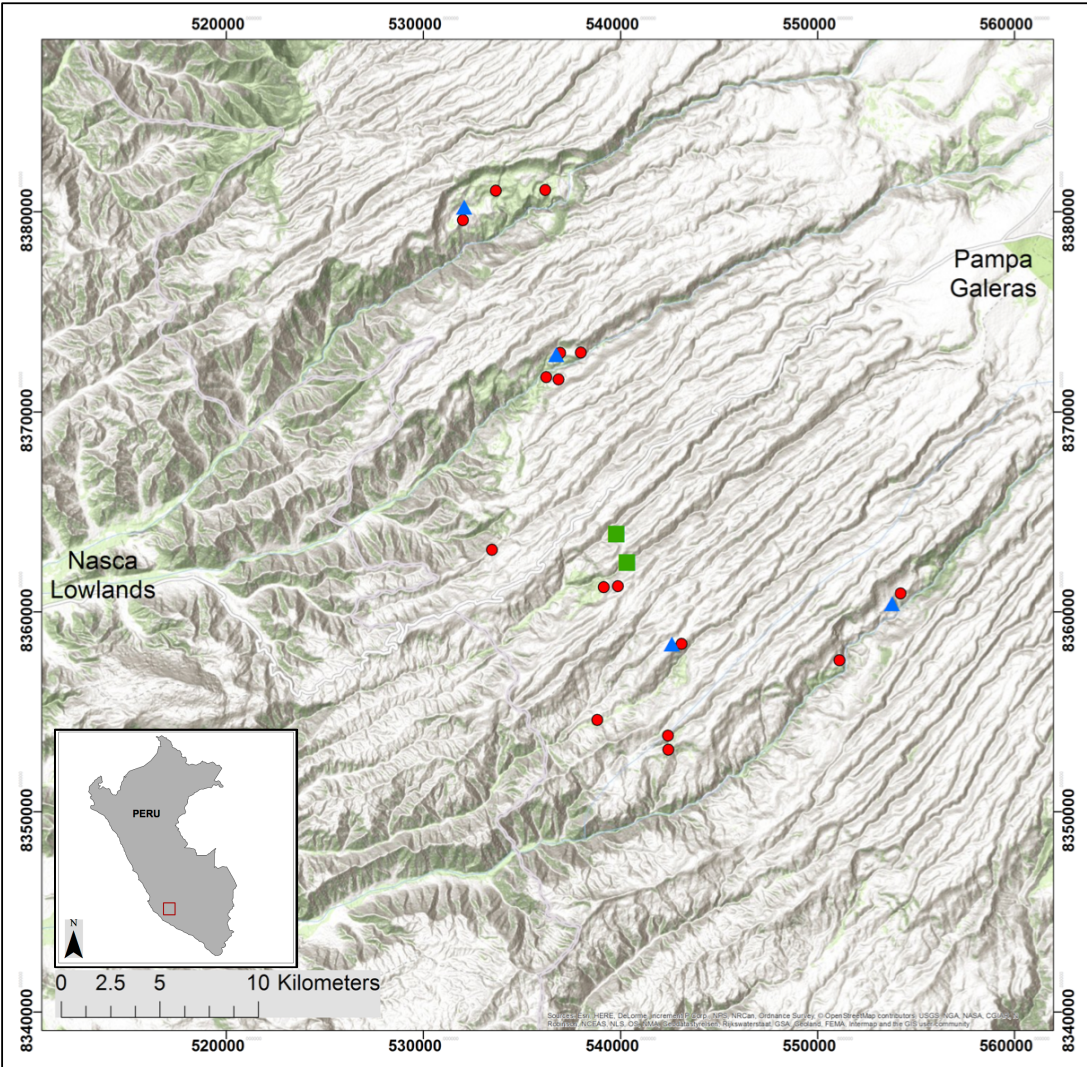


Figure 3.1. Map of the Nasca highlands. Points = LIP residential sites, triangles = chullpa cemeteries, squares = machay cavern tombs.

D. Methods: Measuring Predictor and Response Variables

1. Response: Measuring Violence through Osteological Analysis

The best method for tracking rates of prehistoric violence is the assessment of violent trauma on human remains (Lambert 1997; Walker 2001). To facilitate the creation of an osteological database that could be evaluated for trauma, eleven LIP tombs in the Nasca highlands were excavated in 2018. Excavations produced a human skeletal sample of 325 individuals (determined by number of intact crania) and thousands of post-cranial remains. Of

the 325 crania, all underwent age and sex estimation and an assessment of *cribra orbitalia*. Only 270 individuals, however, were sufficiently well-preserved to assess biological profiles, trauma, and pathology. The commingled nature of the LIP burial contexts prevents us from linking post-cranial remains to the crania. Thus, we restricted our analyses to the sample of crania.

The age-at-death for each individual was estimated using the standards protocols of assessing stages of cranial suture closure, dental formation/eruption and dental wear to estimate age (Bass 2005; Buikstra and Ubelaker 1994). Age-at-death estimations were used to place individuals into one of seven age categories: infant (0–4), child (4–12), adolescent (12–20), young adult (20–35), middle adult (35–50), and old adult (50+) (White and Folkens 2005). Sex was estimated using sexually dimorphic cranial features as per the standards protocol (Bass 2005; Buikstra and Ubelaker 1994; White and Folkens 2005).

Rates of ante-mortem and peri-mortem trauma were recorded using evidence of bone healing as indicating ante-mortem trauma (Lovell 1997; Sauer 1998; Tung 2007). Radiating fractures, discoloration in fracture lines, and bone hinging at fracture margins were used to determine peri-mortem trauma (Ortner 2004; Sauer 1998; Tung 2007). Observations of cranial trauma distinguished between accidents and intentional violence and sharp-force vs. blunt-force trauma (Kurin 2012; Lambert 1997; Lovell 1997; Tung 2007, 2012). Postmortem damage was distinguished from peri-mortem trauma based on the coloration and shape of fracture margins and the presence of hinging bone and radiating fractures (Berryman and Haun 1996; Murphy et al. 2010; Ortner 2008; Sauer 1998). Peri-mortem trauma was further divided into the frequency of “overkill” trauma, defined by the presence of multiple peri-mortem traumas that go beyond what is required to dispatch an individual (Kurin 2012; Simmons 2007; Šlaus et al. 2010). A “critical trauma” metric (Andrushko and Torres 2011) was also developed, defined here by

healed or lethal traumas that are >25mm in diameter, and/or >2.5mm deep. As skeletal trauma can range from life-threatening injuries to hairline nasal fractures, critical trauma provides a more accurate measure of violence than ante-mortem trauma.

One concern is whether the cranial-focused analyses will accurately capture rates of violence. LIP weaponry consisted of maces, hand-axes, and slings, which often requires direct cranial contact to inflict peri-mortem injuries. Previous research in the Andes and elsewhere has used cranial trauma as a standard means of estimating rates of violence (Kurin 2012; Martin and Harrod 2014; Torres-Rouff and Costa Junqueira 2005).

To assess differences in trauma patterns, we compare our data with osteological analyses of 97 Middle Horizon (500 – 950 C.E., henceforth MH) crania recovered from tombs in the Nasca lowlands directly adjacent to the Nasca highlands (Kellner 2002). This comparative sample is used because it immediately predates the LIP and allows an assessment of Wari era levels of violence.

Patterns of LIP Violence

Patterns of violence are thoroughly explored in Chapter one, and only a brief summary of the trends in warfare will be presented here. Overall, 31% of the human skeletal sample exhibits ante-mortem trauma and 13.1% exhibits peri-mortem trauma. Thirty eight percent of individuals exhibit at least one peri-mortem and/or ante-mortem trauma. Of the sub-sample of individuals with peri-mortem trauma, nearly half (49%) exhibit overkill trauma. In addition, 25% of the sample exhibits critical trauma. These results show that a quarter of the population experienced a violent encounter that was very likely life-threatening. The average number of traumas per individual also significantly increases during the LIP ($t = 7.593, p = 0.000$) from 0.10 during the Middle Horizon to 0.80 during the LIP.

Variability in LIP violence

We evaluate temporal fluctuations in LIP violence using a sample of direct radiocarbon dates from 124 individuals (see, Chapter One). Crania that were not directly dated are not included in our analysis, as we cannot accurately bin them into one of the three the LIP phases we establish below. Samples were taken from the vomer and nasal concha when possible or the nasals/styloid process when necessary. In several cases, none of these elements were available, requiring us to sample of the zygomatic arch. Collagen was extracted and ultrafiltered at the Pennsylvania State University and the University of California, Irvine labs, and run at the Keck Carbon Cycle AMS facility (UCI KCCAMS 2007) at the University of California, Irvine (see Chapter Four for isotope protocols). Results were calibrated using the rcarbon package in the R programming environment (Bevan and Crema 2019) with the SHCal13 calibration curve (Hogg et al. 2013). Five individuals dated to the terminal MH (circa 750-950 C.E.) and were removed from the sample. The resulting sample of 119 individuals contains dates that span the entire LIP, permitting an analysis of diachronic changes in violence throughout the 500-year period. The resulting chronology is divided into three LIP Phases. Phase I (950 – 1200 C.E., $n = 22$), Phase II (1200 – 1300 C.E., $n = 26$), and Phase III (1300 – 1450 C.E., $n = 71$). These ranges were selected to ensure each contained a sufficiently large sample size to conduct reliable statistical analyses, and because these temporal divisions mark important changes in climatological, demographic, and sociopolitical conditions.

Within the LIP (Figure 3.2a), trauma rises during Phase I then declines in Phase II, although the decrease is not significant. Violence increases significantly to its highest levels during Phase III, when peri-mortem trauma peaks at 24% (Fisher Exact $p = 0.05$). It is also noteworthy that overkill trauma remains low during the first two phases (4.8% and 3.7%,

respectively) then increases significantly during Phase III to 14% (Fishers Exact $p = 0.049$). Interestingly, ante-mortem trauma varies little throughout the three phases, averaging 28.7% with a range of 26% - 31%. Critical trauma, a more reliable measure of violence, parallels trends in peri-mortem trauma, with an initial spike in Phase I, a decline in Phase II, and a significant rise in Phase III to 38% (Fishers Exact $p = 0.002$). The number of traumas per individual is significantly higher during Phase III than in Phase I ($t = -2.133, p = 0.019$) and Phase II ($t = -2.978, p = 0.002$), showing the intensity of violent encounters and/or trauma recidivism increased during this time (Figure 3.2b). To summarize, the LIP is generally defined by internecine warfare, although rates of violence and the intensity of violence vary significantly through time.

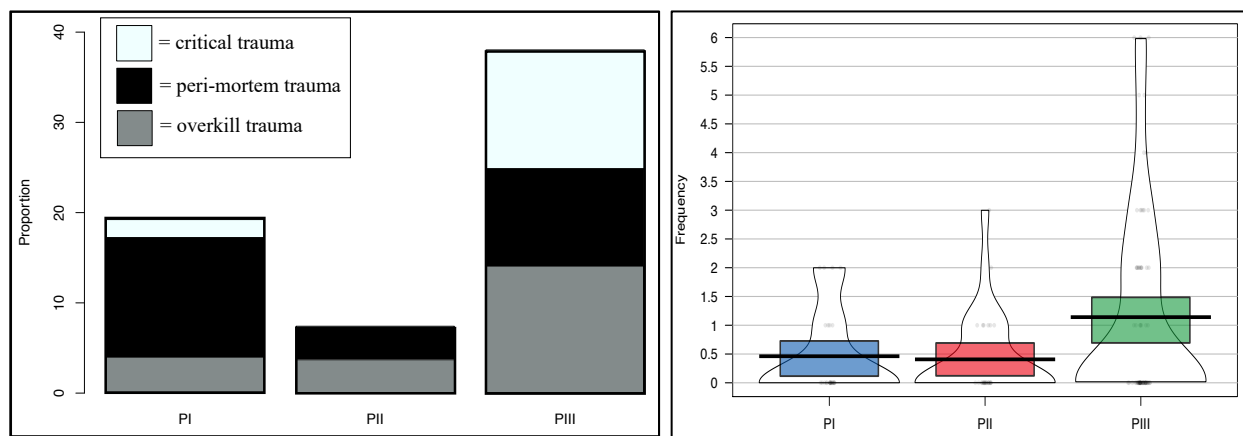


Figure 3.2a (left). Summary of trauma over the three LIP phases. **Figure 3.2b** (right). Sum of trauma per individual over the three LIP phases.

2. Predictor: Population Density

Population density is measured by proxy using the dates as data approach (Crema et al. 2006; Rick 1987; Broughton and Weitzel 2018; Shennan et al. 2013). The dates as data approach rests on the premise that larger populations should produce and deposit greater amounts of datable materials relative to smaller populations. This method has been increasingly refined and updated since its initial application (Rick 1987) and has been successfully used to track

population histories through time and across space (Bevan et al. 2017; Crema et al. 2006; Broughton and Weitzel 2018; Shennan et al. 2013).

The dates as data approach is nonetheless controversial, with several critiques emerging that question whether this method can accurately estimate population (Contreras and Meadows 2014; Culleton 2008; Kennett et al. 2008). These critiques state that the dates as data approach actually tracks activity intensity or settlement aggregation rather than fluctuations in population (Ebert et al. 2017; Hoggarth et al. 2016; Kennett et al. 2014). Another issue stems from the fact that fluctuations in the calibration curve can create artifacts in the data that look like changes in population (Culleton 2008; Shennan et al. 2013; Weninger et al. 2015). To navigate these issues, we only use dates sampled from human skeletal material, the number of which is not affected by activity intensity. We also note that the study region contains highly aggregated groups throughout the time period of interest so that the available sample of skeletons will not fluctuate as an artifact of changes in the aggregation or dispersion of local groups. Finally, we use recent statistical improvements to the dates as data approach (Crema and Bevan 2019) that can assess whether variability in our population estimates are an artifact of the calibration curve.

To estimate population changes in the Nasca highlands we used the rcarbon package (Crema and Bevan 2019) in the R environment to generate summed probability distributions (SPDs) on calibrated radiocarbon dates from our sample of 124 dated human remains. We then followed the Shennan et al. (2013) approach and compared our SPDs to a Monte-Carlo simulation of a null exponential growth model to identify general population trends as well as periods of time where our SPD significantly deviates from the expected null values. Generating the null exponential growth model consists of a three-stage process: 1) fitting a growth model to the observed SPD using a regression model; 2) generating random samples from the fitted

model; and 3) un-calibrating the samples. The resulting set of radiocarbon dates can then be calibrated and aggregated in order to create an expected SPD of the fitted model that accounts for idiosyncrasies of the calibration process. Higher or lower than expected density of observed SPDs for a particular year will indicate a local divergence of the observed SPD from the fitted exponential growth null model, and the significance of these deviations can be used to assess the goodness-of-fit using a global test.

The summed probability distributions show distinct trends throughout the terminal MH and LIP (Figure 3.3). Population density and growth is extremely low during the terminal MH and Phase I of the LIP. Indeed, nearly the entire period deviates significantly below the exponential growth null model. Population begins to grow mildly during the end of Phase I then increases rapidly during Phase II—with growth significantly exceeding the null growth model during the end of Phase II and throughout Phase III. Population density plummets at the end of the LIP circa 1450 C.E., possibly as a result of Inca imperial expansion into the region, as the Inca empire is known to have forcibly relocated populations that actively resisted subjugation (D'Altroy 2002).

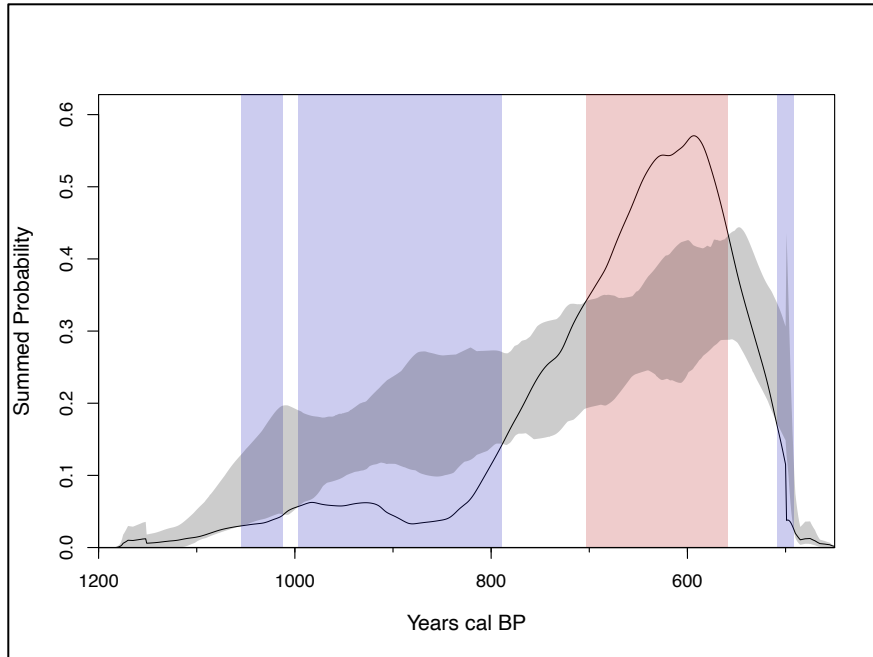


Figure 3.3. Summed probability distribution of ^{14}C dates from the Nasca highlands. The light gray function is the Monte-Carlo simulated null growth model. Blue bars are significant deviations below the null growth model, red bars are significant deviations above the null growth model.

3. Predictor: Environmental Productivity and Climate Reconstructions

The Andean environment is characterized by spatially diverse geocological and climatological conditions. Critical agricultural factors such as altitude, slope, aspect, soil type, moisture, and the amount of solar radiation vary considerably within small areas and over short time periods (Winterhalder and Thomas 1978). In the central and southern Andes, rainfall is constrained to a single season, with peak precipitation during the months of January and February (ONERN 1971). This short season offers limited and variable moisture regimes that make environmental conditions unpredictable. These factors produce patchily distributed and irregularly timed agroecological conditions that are most often defined as marginal (Winterhalder and Thomas 1978). In addition, the young and poorly developed Andean soils have low moisture retention and lack certain crop buffering nutrients (Winterhalder and Thomas 1978). These conditions make food returns highly variable and unpredictable, leading to

challenges maintaining adequate food supply. As a result, many small-scale farmers frequently face resource scarcity and attendant health problems. The probability of resource shortfalls is heightened when climate change produces increasingly cold and arid conditions and/or short-term stochasticity in precipitation (Kennett and Marwan 2015).

Agroecological conditions in the Nasca highlands parallel those of the broader central and southern Andes. Localized environmental stressors substantially affect resource availability and stability. The region's agroecology is defined by marginal, stochastic conditions that are heavily structured by seasonal precipitation (ONERN 1971). The region's five river valleys are steep, narrow, and boulder-strewn, making the majority of the valley untenable for crop production. Within the river valleys arable land is confined to seven small, spatially bounded patches with sufficiently flat topography to permit the construction of terraces and canals. The river valleys are surrounded by arid tablelands that cannot sustain crops due to insufficient precipitation for dry farming, the inability to provide river water for irrigation, and frequent nightly frosts. Local precipitation regimes follow the general patterns of the central Andes and consist of a single rainy season from October to April, with peak precipitation during the months of January and February (ONERN 1971). The regional average of 230 mm of precipitation requires that crops be sustained by irrigation canals that feed water to terraced fields. The entire irrigation water budget is provided by five streams and several seeps that originate in the altiplano to the east. Streams discharge negligible volumes of water and are typically dry for four to eight months of the year (ONERN 1971). The quantity and predictability of river discharge is entirely a product of seasonal precipitation, as headwaters lack permanent lakes, snowpack, or glaciers. Precipitation regimes are variable and unpredictable and can often lead to inadequate or ill-timed rainfall. In addition, substantial diurnal temperature changes can produce crop-killing

frosts almost any time of the year. Local soils are typically shallow and distributed over bedrock, or extremely gravelly where erosion has kept pace with soil formation (FAO Global Database). Unpredictable precipitation combined with marginal growing conditions creates considerable economic risk for local populations today, as it most certainly did during LIP times.

These environmental conditions structure which productivity variables are most important to local farmers. The amount of river discharge, precipitation, and arable land being paramount. River discharge, in addition to providing the critical irrigation supply, also determines the duration of river flow throughout the year. Low discharge streams may only flow four months out of the year while the larger rivers may persist for eight to nine months. Local precipitation is important as it can provide water to crops when irrigation water is either not available or being stored in cisterns for future use. The amount of arable land is critically important as arable patches can vary from several dozen hectares to several hundred, which will influence productivity, speed of density-dependent resource declines, and the ability to fallow fields and scatter them over localized micro-climates (Browman 1987; Golland 1993). Overall, these conditions show that: 1) precipitation is the critically important determinant of productivity; 2) the average environmental productivity is marginal; and 3) the region is extremely ecologically circumscribed. Thus, the region is prone to resource scarcity, particularly when precipitation is low and unpredictable and/or population densities are high.

To estimate environmental productivity, we utilize previously published paleoenvironmental reconstructions that evaluate climate changes throughout the LIP (Schitteck et al. 2015, Figure 3.4). Palynological analysis of a core extracted from the Cerro Llamoca peatland located approximately 30 km northeast of the Nasca highlands tracks the abundance of multiple pollen taxa that are heavily influenced by the amount and variability of precipitation. The authors

find that the pollen family Poaceae provides a representative proxy of precipitation through time as it co-varies with the other pollen taxa analyzed in the core (Schitteck et al. 2015). These data show that Poaceae percentages were very low at the onset of the LIP circa 950 C.E., followed by increasing stochasticity in precipitation regimes leading to an “extreme drought” event circa 1100 – 1225 C.E. (Schitteck et al. 2015:207; Figure 3.4). These diachronic environmental perturbations would have reduced the flows of the rain-driven highland streams, which are critical for delivering irrigation water to the terrace farm systems (McCool 2017; Schitteck et al 2015:39; Sořna 2014). Precipitation rebounds circa 1225 C.E. to pre-drought levels and remains stable throughout the remainder of the LIP.

Broken down by LIP Phases, precipitation averages and standard deviations, as measured by the percentage of Poaceae pollen over time, change significantly. The Phase I climate is defined by declining and volatile precipitation including the period of extreme drought ($m = 50.8\%$, $SD = 11.35$). Precipitation increases significantly in Phase II (Tukey HSD $p = 0.000$) and becomes increasingly predictable ($M = 89.9\%$, $SD = 10.6$). During Phase III precipitation continues to rise ($M = 93.1\%$) while variability decreases substantially ($SD = 1.3$).

To permit robust statistical tests of the relationship between violence and precipitation, each of the 119 dated LIP individuals in our sample is assigned a “Poaceae Score (P.S.).” Scores are assigned based on the average percentage of Poaceae during the calibrated ^{14}C range for each individual. The Poaceae dataset contains a resolution of 25-year intervals, which means many individual ^{14}C ranges overlap multiple intervals. As long as an individual’s ^{14}C range overlaps with a Poaceae interval by five years or more, that interval value was included in the individual’s P.S. For example, if an individual exhibits a date range of 1220 – 1304 C.E., the values for the

1200, 1225, 1250, 1275 intervals were averaged to arrive at a P.S. of 83.4, which measures by proxy the average precipitation during that individuals lifetime.

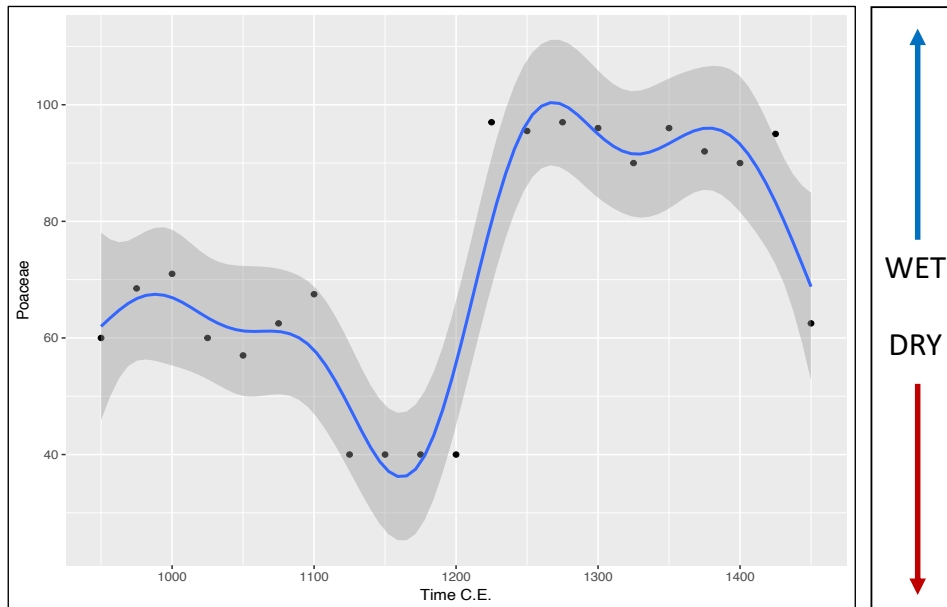


Figure 3.4. A General Additive Model (GAM) showing a regression of the proportion of Poaceae pollen through time as a proxy for precipitation (figure adapted from Schitteck et al. 2015).

4. Predictor: Wari Collapse and Inca Expansion

The timing of Wari collapse and Inca expansion in the Nasca highland region is relatively well documented. All evidence of Wari occupation of the broader Nasca region terminates in the mid-to-late tenth century C.E. (Conlee 2015; Edwards 2010). Indeed, the Nasca region as a whole was largely abandoned in the tenth century and was not reoccupied until the thirteenth century C.E. (Conlee 2015). Ethnohistoric documents point to the Inca invasion of the Nasca region sometime in the mid-to-late fifteenth century C.E. (Conlee 2000). These same accounts mention numerous highland populations that actively resisted Inca incursions by either directly confronting the Inca army or hunkering down in heavily fortified hilltop refuges in the hopes of outlasting an Inca siege.

In either case, we expect patterns of violence to temporally covary with either of these events if Wari collapse or Inca expansion drove patterns of warfare in the study region. If Wari collapse spurred violence, we should expect to see an increase in trauma circa 1000 C.E. and a rapid or gradual decline as political stability was restored. If the Inca incursion drove patterns of violence, we expect trauma to remain low to absent then peak during the terminal LIP circa 1450 C.E.

5. Predictor: Dietary Stress

Dietary stress is measured by proxy using the frequency of cribra orbitalia and porotic hyperostosis and an aggregate pathology measure that includes the frequency of both cribra orbitalia and porotic hyperostosis. While the specific etiology of cribra orbitalia and porotic hyperostosis cannot be determined, as previous research has shown that cranial porosities may be caused by anemia, scurvy, rickets, parasitic infection, as well as hemorrhagic or inflammatory processes (Walker et al. 2009), the Nasca highland's high elevation location, extreme aridity, marginal baseline environmental productivity, and widespread occurrence of pathological conditions make it very likely that the recorded pathologies indicate malnutrition and/or malabsorption. While debate continues as to whether cranial hypertrophy is caused by malnutrition (Piperata et al. 2014; Walker et al. 2009) or malabsorption due to intestinal parasitic infection (Holland and O'Brien 1997; Scaffidi 2018), the fact remains that both of these pathways produce dietary stress. For our purposes here it is not important whether CO and PH are caused by inadequate nutrient consumption or inadequate nutrient absorption, as both produce dietary stress, which we hypothesize should correlate with rates of violence.

Evidence of porous lesions in the orbits (cribra orbitalia) and cranial vault (porotic hyperostosis) were identified by direct macroscopic observation and examination under low

magnification (10x). Cribra orbitalia and porotic hyperostosis were recorded using Buikstra and Ubelaker Standards (1994) in order to facilitate comparison of LIP lesion frequency to previously reported lesion frequency for Middle Horizon burials (Kellner 2002). Lesions were recorded as present even if unilateral, though side was noted in unilateral cases. Lesion activity status at time of death was determined based on criteria laid out by Mensforth and colleagues (1978), and lesion expression was recorded using the Standards Ordinal Index (0 – 3). Each cranium was photo documented to facilitate independent validation of pathological findings by other researchers.

E. Results

Analytical results show interesting, non-linear trends that provide mixed support for the proposed hypotheses. When interaction effects are assessed several trends emerge that support hypotheses one (resource scarcity), three (collapse), four (demography), and lead us to reject hypothesis two (Inca expansion). These results yield salient insights into the motivations for war. The results of the climate and demography tests are shown in Figures 3.5 and 3.6, which plot the residual standard deviations of the trauma measures against precipitation and population density. These graphs show how much the data points spread around the regression line and provide an estimate of each model's predictive power and error.

1. Wari Collapse and Inca Expansion

We can reject the hypothesis that Inca invasion spurred regional violence, as the entire human skeletal sample exhibits ^{14}C ranges prior to the arrival of Inca armies in the region, showing that warfare was in full swing hundreds of years before Inca pressure was felt and persisted right up until 1450 C.E.

The increase in violence during Phase I coincides with the collapse of the Wari empire in the Nasca region. Indeed, while our terminal MH (800 – 950 C.E.) sample is exceedingly small, the five individuals that date to the terminal MH and do not exhibit any peri-mortem or ante-mortem trauma. Further, the Nasca lowland MH sample (Kellner 2002, $n = 97$) exhibits low rates of ante-mortem trauma (9%) and zero instances of peri-mortem trauma. These data may suggest the escalation in violence occurred immediately after Wari abandonment circa 1000 C.E., although our terminal MH sample is too small to make reliable inferences at this time. Nonetheless, levels of violence remain consistently high throughout the LIP, with the decline during Phase II occurring more than 250 years after Wari collapse and the peak in the intensity of warfare occurring during Phase III. Thus, Wari collapse temporally correlates with the initiation of LIP warfare but cannot explain its persistence or temporal variability.

2. Climate and Demography

There is significant collinearity between precipitation and population density (GAM: $R^2 = 0.926$, $p = 0.000$). This result is not surprising, as numerous studies have demonstrated that population densities are often a function of environmental productivity (Coddington and Jones 2013; Fretwell and Lucas 1969; Kennett et al. 2009; Winterhalder et al. 2010). Despite the covariance in our predictor variables, we present the results of the precipitation and population density regression models separately: (1) to illustrate divergences in predictive power; and (2) because of differences in hypothesized expectations regarding the effects of these variables on warfare.

Precipitation (Figure 3.5) does not significantly predict variability in peri-mortem trauma ($R^2 = 0.016$, $p = 0.532$). Precipitation has a non-significant but trending relationship with critical trauma ($R^2 = 0.072$, $p = 0.102$). The association between precipitation and overkill trauma is not

significant ($R^2 = 0.004, p = 0.25$), nor is the relationship with sum of traumas significant ($R^2 = 0.002, p = 0.26$). To summarize, average precipitation has a weak relationship with rates of violent trauma over the LIP as a whole. Nonetheless, violence increases significantly at the onset of the LIP (Fisher's exact: ante $p = 0.027$, peri $p = 0.001$) while average precipitation significantly decreases ($t = 2.054, p = 0.040$), showing that declining precipitation is associated with the high levels of violence during Phase I, but cannot explain the violence during Phases II or III.

The effect of climatic volatility on violence was explored using ANOVA tests comparing the variance in Poaceae Score values with changes in our trauma measures. Variability in precipitation changes significantly over time (PI SD = 11.35, PII SD = 10.6, PIII SD = 1.3; $F = 326.7, p = 0.000$). The high variance in precipitation in Phase I is the result of increasingly volatile regimes trending towards *decreased* average precipitation, while the high variance in Phase II is the result of a rapid *increase* in the abundance of precipitation. Variability in precipitation has a non-significant effect on peri-mortem trauma ($F = 0.002, p = 0.968$), overkill trauma ($F = 1.487, p = 0.225$) critical trauma ($F = 0.702, p = 0.968$) and the sum of traumas per individual ($F = 1.282, p = 0.26$).

Population density is not a significant predictor of peri-mortem ($R^2 = 0.002, p = 0.267$) or overkill ($R^2 = 0.032, p = 0.202$) trauma (Figure 3.6). The lack of a significant relationship between population density and peri-mortem/overkill trauma is partially the result of (a) high level of peri-mortem trauma (20%) during Phase I when population densities are lowest and (b) the low levels of peri-mortem trauma during Phase II when population density is on the rise. Nonetheless, peri-mortem trauma increases significantly during Phase III (Fisher's exact $p = 0.05$) during the temporal interval when population densities significantly deviate above the

growth null model (Figure 3.6). Population density significantly predicts critical trauma ($R^2 = 0.081, p = 0.014$) and the sum of traumas per individual ($R^2 = 0.040, p = 0.016$). These relationships show that violence co-occurs with the population spike in Phase III but is not restricted to it. These results also demonstrate the temporal lag between the population increase and escalations in violence predicted in the demography hypothesis. Results suggest that population density explains much of the variability in regional warfare but does not account for high rates of peri-mortem trauma in Phase I. They also suggest population pressure significantly predicts the intensity of violence, as measured by critical and sum of trauma, but not necessarily the lethality of violence, which may suggest the ability to survive the heinous blunt-force injuries so often seen may have increased during Phase III, when critical trauma and peri-mortem trauma deviate substantially from each other (Figure 3.2a).

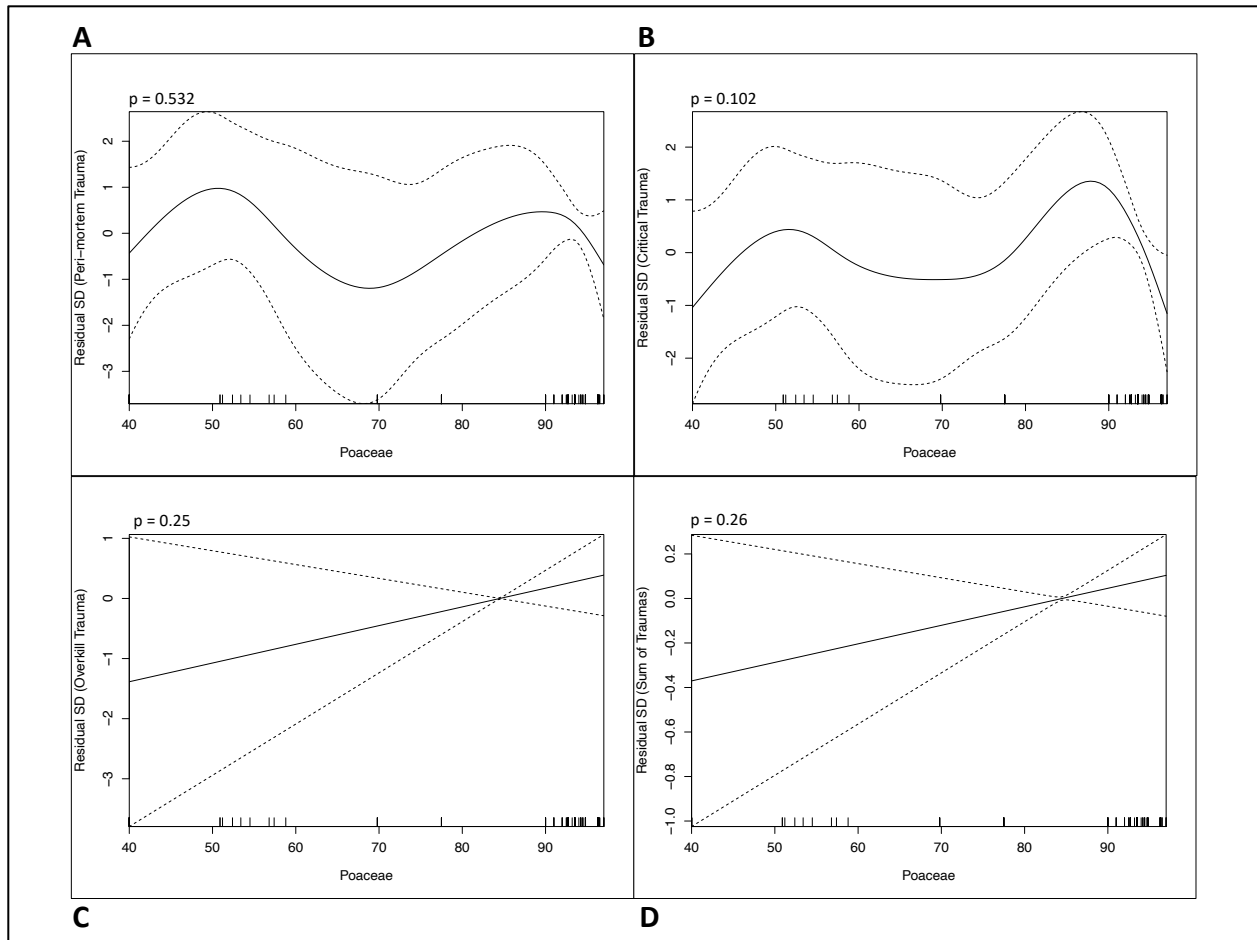


Figure 3.5. General Additive Models (GAMs) comparing the Poaceae proxy for precipitation with the residual standard deviations of (A) peri-mortem trauma, (B) critical trauma, (C), overkill trauma, and (D) Sum of trauma per individual. The GAMs plot the residual standard deviations of the trauma measures (y-axis) against precipitation and population density (x-axes) to show how much the data points spread around the regression line and provide an estimate of each model’s predictive power and error. Tick marks along the x-axis show our observations.

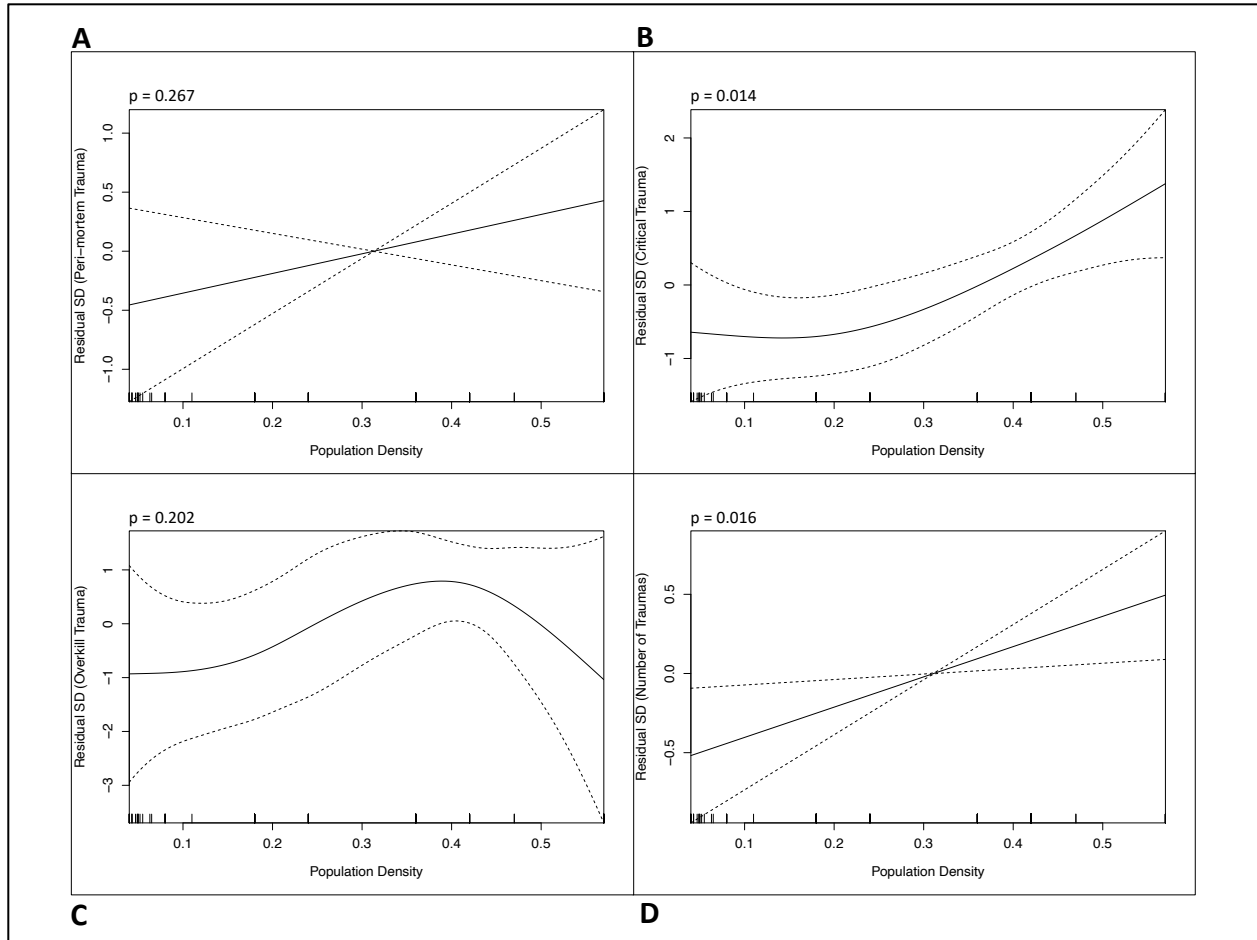


Figure 3.6. General Additive Models (GAMs) comparing the Summed Probability Distribution (SPD) values with the residual standard deviations for (A) peri-mortem trauma, (B) critical trauma, (C) overkill trauma, (D) Sum of traumas per individual.

3. Dietary Stress

Linear and non-linear regression models that compare pathology to trauma do not yield significant results. This is because, regardless of LIP phase, those with peri-mortem trauma are not more or less likely to exhibit pathological lesions. In other words, variability in pathology does not explain differential *susceptibility* to a violent encounter. Pathology, our marker of population stress, does however positively co-vary with all forms of trauma, showing stress and violence are positively associated (Figure 3.7). This is especially true with cribra orbitalia, which closely parallels all recorded forms of trauma (Figure 3.7).

To facilitate a statistical comparison between dietary stress and violence over time, it was necessary to disaggregate our LIP sample from three temporal phases into five. The increase in the number of temporal bins permits correlation tests that can evaluate the association between our measures of pathology with those of trauma. Five phases were created: P1 (950 – 1175 C.E.), P2 (1175 – 1250 C.E.), P3 (1250 – 1325 C.E.), P4 (1325 – 1400 C.E.) and P5 (1400 – 1475 C.E.). The chronological ranges and the number of temporal bins were selected in order to maximize the number of categories for statistical analysis and the sample sizes within each bin. When data are parametric a Pearson’s r test was used while non-parametric data were tested using Spearman’s ρ . The results are listed in Table 3.2. For nearly all tests there is a positive correlation between pathology and trauma that corresponds with the first prediction in hypothesis one. While the p -values are often non-significant due to small sample sizes restricting statistical power, the correlation coefficients trend positively. A follow-up General Linear Model (GLM) comparing the aggregate pathology measure with peri-mortem shows a significant predictive relationship between dietary stress and lethal trauma ($R^2 = 0.875$, $F = 20.91$, $p = 0.0196$). To summarize, pathology does not explain *differential vulnerability* to violence, but it does associate positively with violent trauma throughout the LIP timeframe.

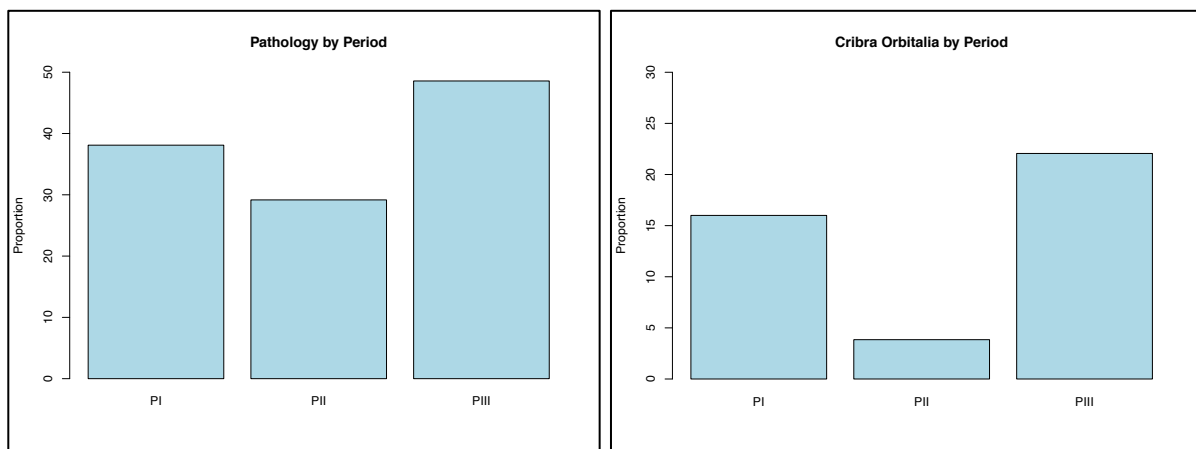


Figure 3.7a (left). The frequency of the aggregate pathology measure over time. **Figure 3.7b** (right). The frequency of cribra orbitalia over time.

Table 3.2. Correlation tests between our pathology and trauma measures. The LIP was broken down into five subphases to permit statistical comparisons. Significant correlation coefficients are highlighted in dark gray while strongly trending coefficients are highlighted in light gray.

Comparison	<i>r</i> coefficient	<i>p</i> -value
Cribra O. ~ Peri	Pearson's <i>r</i> = 0.87	0.057
Cribra O. ~ Critical	Pearson's <i>r</i> = 0.73	0.161
Cribra O. ~ Overkill	Pearson's <i>r</i> = 0.625	0.259
Porotic H. ~ Peri	Pearson's <i>r</i> = 0.59	0.296
Porotic H. ~ Critical	Spearman's <i>rho</i> = 0.10	0.95
Porotic H. ~ Overkill	Pearson's <i>r</i> = 0.223	0.719
Pathology ~ Peri	Pearson's <i>r</i> = 0.935	0.02
Pathology ~ Critical	Spearman's <i>rho</i> = 0.60	0.35
Pathology ~ Overkill	Spearman's <i>rho</i> = 0.56	0.322

4. Climate, Demography, and Dietary Stress

While dietary stress clearly associates with violence, to what degree is dietary stress a result of fluctuations in precipitation and/or population pressure? There is a non-significant association between precipitation and pathology ($p = 0.315$), cribra orbitalia ($p = 0.243$), and porotic hyperostosis ($p = 0.238$). The relationship between population density and pathology and porotic hyperostosis is also non-significant ($p = 0.281$, $p = 0.705$, respectively), while there is a trending association between population density and cribra orbitalia ($p = 0.095$). Weak associations between climate, demography, and dietary stress are the result of multivariate driving processes. Dietary stress was high during Phase I when population density was low, and precipitation was declining. Stress was also high in Phase III when precipitation was abundant and population density peaked. During Phase II, cribra orbitalia declined while porotic hyperostosis increased. We argue that the significant increase in dietary stress at the onset of the LIP and its persistence throughout the period suggests precipitation, population density, and

violence all contributed to the high rates of stress. The persistence of chronic stress combined with the heterogeneous trends for cribra orbitalia and porotic hyperostosis prevent us from running more robust tests as the variability in pathology is neither uniform nor consistent. What appears clear, however, is that high rates of dietary stress predict high rates of violence, during periods of low population density and drought, as well as times of abundant rainfall and high demographic pressure.

F. Discussion and Conclusion

1. Wari Collapse

Temporal trauma patterns suggest violence in the region remained low until Wari abandonment. The significant rise in warfare during the onset of the eleventh century C.E. indicates a connection with Wari collapse. Nevertheless, the persistence of internecine warfare centuries after Wari's departure paired with the significant increase in violence circa 1300 C.E. show that while Wari collapse may have partially incentivized the initiation of warfare, it cannot explain the long-term perpetuation of warfare. The temporal association with Wari collapse and the emergence of warfare provides tentative support for Hypothesis 2—however, this single event cannot explain variability within Phase I, the decline in violence during Phase II, or the dramatic increase during Phase III. As such, we focus our discussion on the alternative hypotheses that better capture variability in warfare throughout the 500-year LIP.

2. Climate and Demography

Results yield interesting associations that point to multivariate causal processes. The associations between violence, climate, dietary stress, and demography illustrate a complicated picture that connects variability in violence to fluctuations in resource availability.

Warfare in Phase I coincides with a period of emergent drought conditions and considerable dietary stress. Demographic reconstructions for Phase I demonstrate low relative population densities and thus low resource demand during this phase of diminishing and increasingly unpredictable productivity. Despite low resource demand, the significant rise in dietary stress during Phase I suggest resources were nevertheless inadequate. Results show that the combination of drought conditions, dietary stress, and political instability wrought by Wari collapse produced socioecological conditions that promoted warfare, conditions which are consistent with the expectations laid out in Hypotheses 1 and 3.

The marked decrease in violence during Phase II must first be framed in a broader context. While trauma falls to its lowest levels during this time, warfare continued, with ante-mortem and peri-mortem trauma rates remaining at levels consistent with chronic warfare (Chapter 1). The decrease in violence during this time appears to be the result of increasingly abundant and predictable rainfall. It is possible that the political climate may also have been improving as the effects of Wari collapse diminished. The increasing population densities at this time may have actually improved resource conditions and reduced the incentives for conflict via economies of scale and allee effects (Coddling et al. 2017). Thus, the Phase II population experienced a reprieve, during which time productivity likely improved, average dietary stress declined, and the regional population began to grow. Nonetheless, warfare persists throughout this phase, likely driven by the continuation of resource stress (which can only be considered low in relative terms to Phases I and III) and the in-filling of the highly circumscribed highland region (McCool 2017), which may have incentivized territoriality (McCool and Yaworsky 2019).

Violence in Phase III rises to levels rarely seen among prehistoric populations. The large proportion of warfare-related casualties had dramatic effects on population structure, behavioral strategies, economic outcomes, and health. Environmental productivity was at its zenith during this time, resulting from abundant and predictable precipitation; however, the per capita resource abundance was declining as evidenced by increased dietary stress concomitant with the dramatic spike in population density. Thus, results yield support for the demography and resource scarcity hypotheses (#1 and #4), whereby demographic pressure strongly predicts patterns of Phase III warfare and much of the variability in violence throughout the LIP. Increasing demographic pressure led to density-dependent declines in net resource returns in a context of extreme circumscription. This combination of conditions promoted warfare and intensified territorial strategies. These findings are in line with recent economic research that has shown a link between climate and conflict via a population density pathway (Burke et al. 2015; Hsiang et al. 2013). These studies show that improved climatic conditions often facilitate large influxes of people that reduce per capita resources below demand thresholds, and thus incentivize many forms of violence (Burke et al. 2015; Hsiang et al. 2013).

We summarize the proposed causal relationships by developing a post-hoc explanatory model using subsistence productivity and resource demands curves that illustrate the relationship between resource availability and violence (Figure 3.8). In this model, the primary driver of warfare is resource scarcity, which in turn is influenced by ever-changing factors (climate, demography, and violence) in a series of feedback cycles (see below). Violence is high whenever the supply curve intersects or falls below the demand curve, with the intensity of violence being a function of the distance between the supply and demand curves.

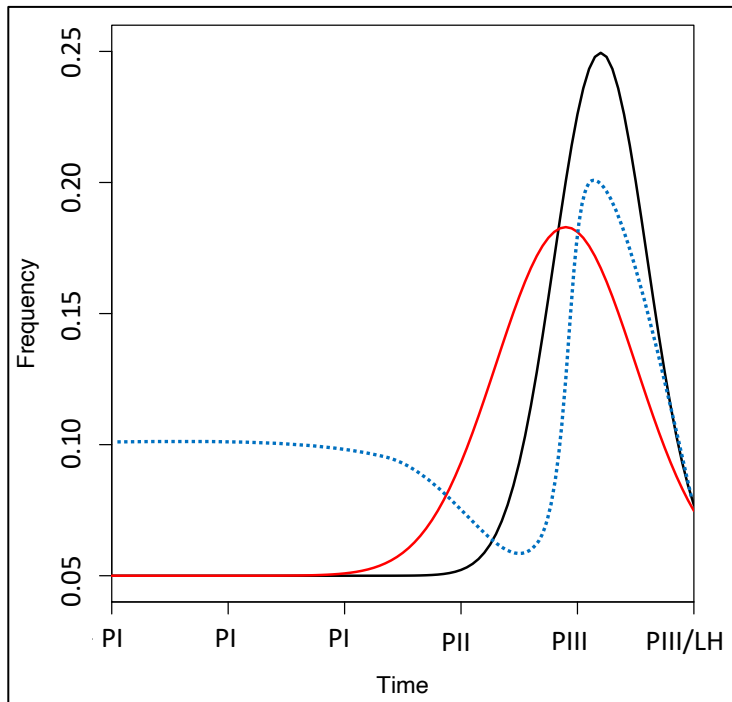


Figure 3.8. A hypothesized explanatory model. The red (left-shifted) distribution represents subsistence productivity, the black (right-shifted) distribution represents resource demands, and the dotted blue line represents violence. The x-axis presents our chronological scheme while the y-axis presents arbitrary frequency values.

3. Phase II and Phase III Population Expansion: *in-situ* growth or immigration?

Existing data strongly suggest that the observed population increase beginning in Phase II and peaking in Phase III was the result of in-migration, likely of populations from the high Sierra regions to the east. Around 1200 C.E., Sierra populations were on the move as a result of chronic warfare and drought conditions that afflicted the region but missed the coastal and near-coastal highland regions (Eitel et al. 2005; Hillyer et al. 2009; Kennett and Marwan 2015; Thompson et al. 1985). Indeed, LIP investigations of the Andahuaylas region to the east of the Nasca highlands report missing populations in the latter half of the LIP, with the vast majority of sites dating to the first two centuries of the LIP (Kurin et al. 2012; Lofaro et al. 2018). Recent mtDNA studies in the Palpa region directly north of the Nasca highlands have shown that the entire

region was abandoned during the terminal MH circa 850 C.E. and was reoccupied in the 1200s by a population with a highland mtDNA signature (Fehren-Schmitz et al. 2014). As mentioned earlier, the Nasca lowlands were also abandoned in the mid to late 900s C.E. and only reoccupied in the 1200s by populations thought to be of Sierra origin (Conlee 2015). Thus, there is evidence of populations emigrating from the Sierra regions into the near-coastal highland regions directly neighboring the Nasca highlands. These factors point to a similar migratory process playing out in the Nasca highland region that may have spurred the rapid population increase seen during Phases II and III.

In addition to the evidence from surrounding regions, the conditions present in the Nasca highlands during Phases II and III make an *in-situ* population increase unlikely due to the high mortality and morbidity (see, Chapter 2). During the entire period of population growth, the Nasca highland population was experiencing dietary stress, chronic violence, high mortality, population packing in confined hillforts, and other factors that suggest any increase in fertility during this time would be outpaced by mortality. Given such constraints, it is most probable that the influx of people during Phase III was the result of mass migrations that put increasing pressure on the limited and circumscribed Nasca highlands resource base.

4. Feedback Systems and the Scale of Selection

Results show a significant relationship between dietary stress and violence under climatological, political, and demographic conditions known to produce resource scarcity. Disentangling the causal web between violence and resource scarcity is notoriously challenging. Many scholars have commented on the difficulty of parsing out whether resource shortfalls are a cause or consequence of violent conflict. Indeed, the equifinality inherent in many archaeological assemblages ensures that violence and resource shortfalls will emerge simultaneously in terms of

archaeological time. We argue however that this chicken and egg problem is better framed as a feedback system rather than a monocausal chain of events. Clearly, there are many recorded instances of resource shortfalls provoking violence (Allen et al. 2016; Ember and Ember 1992; Ember et al. 2013; Gat 2009; Kelly 2000; Kohler et al. 2014; LeBlanc 1999) and, in turn, violence creating resource shortages (Kurin 2016; Glowacki and Wrangham 2013; Lambert 1997, 2002; Maschner and Reedy-Maschner 1998; Milner et al. 1991; Ortner 2008; Steadman 2008; Tung et al. 2016; Walker 2001). However, there is sufficient existing data to demonstrate that these two phenomena feedback on one another, with scarcity promoting violence, and resource theft and the threat of violence reducing supply (Allen et al. 2016; Glowacki and Wrangham 2013; Keeley 1996; LeBlanc 1999; VanDerwarker and Wilson 2016). This is not to say that intergroup violence is incapable of ameliorating short-term resource scarcity or generating resource wealth, there is certainly evidence for this outcome (Glowacki and Wrangham 2013, 2014). After all, successful aggressions can lead to “winning” outcomes via annexed territory, theft of food, forced tribute, etc. Rather, what appears empirically clear is that small-scale warfare is often motivated by resource benefits while consistently reducing the average population-level resource supply and increasing dietary stress.

The consistent finding that resource scarcity is both a cause and consequence of warfare provokes a potential evolutionary paradox: if the goal of coalitional violence is to overcome resource shortages, why does this behavioral strategy consistently lead to the opposite outcome? In other words, if intergroup violence evolved as a means of procuring subsistence resources, would we not expect this behavior to predictably alleviate resource shortages and dietary stress rather than exacerbate them?

The solution to this paradox may stem from two core concepts of evolutionary biology: the scale of selection and the status quest. We have known for decades that natural selection operates on the “selfish gene” rather than the individual or the group (Dawkins 1976). Behavioral ecology has shown that selection will consistently favor individual behaviors that enhance inclusive fitness, even at the expense of group survival (Bird and O’Connell 2006; Coddington and Bird 2015). If intergroup violence leads to a disproportionate share of resource rewards for those participating, selection will favor this strategy even if it leads to reduced group-level food abundance or resource scarcity in the long-term (Glowacki and Wrangham 2013). We hypothesize that selection will favor participation in resource-based violence so long as the fitness rewards are directed at participants, even if this strategy decreases group well-being or survival (Wrangham and Glowacki 2012; Glowacki and Wrangham 2013). Subsequently, warfare-induced resource scarcity should not necessarily be used to infer non-resource-based motivations. In order to reject a resource-motivated hypothesis, it must be demonstrated that those doing the fighting are receiving non-material benefits or are coerced into participation through structural means (e.g., drafts).

Thus, we do not consider it problematic that warfare in the LIP Nasca highlands appears to consistently positively covary with dietary stress. We contend that violence may beget violence via motivating factors that favor individual material benefits over the welfare of the group. Warfare may emerge as a strategy for procuring subsistence resources, with the effect of providing rewards for some and creating or exacerbating resource scarcity for most. Subsequently, the long-term perpetuation of warfare in the Nasca region coupled with the persistently high levels of dietary stress most likely reveal a feedback system that provided

fitness-related motivations for continual participation in intergroup violence, thus creating a tragedy of the commons.

5. The Status Quest

Ample evidence shows that participation in conflict can yield rewards in the form of status (Chagnon 1988; Gat 1999; Glowacki and Wrangham 2013, 2014; Patton 1996), which reliably tracks fitness (Chagnon 1988; Cronk 1991; Glowacki and Wrangham 2013; Kaplan and Hill 1984; Hopcroft 2006; Von Rueden et al. 2011). Individual motivations for participation in intergroup conflict may stem from status incentives that provide avenues to enhanced fitness but may also negatively impact the group. The ability of archaeologists to track the effect of status on rates of violence is expressly difficult. Status is manifested in individuals rather than groups and can be achieved through any number of differing pathways. Discerning whether or not enhanced status derives from participating in warfare is difficult enough, determining whether the status pursuit explains variability in population-level violence has proven to be an immensely challenging task. To what degree may we expect intragroup status competition to drive the observed patterns of warfare in the Nasca highlands?

Ethnohistoric records of the LIP Andes certainly point to status competition through war. Indeed, the Spanish colonial accounts are rife with tales of LIP warlords using conflict to create and maintain their status as chiefs (Cobo 1979 [1653]; Guaman Poma 1980 [1613]). Nevertheless, these records report the LIP through the colored lens of Inca chroniclers and the biased pen of Spanish colonists. The Inca who provided the narratives for these records paint the pre-Inca Andes as a dark age of petty warlords with humans living nasty, brutish, and short lives. This view, of course, provides a moral justification for Inca conquest and subjugation of the

Andes, and should be seen as the winner's perspective on history. To what degree these records correlate with LIP actualities is largely unknown.

From a processual perspective, an association between status seeking and violence may be seen indirectly when exogenous causal factors fail to explain variability in violence. The patterns of warfare in the Nasca highlands do not meet this criterion. While the relative influence of climatological, political, and demographic drivers varies through time, patterns of warfare significantly co-vary with these forces in ways our hypotheses predict. While the status quest may be responsible for explaining some of the residual variation not captured by our models, we believe the combination of climate, dietary stress, demography, and political instability provide a compelling explanation of LIP warfare in the Nasca highlands. Future research will explore whether our model predictions will hold up when tested using a multiregional dataset.

6. Conclusion

Results show a multivariate causal process driven by fluctuations in rainfall, population pressure, and resultant dietary stress. During the first 150 years of the LIP, high rates of violence are associated with declining precipitation, dietary stress, and the regional abandonment of the Wari empire. From 1200 – 1300 C.E., climate conditions ameliorated, dietary stress declined, and the population began to grow, all of which reduced the incentives for warfare and led to a reduction in violence. The success created by improving environmental productivity and rapid population expansion circa 1300 – 1450 C.E. ultimately led to declining resource availability, shown by a significant increase in dietary stress. In the highly circumscribed environment of the Nasca highlands the demographic pressure combined with resource scarcity stimulated an escalation in violence, which resulted in nearly 150 years of internecine warfare.

This study adds to a growing body of research evaluating the climatological, political, and demographic drivers of intergroup violence. Our own evaluation led us to develop general predictive models that can explain variability in warfare across time and space. Hypothesis tests included interactions between independent variables, going beyond monocausal explanations of conflict. By developing and testing predictive models using case studies we will be better able to predict whether similar conditions will favor conflict in the future (Burke et al. 2015; Hsiang et al. 2013; Zhang et al. 2007b). With increasingly stochastic and severe climate change occurring in the present day along with dramatic population pressure, we need to develop research programs to evaluate human responses to socioenvironmental change (e.g. Burke et al. 2015; Scheffren et al. 2012; Zhang et al. 2007b). This can be accomplished through the development of increasingly sophisticated models that can assess heterogeneity in conflict-promoting conditions and predict which areas have the highest probability of violent outcomes. The application of these models may help with current conflict mitigation, and future prevention.

IV. Examining Trade-offs between Food Acquisition and Violence Avoidance: population-level effects and variability in risk-preference

A. Introduction

Resource procurement and avoidance of interpersonal violence are critical features of human survival strategies. Yet these two features are often competing, requiring individuals to make trade-offs in order to maximize fitness. Understanding how individuals optimize this trade-off will yield insights into the evolution of violence avoidance behaviors, as well as general patterns of population mortality and morbidity. Nevertheless, this particular trade-off has gone largely unexplored in anthropology.

Outside the anthropological literature the trade-off between subsistence and violent mortality has received broad attention under the umbrella of non-human “predation risk” studies (Bachman 1993; Bøving and Post 1997; Brown and Kotler 2004; Cowlshaw 1997; Creel et al. 2014; Stanford 2002; Switalski 2003; Wolf and Van Horn 2003). Predation risk research assesses spatial and temporal heterogeneity in risk with the goal of explaining how individual’s cope with the trade-off between predation avoidance behaviors and competing fitness demands (Brown and Kolter 2004; Creel et al. 2014; Wolf and Van Horn 2003). The majority of predation risk studies find that as the probability of predation rises, organisms increasingly engage in avoidance behaviors at the cost of competing requirements such as foraging (Bachman 1993; Bøving and Post 1997; Brown and Kolter 2004; Creel et al. 2014; Stanford 2002; Swatalski 2003; Wolf and Van Horn 2003). Predation risk studies seek to elucidate “risk effects” on individual fitness and population-level dynamics (Brown and Kotler 2004; Creel et al. 2014), as well as explain inter-specific and individual variation in the types of predation avoidance tactics and the degrees to which organisms invest in them (Creel et al. 2014).

While humans can be affected by the risk of becoming prey, our behavior is more heavily influenced by the risk of interpersonal lethal and sublethal violence (Allen et al. 2016; Arkush and Tung 2013; Gat 1999, 2006; Glowacki and Wrangham 2013; Glowacki et al. 2017; Hickerson 1970; Keeley 1996; Kelly 2000; Otterbein 1999; Pinker 2011; Walker 2001; Walker and Bailey 2013; Wrangham 1999; Wrangham et al. 2006; VanDerwarker and Wilson 2016). Despite these differences the conceptual framework of predation risk research can be operationalized to investigate how the risk of violence affects human behavior and health. The benefits of applying a modified predation risk model to human behavior stem from the ability to generate and test formal expectations regarding population- and individual-level risk-avoidance tactics and their fitness effects. Modified to humans, predation risk studies suggest that increasing risk of interpersonal violence (henceforth RIV) favors behaviors that decrease the RIV at the cost of competing demands such as food acquisition.

1. Trade-offs between Food Security and Personal Safety

The last twenty-five years of anthropological research has seen a dramatic increase in studies on intergroup lethal aggression among humans (Allen et al. 2016; Arkush and Allen 2006; Arkush and Tung 2013; Gat 2006; Glowacki and Wrangham 2013; Glowacki et al. 2017; Keeley 1996; Kelly 2000; LeBlanc 1999; Milner 1999; Tung 2012; VanDerwarker and Wilson 2016; Walker 2001). This research has produced ample evidence showing lethal and sublethal violence to be a pervasive, albeit variable, feature of the human career. As such, it is becoming increasingly clear that interpersonal violence was a persistent threat and thus an important selection pressure throughout much of human prehistory. High levels of violence raise the inevitable question as to what behaviors evolved to reduce the RIV, and at what cost?

Archaeological and ethnographic data suggest that the costs of violence avoidance are largely manifested as subsistence constraints and related dietary stress (Glowacki and Wrangham 2013; Hickerson 1970; Human Security Report 2005; Keeley 1996; Kelly 2005; Kurin 2016; Meggitt 1977; Netting 1973; Roscoe 1996; VanDerwarker and Wilson 2016). Numerous studies on small-scale warfare show that when the risk of interpersonal violence is high, travel is dangerous and should be avoided when at all possible (Glowacki and Wrangham 2013; Hickerson 1970; Keeley 1996; Kelly 2005; Kurin 2016; Milner 1999; Meggitt 1977; Netting 1973; Roscoe 1996; VanDerwarker and Wilson 2016). Unfortunately, basic biological demands necessitate a compromise between violence avoidance and resource acquisition. How do individuals' trade-off these competing demands in ways that maximize fitness? In the following section we develop a risk-sensitive model to formulate predictions regarding population-level risk avoidance tactics and individual variability in risk preference.

B. A Risk-sensitive Patch-choice Model

We generate a risk-sensitive marginal value theorem (MVT) model that stipulates how RIV structures the payoffs for various subsistence behaviors. The MVT is a patch-choice model that specifies how long an individual should stay in a patch so as to maximize their overall energetic return rate, with the expectation that the optimal time in-patch increases with patch distance from a central place or neighboring patch (Bettinger and Grote 2016; Charnov 1976). The MVT specifies an energetic gains function, $G(t)$, which we define following Charnov and Parker (1995) as

$$G(t) = E[1 - e^{-ct}]$$

where

E = total energy in patch,
 c = gain rate in patch
 t = total time in patch

The return rate at any time t is, thus, the slope of G(t) at t, with the optimal leave time being the point where the slope is greatest (Figure 1a). Here, we extend G(t) to include costs of RIV avoidance strategies using the function, P(t), which we define as

$$P(t) = e^{-mt}$$

where

m = risk of interpersonal violence, with $0 \leq m \leq 1$
 t = total time in patch

P(t) specifies the proportion of t actually spent foraging as opposed to engaging in violence avoidance behaviors. Thus, the total amount of energy recovered from a patch with RIV included is given by

$$G(t) * P(t)$$

This equation specifies how the risk of interpersonal violence discounts the gains curve as individuals increasingly invest time in RIV avoidance tactics (Figure 4.1a and 4.1b). The risk-affected gains curve is discounted so that the derivative intersects the gains curve at a lower efficiency and net energetic return, suggesting that individuals will leave patches sooner. Thus, the model's goal is to optimize two variables: to maximize energetic returns while minimizing the RIV.

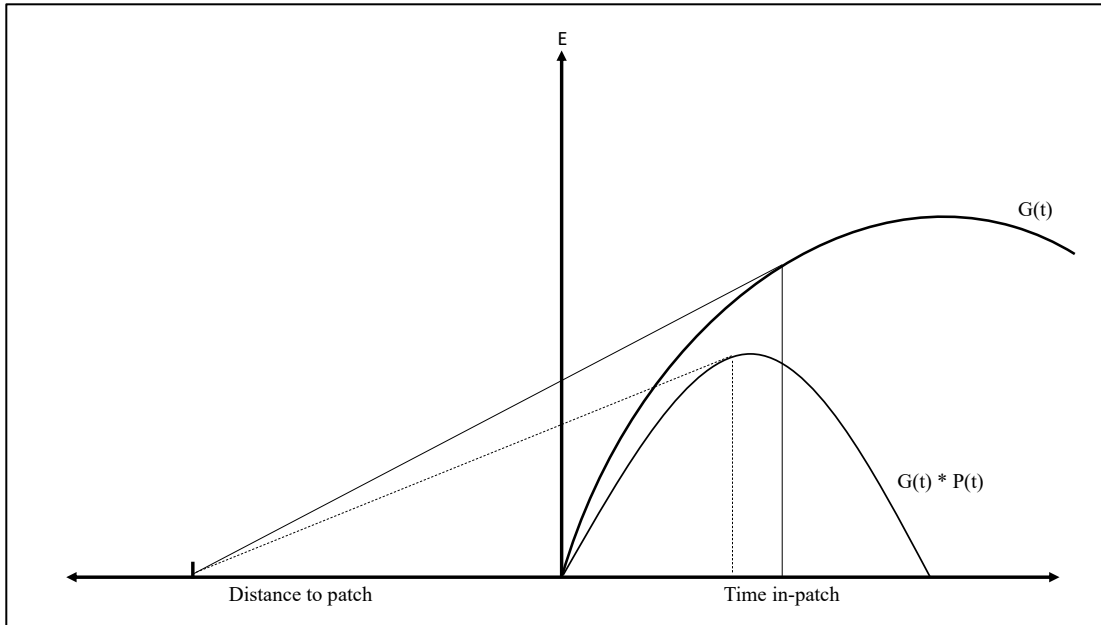


Figure 4.1a. A risk-sensitive Marginal Value Theorem model. $G(t)$ = energy, $P(t)$ = the proportion of t actually spent foraging as opposed to engaging in violence avoidance behaviors, $G(t) * P(t)$ = the total amount of energy recovered from a patch with RIV included.

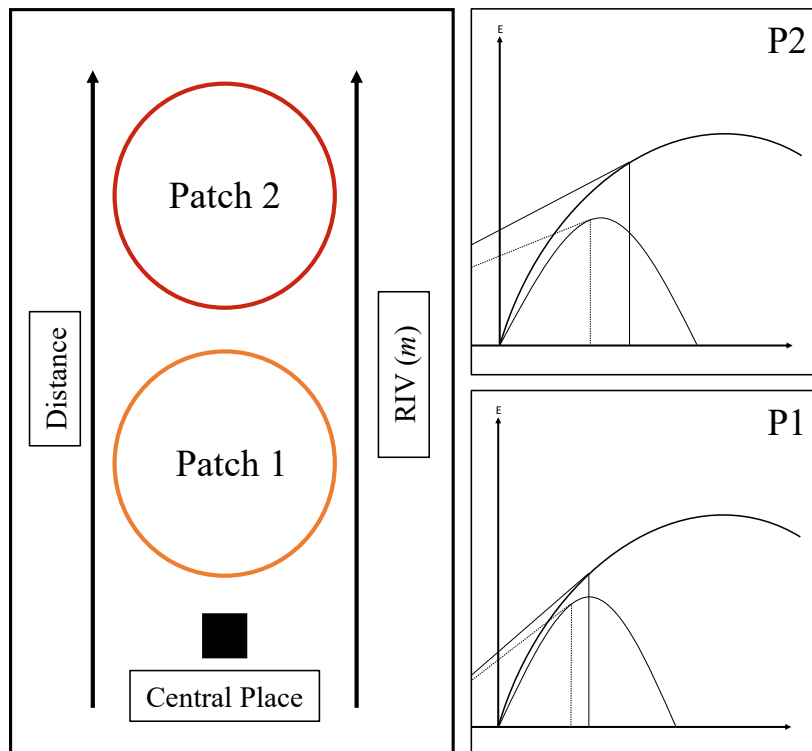


Figure 4.1b. This figure operationalizes the model to articulate how distance from a home base to a patch discounts the gains curve as a function of violence avoidance tactics.

1. Measuring Risk and Returns

To measure RIV for the present case study we use: 1) a spatially independent probability measure, and 2) a spatially dependent measure of patch-use variance. The *independent* measure is the average probability of a violent encounter. The spatially *dependent* measure evaluates how RIV varies by distance of a patch from a central place. Our model makes the relatively safe assumption that as the frequency and severity of *intergroup* violence increases, the probability of an *interpersonal* violent encounter will increase disproportionately based on an individual's distance from a central place (Figure 4.1b), with more distant resource patches exhibiting a higher probability of a violent confrontation. This is due to three salient factors: (1) patches further from a central place will favor longer in-patch residence times, (2) humans generally practice a fission/fusion subsistence system whereby aggregations of people temporarily disperse into smaller parties that are more vulnerable to attack or ambush (Gat 2015; Glowacki and Wrangham 2013; Keeley 1996; Kelly 2000, 2005; Milner et al. 1991; Roscoe 1996, 2008), and (3) there is safety in numbers at a home base. This is also based on extensive ethnographic and archaeological data showing that the majority of victims of intergroup violence are isolated individuals or small groups moving outside of central places (Bayham et al. 2019; Gat 2015; Glowacki and Wrangham 2013; Heider 1979; Hendrickson et al. 1996; Keeley 1996; Kelly 2000, 2005; Milner et al. 1991; Netting 1973; Roscoe 1996, 2008).

From this model we predict that a patch will be abandoned or avoided when the risk-effect reduces energetic returns below that of an alternative patch. An attractive alternative patch is that which has less deleterious risk-effects, likely as a result of a lower RIV. A patch will continue to be utilized at a lower efficiency when the risk-effect does not reduce energetic returns below alternative patches. As the potential fitness consequences of violent encounters are often more salient than reduced energetic returns (starvation takes time, a lethal encounter is

immediate), we expect that when the RIV is high populations will average towards risk-averse behavior.

An important implication of our model is its deviation from the predictions of the Central Place Foraging model, which predicts foragers/farmers will spend *more* time in distant patches. Conversely, our model predicts that when RIV is high, individuals will spend *less* time in distant patches and *more* time in patches close to a central place.

2. Variability in Risk-preference

To specify variability in risk-preference we define the risk-averse strategy as that which accepts reduced energetic efficiency in order to decrease the RIV (the $G(t) * P(t)$ gains curve in Figure 4.1a) and the risk-prone strategy as that which continues to maximize energetic efficiency at the cost of an increased RIV (the $G(t)$ gains curve in Figure 4.1a).

While our model predicts straight-forward population-level risk-effects, it is necessary to generate expectations regarding variability in risk-preference. As a first effort, we expect that sex, age, and the quality of local environments (along with the level of equality in food distribution) will most heavily influence variability in risk-preference. Young males tend to exhibit risk-prone behavior (Ermer et al. 2008; Kruger and Nesse 2006; Wang et al. 2009; Wilson and Daly 1985), partially due to status incentives associated with participation in dangerous activities (Bishop and Lytwyn 2007; Chagnon 1988; Glowacki and Wrangham 2013; Patton 1996), and partially due to competition with other males for material gains (Glowacki and Wrangham 2013). Further, in many foraging societies men tend to travel further during foraging bouts relative to women, often in pursuit of highly mobile game (Grimstead 2010; Hawkes and Bliege Bird 2002; Zeahan 2004). As such, we predict that some young adult males will continue using high-risk patches in order to acquire material gains or to signal their fitness quality to other

members of the population. Individual phenotypic quality (health status) as well as environmental quality will also structure the payoffs for alternative risk-preferences. Individuals who are in poor health or living in a marginal environment will be closer to their starvation threshold relative to healthier members of the population or to groups living in more productive areas. We predict that individuals in poor phenotypic condition will exhibit risk-prone behavior because they cannot afford the somatic penalty of reduced energetic returns. We also predict that individuals living in marginal environments will tend towards risk-prone behaviors relative to those living under more productive conditions (Kuznar 2001; Winterhalder et al. 1999).

C. Case Study

We test our model predictions using data from a small-scale population of agropastoralists that lived in the Nasca highlands of Peru circa 950 – 1450 C.E. (McCool 2017). This population resided in densely clustered fortified communities located throughout five small river valleys (Figure 4.2). This population was selected for the present study because of the spatial heterogeneity in economic activities (see below), and because the region experienced chronic warfare throughout the 500-year study period, known as the Late Intermediate period (LIP; 950 – 1450 C.E.) (McCool 2017). Previous research on warfare in the region has shown that lethal and sublethal violence is not concentrated on any single age or sex cohort (see, Chapter one). Rather, it appears that all members of this population were targeted for violence, suggesting an internecine pattern of warfare defined by social substitutability (Kelly 2000) and a lack of defined structural rules governing who should be the targets of violence (see, Chapter one). Thus, we have an empirically derived *a-priori* expectation that members of this population are targets of violence based on their vulnerability, which we expect to be primarily a function of

subsistence and other socioeconomic activities that put individuals in harm's way. In the following section we present the population data as well as the evidence for chronic warfare, which we use as the spatially independent measure of RIV.

To compare our results with those of a population who did not experience a high RIV, we utilize the results of trauma, pathology, and stable isotope research on a Middle Horizon (MH; 500 – 950 C.E.) population from the Nasca lowlands directly adjacent to our highland study region. The MH sample exhibits very low levels of healed trauma (9%) and zero cases of perimortem trauma (Kellner 2000), showing an absence of warfare. The sample also exhibits low rates of dietary stress with cribra orbitalia at 8.2% and porotic hyperostosis at 8.2% (Kellner 2000). These factors make the MH sample an excellent comparative baseline.

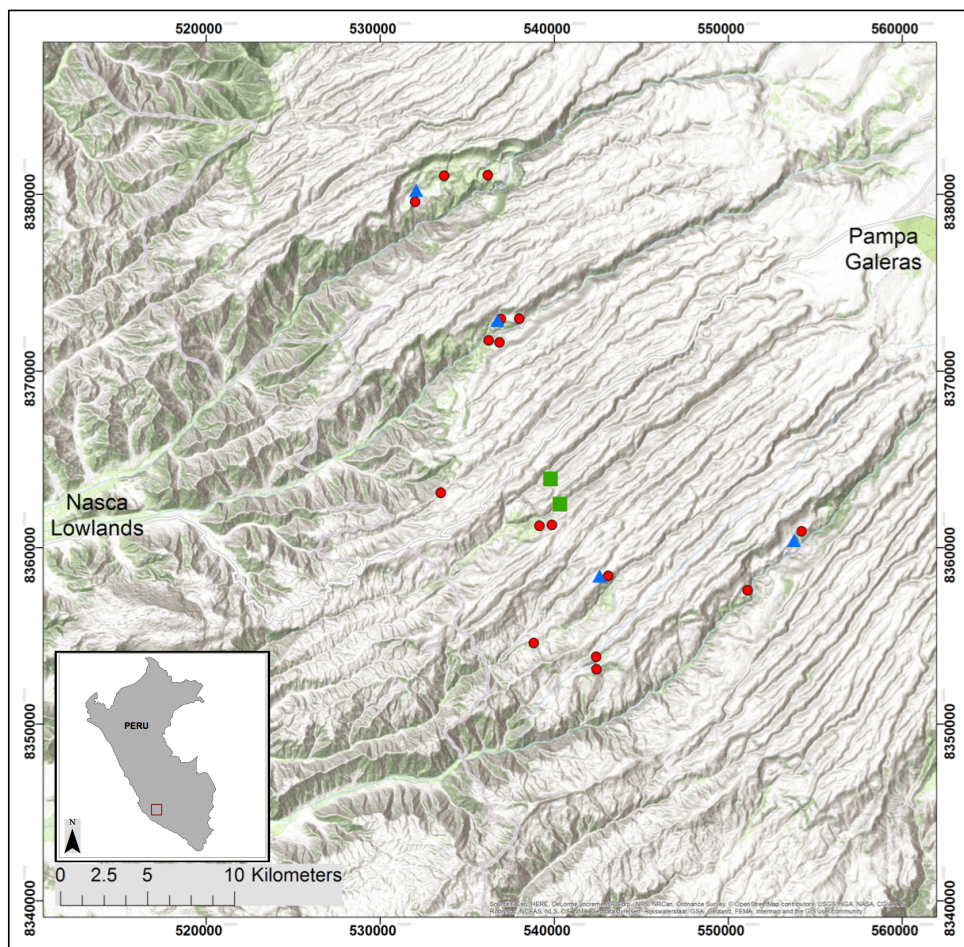


Figure 4.2. The study area. Points = residential hillforts. Triangles and squares = tombs. Note the clusters of sites within the agricultural zones and the distance to the Pampa Galeras in the upper right corner.

1. Human Skeletal Data

In order to assess rates of violence and their demographic patterning, in the fall of 2018 we excavated eleven LIP tombs in the Nasca highlands, producing a human skeletal sample of 325 individuals (determined by number of intact crania). Of the 325, 270 were sufficiently intact to assess age, sex, trauma, and pathology. The commingled nature of the LIP burial contexts prevents us from linking post-cranial elements to those on the cranium. As such, we restricted our osteological analyses to the sample of crania.

The age-at-death for each individual was estimated using the standards protocols for assessing stages of cranial suture closure, dental formation/eruption and surface wear (Bass 2005; Buikstra and Ubelaker 1994). Age-at-death estimations were completed for seven age cohorts: infant (0–4), child (4–12), adolescent (12–20), young adult (20–35), middle adult (35–50), and old adult (50+) (White and Folkens 2005). Sex was estimated using sexually dimorphic cranial features as per the Standards protocol (Bass 2005; Buikstra and Ubelaker 1994; Murphy et al. 2010; Vercellotti et al. 2014; White and Folkens 2005).

Rates of ante-mortem and peri-mortem trauma were recorded using evidence of bone healing as indicating ante-mortem trauma (Lovell 1997; Sauer 1998; Tung 2007). Radiating fractures, discoloration in fracture lines, and bone hinging at fracture margins were used to determine peri-mortem trauma (Ortner 2008; Sauer 1998; Tung 2007). Observations of cranial trauma distinguished between accidents and intentional violence and sharp-force vs. blunt-force trauma (Kurin 2016; Lambert 1997; Lovell 1997; Tung 2007, 2012). Postmortem damage was distinguished from peri-mortem trauma based on the coloration and shape of fracture margins

and the presence of hinging bone and radiating fractures (Berryman and Haun 1996; Murphy et al. 2010; Ortner 2008; Sauer 1998). Peri-mortem trauma was further divided into the frequency of “overkill” trauma, defined by the presence of multiple peri-mortem traumas that go beyond what is required to dispatch an individual (Kurin 2016; Šlaus et al. 2010). A “critical trauma” metric (Andrushko and Torres 2011) was also developed, defined here by healed or lethal traumas that are >25 mm in diameter, and/or >2.5 mm deep. As skeletal trauma can range from life-threatening injuries to hairline nasal fractures, critical trauma provides a more accurate measure of violence than ante-mortem trauma.

One concern is whether the cranial-focused analyses can accurately capture rates of violence. LIP weaponry consisted of maces, hand-axes, and slings, which often requires direct cranial contact to inflict peri-mortem injuries. Previous research in the Andes and elsewhere has found cranial trauma analysis to be an effective means of establishing rates of violence (Kurin 2016; Martin and Harrod 2014; Torres-Rouff et al. 2005).

Patterns of LIP Violence

We evaluate temporal fluctuations in LIP violence using a sample of direct radiocarbon dates from 124 individuals (see, Chapter one). Samples were taken from the vomer and nasal concha when possible or the nasals/styloid process when necessary. In several cases, none of these elements were available, requiring the sampling of the zygomatic arch. Collagen was extracted and ultrafiltered in the Paleoecology and Isotope Geochemistry Laboratory at the Pennsylvania State University and analyzed on the W.M. Keck Carbon Cycle AMS at the University of California, Irvine. Resulting ^{14}C values were calibrated using the southern hemisphere calibration curve and the rcarbon package in the R environment (Crema and Bevan 2020). Five individuals dated to the terminal MH and were removed from the sample. The

resulting sample of 119 individuals contains dates that span the entire LIP, permitting an analysis of diachronic changes in violence throughout the 500-year period. The resulting chronology is divided into three LIP Phases. Phase I (950 – 1200 C.E.), Phase II (1200 – 1300 C.E.), and Phase III (1300 – 1450 C.E.). These ranges were selected to ensure each contained a sufficiently large sample size to conduct reliable statistical analyses, and because these temporal divisions mark important changes in climatological, demographic, and sociopolitical conditions (see Chapter One).

Compared to the MH sample, trauma increases significantly during LIP Phase I. During Phase II violence declines (Figure 4.3a), although the decrease is not significant. During Phase III, violence increases significantly to its highest levels, and peri-mortem trauma peaks at 24% (Fisher Exact $p = 0.05$). It is also noteworthy that overkill trauma (see, Chapter one) remains low during the first two phases (4.8% and 3.7%, respectively) then increases significantly during Phase III to 14% (Fishers Exact $p = 0.049$). Interestingly, ante-mortem trauma varies little throughout the three phases, averaging 28.7% with a range of 26% - 31%. Critical trauma (see, Chapter one), a more reliable measure of violence, parallels trends in peri-mortem trauma, with an initial spike in Phase I, a decline in Phase II, and a significant rise in Phase III to 38% (Fishers Exact $p = 0.002$). The number of traumas per individual is significantly higher during Phase III than in Phase I ($t = -2.133, p = 0.019$) and Phase II ($t = -2.978, p = 0.002$), showing the intensity of violent encounters and/or trauma recidivism increased during this time (Figure 4.3b). To summarize, the average (spatially independent) risk of interpersonal violence (RIV) changes significantly throughout the LIP, with the RIV being lowest in Phase II, higher in Phase I and peaking during Phase III. As such, we expect population-level violence avoidance tactics to vary in accordance with fluctuations in the average RIV.

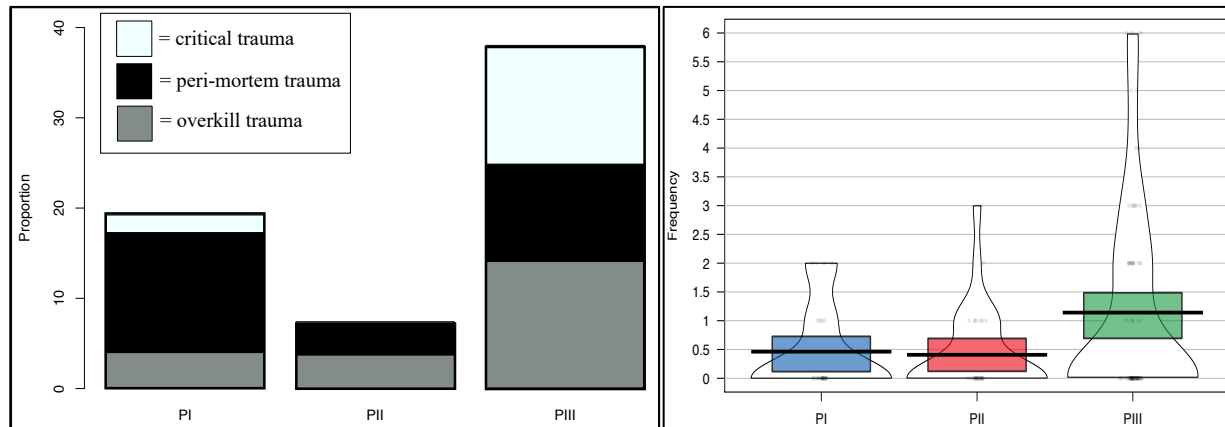


Figure 4.3a (left). Summary of trauma over the three LIP phases. **Figure 4.3b (right).** Sum of trauma per individual over the three LIP phases.

2. Measures of RIV and Resource Returns

In order to establish spatially dependent measures of RIV, it is first necessary to characterize the environment as it relates to subsistence activities. This will permit expectations to be drawn about the RIV in different resource patches. The Nasca highland environment promotes economic adaptations that are largely comprised of intensive agriculture mixed with herding llama (*Lama glama*) and Alpaca (*Vicugna pacos*), which we refer to collectively as *camelids* (McCool 2107; ONERN 1971). The Nasca highland region encompasses five river valleys that form the southern drainage of the Río Grande de Nasca. Situated along the *chaupiyunga* (1200–2500 meters above sea level, MASL) and *quechua* (2500–3300 MASL) vegetation zones, the region straddles both coastal and sierra ecologies (Denevan 2001). Running down the valleys are seasonal streams that discharge a negligible volume of water and are prone to desiccation for four-to-eight months a year (ONERN 1971; Schreiber and Lancho Rojas 1995).

Nasca highland valleys are steep, narrow, and boulder-strewn, restricting substantial human occupations to several arable patches of land with relatively gradual and open topography compared to the otherwise steep valleys (Figure 4; McCool 2017). These patches are situated roughly 2,300 to 3,000 MASL and rapidly gain elevation as they extend east. Previous environmental research in the region has defined the highland region as marginal for agriculture with poor soils and scarce, highly variable water availability (ONERN 1971). Nonetheless, intensive agriculture is possible in these open patches with the construction of terraces and canals. These patches are the only areas in the region where intensive agriculture is possible due to their relatively gentle slopes, potential for irrigation, and seasonal precipitation from January through March (McCool 2017, Figure 4.4). During the nine month-long dry season, the farming zones and surrounding areas contain insufficient grazing resources to maintain camelid herds, requiring herders to make seasonal trips to high elevation plains with abundant bunch grasses.



Figure 4.4. A Google Earth image of the Chauchilla agricultural zone. The hillfort Cerro

Ayapata is shown with a white-and-black point. Note the open area of arable land and the otherwise constricted canyon.

Located to the east of the Nasca highland farming zones, the *puna* high plain extends east across the continental divide into the sierra. The *puna* is an ideal environment for herding due to its flat topography and abundant *ichu* bunch grasses. This is especially the case on the *Pampas Galeras*, a high elevation plain several dozen kilometers east of the highland residential sites that contains abundant bunch grasses due to elevated levels of precipitation. The *puna* is not viable for agriculture due to its frequent nightly frosts, insufficient rainfall, and the inability to irrigate fields. Together these factors concentrate agricultural zones—where all human settlements are located—into clearly defined, resource-dense patches, surrounded by areas devoid of crops and large human settlements. The two primary economic activities – farming and herding – are typically spatially heterogeneous for up to nine months a year, with farming taking place on the dense arable patches surrounding the hillfort residential sites and herding taking place up to 45 km away on the Pampa Galeras.

As a result of these divergent economic activities, the Nasca highlands can be roughly divided into two distinct, bounded patches that vary in their resource returns and RIV. The first patch is comprised of the arable zones that surround each of the fortified residential sites (Figure 4.2). This patch contains all of the land that can be brought under cultivation in the region and provides the bulk of dietary staples (ONERN 1971). The second patch is the herding/hunting patch known as the Pampas Galeras, located several dozen kilometers away from the residential centers (Figure 4.2). Camelid herds generally provide a meat staple that supplements agricultural returns and provides a backup source of calories when unexpected events lead to crop shortfalls (Browman 1987, 1997). Population density-dependent resource depression is sure to occur in

both the farming and herding patches, which will favor field rotation in a fallow/fertile system and the movement of herds from one grazing area to another within the Pampa Galeras.

Nevertheless, the two patches are maintained permanently when under risk-free conditions, as demonstrated by their continual use during prehistoric periods lacking conflict and in modern times (Conlee 2015; Kellner 2002; ONERN 1971). Our test evaluates whether the use of either patch is predictably constrained or curtailed as a function of the RIV.

Tying these measures into our predictions, we expect the following:

- 1) As violence increases the spatial dependent RIV will be disproportionately high for the herding patch compared to the farming patch (greater distance from a home base equals greater RIV). As a result, we expect activity in the herding patch to be either constrained or curtailed.
- 2) The population average for camelid meat consumption should negatively co-vary with the RIV, with risk-prone individuals being those who exhibit isotopic values that show an increased reliance on camelid meat relative to the population average.
- 3) As a result of underutilizing or abandoning the herding patch we expect decreasing net returns as reflected by increasing dietary stress.
- 4) The risk-prone cohorts to exhibit significantly higher rates of cranial trauma relative to risk-averse individuals.
- 5) As a result of decreased use of the herding patch, we expect agriculture intensification in order to compensate for the lost resource returns

4. Mobility, Patch-use, and the RIV in the Andes

The Andean highlands are an exceedingly challenging environment in which to live. For our purposes here the Andean environment is interesting because it promotes human subsistence adaptations defined by high mobility and frequent long-distance travel—two strategies that, as

discussed above, will increase the RIV during wartime. To understand the link between violence avoidance tactics and human health it is necessary to characterize the Andean environment in order to understand how reducing the RIV will affect subsistence, dietary stress, and health.

The Andean environment is characterized by spatially diverse geocological and climatological conditions. Critical agricultural factors such as altitude, slope, aspect, soil type, moisture, and the amount of solar radiation vary considerably within small areas and over short time periods (Winterhalder and Thomas 1978). In the central and southern Andes, rainfall is constrained to a single season, with peak precipitation during the months of January and February (ONERN 1971). This short season offers limited and variable moisture regimes that make environmental conditions unpredictable. These factors produce patchily distributed and irregularly timed agroecological conditions that are most often defined as marginal (Winterhalder and Thomas 1978). In addition, the young and poorly developed Andean soils have low moisture retention and lack certain crop buffering nutrients (Winterhalder and Thomas 1978). These conditions make food returns highly variable and unpredictable, leading to challenges maintaining adequate food supply. As a result, many small-scale farmers frequently face resource scarcity and attendant health problems. The probability of resource shortfalls is heightened when climate change produces increasingly cold and arid conditions and/or short-term stochasticity in precipitation (Kennett and Marwan 2015).

Agroecological conditions in the Nasca highlands parallel those of the broader central and southern Andes. Localized environmental stressors substantially affect resource availability and stability. The region's agroecology is defined by marginal, stochastic conditions that are heavily structured by seasonal precipitation (ONERN 1971).

Small-scale Andean societies cope with this challenging environment by employing a surprisingly patterned suite of economic strategies (Browman 1987; Goland 1993; Kellett 2010; Marston 2011; Parsons et al. 1988). These include: (1) storing “bumper” crops so that years of abundance can subsidize low-yield seasons (Browman 1987; Kellett 2010); (2) scattering agricultural fields across the landscape in different macro- or micro-environments to reduce the probability that loss at one field will impact others (Chibnik 1990; Goland 1993; Marston 2011; Valdivia et al. 1996); (3) a mixed agropastoral strategy that minimizes the risk that a catastrophic event will adversely affect both strategies (Browman 1987; Parsons et al. 1988; Kellett 2010; Kuznar 2001; Winterhalder and Thomas 1979); (4) reciprocal exchanges of resources between groups living in different ecological zones to increase the probability of stable food returns (often termed “verticality”) (Brush 1976; Marston 2011; Murra 1972); and (5) intra-field crop diversification to reduce the chance that harmful stochastic events will impact all crop types equally (Goland 1993; Marston 2011). Collectively, these strategies decrease the probability of food shortages, but many require high degrees of mobility, including frequent long-distance travel.

During times of climatic upheaval and drought, subsistence risk can dramatically increase, further incentivizing and perhaps intensifying high mobility risk-mitigation strategies (Kennett and Marwan 2015). However, as discussed above, highly mobile activities become dangerous during wartime as they require individuals to leave the safety of protected centers and temporarily disperse into smaller, more vulnerable groups (Kurin 2012; McCool 2017; VanDerwarker and Wilson 2016b). As a result, we predict that the Nasca highland population will reduce mobility and conduct subsistence activities in close proximity to protected centers (Kurin 2012; VanDerwarker et al. 2013; VanDerwarker and Wilson 2016b). Thus, the

application of our model to the Andean case study suggests that the typical violence avoidance tactics of reduced mobility and long-distance travel will dramatically increase the variability and unpredictability of subsistence returns, both of which may increase the probability of recurrent food shortfalls. We expect that the costs of reducing the RIV will be especially high in the Andes and the trade-off between food acquisition and violence avoidance to be especially salient.

D. Isotope Methods

1. Stable Carbon and Nitrogen Isotopes

Bone collagen for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analysis was extracted and purified using the modified Longin method (Brown et al. 1988) following protocols of the Pennsylvania State Carbon Cycle AMS Facility (Kennett et al. 2017). Bone samples were initially cleaned of adhering sediment and the exposed surfaces were removed by scraping with an X-acto® blade. Samples (400 – 700 mg) were demineralized for 24–36 hr in 0.5N HCl at 5 °C. Collagen was rinsed to neutrality in multiple changes of ultrapure Millipore water, and then gelatinized for 12 hours at 70 °C in 0.01N HCl. Gelatin solution was frozen using liquid nitrogen then lyophilized after which ultrapure Millipore water was pipetted into the tubes to liquify the gelatin solution. The gelatin solution was then pipetted into precleaned Amicon Centriprep® 30 ultrafilters (retaining >30-kD molecular weight collagen) and centrifuged 3 times for 30 min, diluted with ultrapure Millipore water and centrifuged 3 more times for 30 min to desalt the solution. Ultrafiltered collagen was lyophilized and weighed to determine percent yield. The recognition that foreign carbon could be introduced to samples during ultrafiltration by humectants (e.g. glycerol, glycerin) or filter material (e.g. reconstituted cellulose, polyethersulfone) has spurred much recent methodological work to determine effective precleaning protocols (Bronk Ramsey

et al. 2004; Higham et al. 2006; Brock et al. 2007; Hüls et al. 2007). To remove the glycerol coating from the Centriprep filters, the inner and outer portions of the filters were filled with .01N HCl and sonicated at ~60 °C for 1 hr and rinsed with ultrapure Millipore water. Ultrapure Millipore water was centrifuged through the filters 3 times for 30 min each, and the inner and outer portions were refilled with ultrapure Millipore water and sonicated for 1 hr at ~60 °C. After 3 further centrifuge runs with ultrapure Millipore water, the filters were kept wet until use, no more than 48 hr after precleaning. Results on Pleistocene and historic age bone standards processed along with the unknowns indicate no contamination from either modern or ancient carbon.

2. AMS Dating of Human Bone from the Nasca Highlands

^{14}C samples (~2.5 mg) were combusted for 3 hr at 900 °C in vacuum-sealed quartz tubes with CuO wire and Ag wire. At KCCAMS, sample CO_2 was reduced to graphite at 550°C using H_2 and a Fe catalyst, with reaction water drawn off with $\text{Mg}(\text{ClO}_4)_2$ (Santos et al. 2004). Graphite samples were pressed into targets in Al boats and loaded on the target wheel for AMS analysis. ^{14}C ages were $\delta^{13}\text{C}$ -corrected for mass dependent fractionation with measured $^{14}\text{C}/^{13}\text{C}$ values (Stuiver and Polach 1977), and compared with samples of Pleistocene horse bone (background, >48 ^{14}C kyr BP), middle Holocene pinniped bone (~6500 ^{14}C BP), late AD 1800s cow bone, and OX-1 oxalic acid standards for calibration. Stable isotope samples (~0.7 mg) were analyzed on a Fisons NA1500NC elemental analyzer/Finnigan Delta Plus isotope ratio mass spectrometer with a precision of <0.1‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

3. Stable Carbon (apatite)

Preparation of bone carbonate samples occurred at the Pennsylvania State University and the University of California, Santa Barbara (UCSB) in the Human Paleoecology and Isotope

Geochemistry Laboratories. Because of the increasing awareness that interlaboratory differences in bone sample processing and analysis can result in significantly different stable isotope ratios (Pestle et al., 2014), data from both laboratories are presented here to assess interlab comparability of $\delta^{13}\text{C}$ apatite values. Pestle et al. (2014) demonstrated that interlab differences in isotope ratios derived from collagen are less variable than those from bone apatite, and thus this study did not compare inter-lab differences in $\delta^{13}\text{C}$ collagen and $\delta^{15}\text{N}$ collagen. Bone apatite preparation at both universities followed procedures similar to those of Koch et al. (1997). Samples were finely powdered in an agate mortar and pestle and treated with 0.4 mL of 2% bleach (NaOCl). For each milligram of bone, 0.04 mL of 2% NaOCl was added to the 2 mL centrifuge tube containing the bone powder. Samples were sonicated for 10 minutes, mixed on a mini-vortexer for 60 seconds and left at room temperature for 24 h. Treated samples were rinsed with either ultrapure Millipore water (H_2O) at PSU or double-distilled deionized water at UCSB. Next, for each milligram of bone powder, 0.04 mL of 0.1M acetic acid (CH_3COOH) was added to the centrifuge tubes. These were sonicated for 15 minutes, mixed on a mini-vortexer for 60 seconds, and then left at room temperature for 24 h. Treated samples were rinsed with either ultrapure Millipore water at PSU or double-distilled deionized water at UCSB, and then dried at 50.8°C in a laboratory oven for 24 hours.

The samples were then dried overnight at 60°C and subsequently analyzed at the Center for Stable Isotopes, University of New Mexico by continuous-flow isotope ratio mass spectrometry using a GasBench device coupled to a Thermo Fisher Scientific Delta V Plus isotope ratio mass spectrometer. The results are reported using the delta notation measured against VPDB. Reproducibility was better than 0.1‰ for both $\delta^{13}\text{C}$ based on repeats of a

laboratory standard (Carrara Marble). The laboratory standard is calibrated versus NBS-19, for which the $\delta^{13}\text{C}$ is 1.95‰.

4. Stable Isotope Biogeochemistry

Stable carbon and nitrogen isotope ratios in human tissues reflect the isotope ratios of consumed foods, and have been used to reconstruct human diet for decades (Ambrose and Norr 1993; DeNiro and Epstein 1978, 1981; Froehle et al. 2012; Howland et al. 2003; Jim et al. 2004; Lee-Thorp et al. 1989; Schoeninger and DeNiro 1984; Tieszen and Fagre 1993;). Variation in stable carbon isotope ratios is primarily the result of differential fractionation rates among three alternative plant photosynthetic pathways. C_3 photosynthetic pathway plants are ^{13}C depleted relative to C_4 and CAM plants, and include most fruits, vegetables, shrubs, and grasses from temperate regions (O’Leary 1988; Smith and Epstein 1971). C_4 photosynthetic pathway plants are $\delta^{13}\text{C}$ enriched and include grasses adapted to dry environments, maize, and amaranth. Plants using the less common CAM photosynthetic pathway exhibits $\delta^{13}\text{C}$ values between C_3 and C_4 but trend towards—and sometimes overlap with— C_4 values (Tung and Knudson 2018). CAM plants typically include dry or desert adapted taxa such as cacti and agave and several tropical plants such as pineapple.

$\delta^{13}\text{C}$ values in human tissues are a function of the proportion of C_3 , C_4 , and CAM plants in the human diet, as well as the consumption of marine resources that are $\delta^{13}\text{C}$ enriched. When bone is sampled to obtain stable isotope ratios the resulting values differ between bone mineral apatite (hydroxyapatite) and organic bone collagen. Stable $\delta^{13}\text{C}$ isotopic ratios from bone apatite tend to reflect the $\delta^{13}\text{C}$ of all energy sources in total diet, while $\delta^{13}\text{C}$ from bone collagen primarily reflects the protein component of the diet (Ambrose and Norr 1993; Froehle et al. 2010; Howland et al. 2003; Kellner and Schoeninger 2007; Tieszen and Fagre 1993).

Nitrogen is incorporated into human tissues primarily through the plants and animals they consume. Plants obtain nitrogen from soil nitrates and as a result exhibit $\delta^{15}\text{N}$ values higher than atmospheric nitrogen. Nitrogen isotope values in organisms are relative to the $\delta^{15}\text{N}$ values of the plants and animals they consume, resulting in $\delta^{15}\text{N}$ values that are typically 3-5‰ higher than their diets (Minagawa and Wada 1984; Schoeninger and DeNiro 1984). For example, herbivores exhibit $\delta^{15}\text{N}$ values 3-5‰ higher than their plant diet, while carnivores are enriched 3-5‰ relative to the animals they consume. Because there are many more trophic levels in the marine environment, marine vertebrates exhibit $\delta^{15}\text{N}$ values 6-8‰ higher than terrestrial vertebrates at similar trophic levels (Schoeninger and DeNiro 1984). Thus, human diets reliant on marine vertebrates will exhibit $\delta^{15}\text{N}$ values well above those composed of terrestrial vertebrate resources. As a result of this patterned fractionation $\delta^{15}\text{N}$ ratios distinguish an organism's trophic level and differentiate the proportion of terrestrial and marine food in the diet. This latter feature of $\delta^{15}\text{N}$ isotope data is especially crucial, as $\delta^{13}\text{C}$ values in marine foods are similar to those of C_4 plant protein sources, making it difficult to distinguish consumed dietary protein from C_4 plants or marine resources using $\delta^{13}\text{C}$ analysis alone (Froehle et al. 2010; Kellner and Schoeninger 2007; Somerville et al. 2013)².

To enable stable isotope analysis of the Nasca highland population a sample of 124 individuals underwent bone collagen and bone carbonate extraction at the laboratory facilities at the Pennsylvania State University, the University of California at Santa Barbara, and underwent

² In addition to dietary composition, many other processes can alter stable isotope ratios, such as starvation (Beaumont and Montgomery 2016), breastfeeding (Eerkens et al. 2017), the use of dung fertilizers (Szpak et al. 2012), and much more. We reserve outlining these alternative ratio-altering pathways until the discussion section, when we explore the mechanisms driving the observed isotope ratios.

analysis at the University of California at Irvine and the University of New Mexico. The resulting dataset contains $\delta^{13}\text{C}_{\text{collagen}}$, $\delta^{13}\text{C}_{\text{apatite}}$, and $\delta^{15}\text{N}_{\text{collagen}}$ for all 124 individuals that include the child, adolescent, young adult, middle adult, and old adult age-cohorts as well as proportionate number from each sex.

5. Modeling Stable Isotope Data

A Simple Carbon Model

Using $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{13}\text{C}_{\text{apatite}}$ alone will fail to capture the full range of dietary energy or protein sources (Kellner and Schoeninger 2007; Froehle et al. 2010). Plotting $\delta^{13}\text{C}_{\text{collagen}}$ against $\delta^{13}\text{C}_{\text{apatite}}$ allows for a more complete picture of total diet and dietary plant protein. As previously stated, published experimental data on rats, mice, and pigs show that $\delta^{13}\text{C}_{\text{collagen}}$ is biased towards dietary protein while $\delta^{13}\text{C}_{\text{apatite}}$ reflects the total diet. Kellner and Schoeninger (2007) and Froehle et al. (2010) utilized the experimental feeding data and dietary data from human populations with reasonably known diets to generate regression lines that reflect C_3 vs. C_4 /marine protein sources. When applied to human dietary reconstructions the position of an individual's stable carbon signature relative to the $\delta^{13}\text{C}_{\text{collagen}}$ regression line reveals information on protein sources while their position relative to the $\delta^{13}\text{C}_{\text{apatite}}$ line shows the ratio of C_3 to C_4 plants in the total diet. The result is a more holistic understanding of dietary constituents than was afforded by previous methods.

Nonetheless, the simple carbon model has two important shortcomings. First, the model struggles to differentiate C_4 from marine protein sources. Second, it is unclear as to what information can be inferred when an isotopic signature is positioned in-between the two regression lines (Froehle et al. 2012). As such, a more complete model was used to clarify this potential equifinality (see, Froehle et al 2012).

A Multivariable Carbon/Nitrogen Model

Froehle et al. (2012) produce a multivariate model that provides clarification by using cluster analysis and discriminant functions to differentiate marine and C₄ protein sources along with more effectively tracking C₃/C₄ dietary sources. The authors employ a k-means cluster analysis on archaeological populations with well-defined diets to generate dietary groupings based on ratios in stable carbon and nitrogen isotopes, resulting in five distinct dietary clusters. Froehle et al. (2012) then develop a discriminant function model to “flatten” the three isotope variables ($\delta^{13}\text{C}_{\text{collagen}}$, $\delta^{13}\text{C}_{\text{apatite}}$, $\delta^{15}\text{N}$) into two-dimensional plotting space. The two discriminant function equations employed account for 98.8% of the variance in the five dietary clusters. The resulting plot space contains the previously generated dietary clusters where each cluster is characterized by a box that represents the range of isotope values for each function within the clusters. The location in plotting space where an individual’s isotopic signature falls reveals information about protein sources and total diet, including whether or not an individual diet contained marine protein sources.

$$\begin{aligned} \text{Carbon: } F1 &= (0.322 * \delta^{13}\text{C}_{\text{carbonate}}) + (0.727 * \delta^{13}\text{C}_{\text{collagen}} \\ &\quad + (0.219 * \delta^{15}\text{N}) + 9.354 \\ \text{Nitrogen: } F2 &= (-0.393 * \delta^{13}\text{C}_{\text{carbonate}}) + (0.133 * \delta^{13}\text{C}_{\text{collagen}} \\ &\quad + (0.622 * \delta^{15}\text{N}) - 8.703 \end{aligned}$$

5. Evaluating Subsistence Strategies using Stable Isotopes

Patch use is evaluated using stable nitrogen, carbon, and oxygen isotope chemistry of human bone collagen and carbonate.

Stable Nitrogen isotopes ($\delta^{14}\text{N}/\delta^{15}\text{N}$) track an individual’s trophic level of consumed protein sources (DeNiro and Epstein 1981; Schoeninger et al. 1983). The available animal protein for highland agriculturalists is largely confined to camelids of both the domestic (llama

and alpaca) and wild (guanaco and vicuña) varieties, in addition to domestic guinea pig (*Cavia porcellus*) (Finucane et al. 2006; Parsons et al. 1997). Guinea pigs (*cuy*) are fed off domestic organic waste and are raised and consumed within the household (Finucane et al. 2006). Because of their small body size, Guinea pigs provide small amounts of meat protein and tend to exhibit a more $\delta^{13}\text{C}$ enriched signature when compared to camelids that eat wild C_3 grasses (Kurin 2016). The alternative protein source is domestic camelids and wild hunted camelids. Guanaco (*Lama guanicoe*) and vicuña (*Vicugna vicugna*) are largely distributed throughout the Puna grasslands and range from small extended family herds to large aggregates, especially in the case of vicuña. Domestic camelids can be corralled in locations inside or adjacent to residential areas but typically require seasonal rotations to *Ichu* bunchgrass habitats on the Puna's grasslands 30-50 km from the Nasca highland residential sites (Finucane et al. 2006; McCool 2017; Parsons et al. 1997; Winterhalder and Thomas 1978). Camelids can thus provide a greater amount of dietary protein but require frequent travel to distant grazing patches.

In order to parse out the relative contribution of plant versus animal protein to $\delta^{15}\text{N}$ enrichment, we conduct General Additive Models (GAMs) comparing $\delta^{13}\text{C}_{\text{collagen}}$ to $\delta^{15}\text{N}$ to evaluate how much effect the consumption of protein-rich plant resources has on overall ^{15}N enrichment. Because $\delta^{15}\text{N}$ is capable of tracking relative protein intake, we expect $\delta^{15}\text{N}$ values to decrease when the RIV is high and increase when RIV is low. As per the model expectations we define our risk-prone cohort as those who exhibit higher $\delta^{15}\text{N}$ values and we predict this cohort will exhibit higher rates of violent trauma by engaging in the high-risk herding activities.

Finally, we expect compensating adaptations designed to mitigate the impacts of RIV-induced resource loss. These strategies should be structured to reduce resource loss while preventing an increase in RIV. In the Andean highland environment, a straightforward strategy

for reducing subsistence risk while keeping mobility constant is intra-field crop diversification (Goland 1993; Marston 2011). Planting a variety of crops in a single parcel reduces the variance in economic returns by scattering the probability of loss among a suite of crop types, all of which have different loss parameters. We may expect to see this strategy via stable $\delta^{12}\text{C}/\delta^{13}\text{C}$ isotope ratios, whereby a high RIV promotes a mixed C_3/C_4 strategy while low RIV incentivizes a more C_4 (maize based) strategy. This strategy should be reflected in a $\delta^{13}\text{C}$ signature indicative of mixed C_3/C_4 plant consumption during period of high violence and a depleted $\delta^{13}\text{C}$ signature when levels of violence decrease.

6. Evaluating Dietary Stress

Evidence of porous lesions in the orbits (cribra orbitalia) and on the ectocranial surface of the cranial vault (porotic hyperostosis) were identified by direct macroscopic observation and examination under low magnification (x10). Cribra orbitalia and porotic hyperostosis were recorded using Buikstra and Ubelaker Standards (1994) in order to facilitate comparison of LIP lesion frequency to previously reported lesion frequency for Middle Horizon burials (AD 500 – 1000, Kellner 2002). Lesions were recorded as present even if unilateral, and side was noted in unilateral cases. Lesion activity status at time-of-death was determined based on criteria laid out by Mensforth et al. (1978), and lesion expression was recorded using the Standards ordinal index (0-3). Each cranium was photo documented to facilitate independent validation of pathological findings by other researchers.

Cribra orbitalia and porotic hyperostosis are well documented indicators of nutritional stress (Billman et al. 2000; Kurin 2016; Lambert 2002; Milner et al. 1991; Ortner 2008; Tung et al. 2016, Tung et al. 2017; Walker 2001), however their exact etiologies can be complicated (Walker et al. 2009). Nonetheless, the Nasca highland's high elevation location, extreme aridity,

and pronounced drought conditions make it most likely that the observed pathologies are the result of malnutrition and/or malabsorption due to parasitic infection rather than hemorrhagic or inflammatory processes (see, Chapter two).

Finally, there are issues relating to the osteological paradox. As I have demonstrated in Chapter two, the frequency and severity of cribra orbitalia and porotic hyperostosis indicate frailty rather than robusticity or longevity. As a result, we argue that these pathological conditions effectively track nutritional status and can be used to evaluate dietary stress.

E. RESULTS

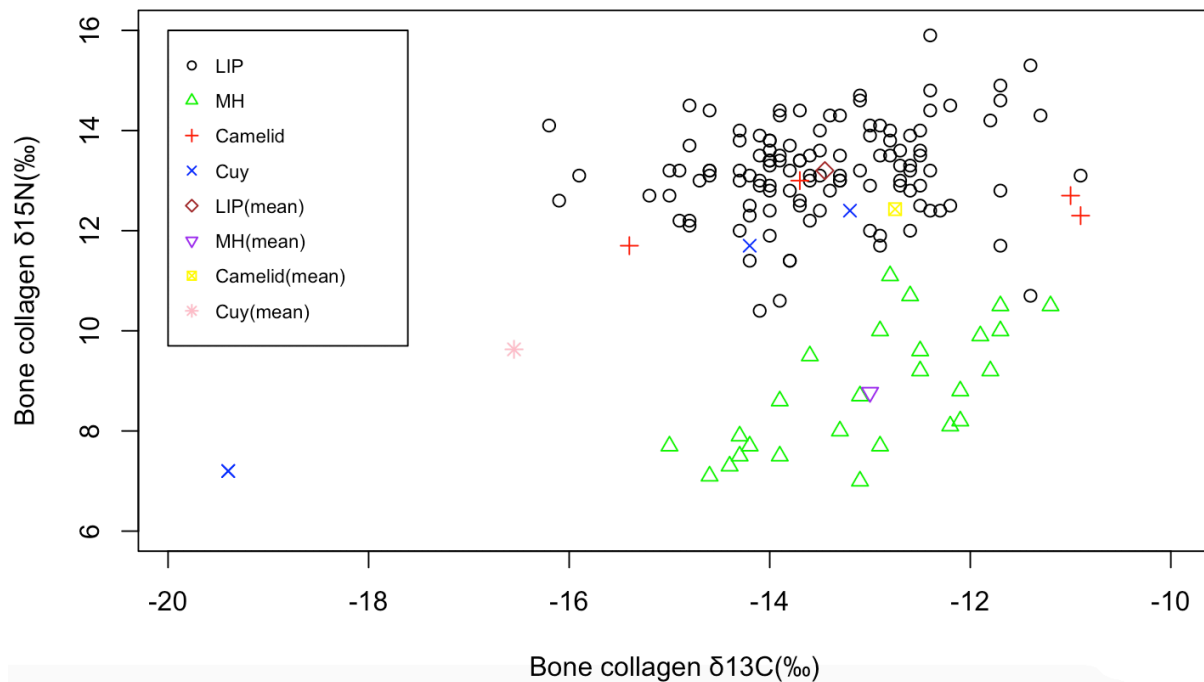


Figure 4.5. Stable $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}$ isotope values for the LIP and MH (Kellner and Schoeninger 2008) samples as well as four Camelids and four Guinea pigs (cuy) excavated from LIP tombs.

1. Stable $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ Isotope Results

The LIP $\delta^{15}\text{N}$ values are unexpectedly high and consistent for an inland agropastoralist population ($m = 13.2\text{‰}$ $\sigma = 0.94$, Figures 4.5, 4.6). Average $\delta^{15}\text{N}$ values remain surprisingly consistent throughout the LIP (Phase I = 13.2‰ , Phase II = 13.5‰ , Phase III = 13.1‰). Phase II values are significantly enriched relative to Phase III ($p = 0.05$), however this is well within a single trophic level (i.e. $3\text{--}5\text{‰}$). While sex-based values are significantly different ($p = 0.001$) they are also well within a single trophic level (females = 13.0‰ , males = 13.6‰). Even when comparing all age-cohorts, $\delta^{15}\text{N}$ values are surprisingly steady, and a Tukey HSD test results in only one significant difference with children being depleted relative to old adults (children versus old adults $p = 0.031$). LIP $\delta^{15}\text{N}$ values are nevertheless significantly higher than the preceding Middle Horizon average of 8.8‰ (Kellner and Schoeninger 2008) ($p = 0.000$). Overall, $\delta^{15}\text{N}$ data exhibit remarkably high values and consistency throughout the 500-year LIP. As such, we will focus our discussion on differences in nitrogen values between the MH and LIP samples, where significant differences in average values are observed.

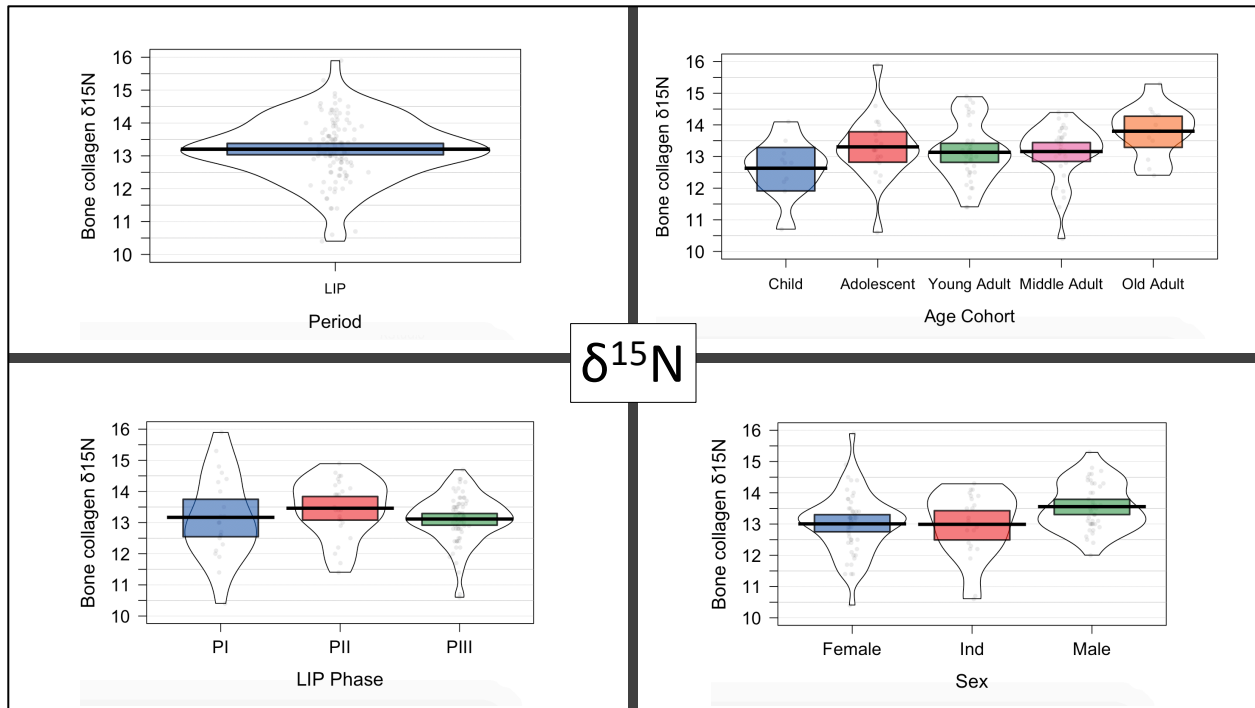


Figure 4.6. Comparing $\delta^{15}\text{N}$ values during the LIP, by age-cohort, over time, and among the sexes.

The average $\delta^{13}\text{C}_{\text{collagen}}$ value for bone collagen is -13.5‰ with a standard deviation of 1.01‰ . Similar to $\delta^{15}\text{N}$ values, $\delta^{13}\text{C}_{\text{collagen}}$ signatures are consistent through the LIP (Phase I = -13.4‰ , Phase II = -13.3‰ , Phase III = -13.5‰), by sex (females = -13.7 , males = -13.3), and across age cohorts (Tukey HSD test reveals no significant differences) (Figure 4.7). These consistent values show a primarily C_4 based (maize) diet that includes slightly more C_3 plants in the diet than the previous Middle Horizon population (mean of $\delta^{13}\text{C}_{\text{collagen}} = -13.0$) (Kellner and Schoeninger 2008). The difference between MH and LIP $\delta^{13}\text{C}_{\text{collagen}}$ values is trending towards significant ($p = 0.051$) albeit within a single trophic level.

The average $\delta^{13}\text{C}_{\text{carbonate}}$ value for bone carbonates is -8.0‰ with a standard deviation of 1.2‰ . $\delta^{13}\text{C}_{\text{carbonate}}$ values exhibit slightly more temporal variability than the other isotopic averages (Phase I = -7.7‰ , Phase II = -7.6‰ , Phase III = -8.3‰) as well as sexed-based

differences (females = -8.21‰, males = -7.83‰) (Figure 4.7). A Tukey HSD test however did not reveal any significant differences among average $\delta^{13}\text{C}_{\text{carbonate}}$ values between age cohorts. The lack of MH $\delta^{13}\text{C}$ data from bone carbonates prevents us from comparing these data with the MH sample.

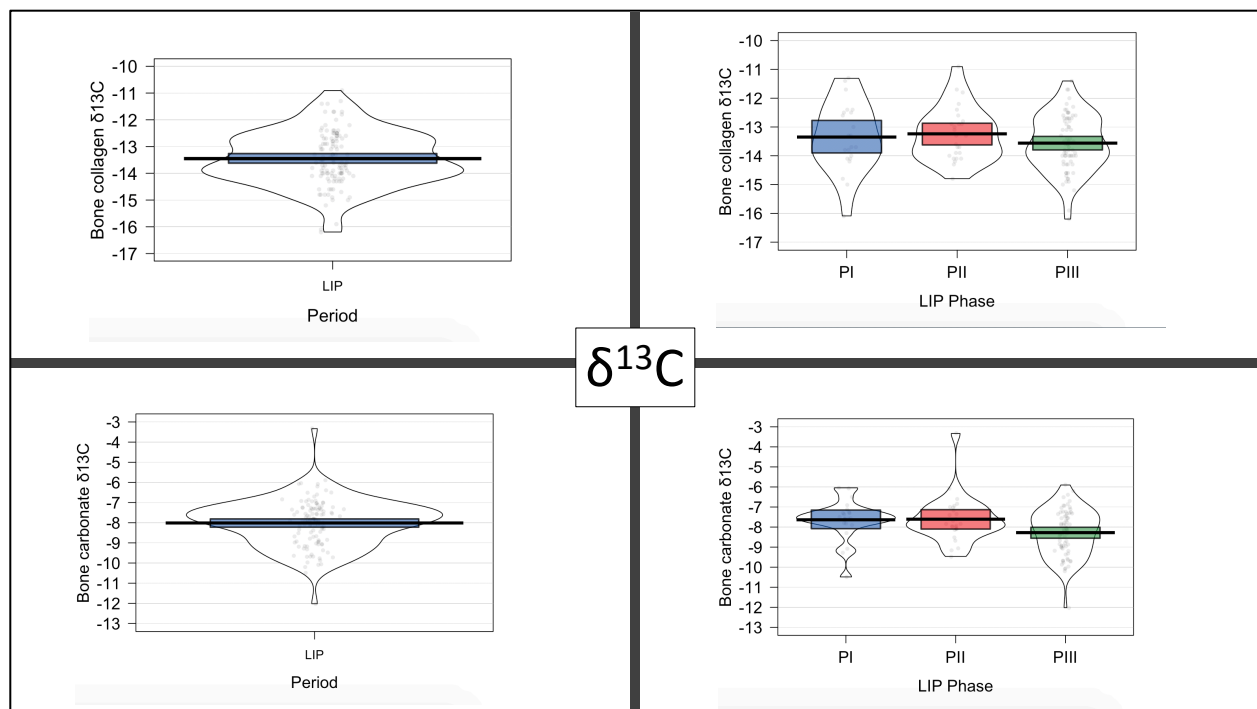


Figure 4.7. Comparing $\delta^{13}\text{C}$ values during the LIP and over time.

2. Carbon and Nitrogen Models and Inter-isotopic Relationships

A simple carbon model was generated using the methods outlined in Froehle et al. (2010), which compares the $\delta^{13}\text{C}$ values of bone collagen and carbonate to experimentally derived regression lines which spatially demarcate C_4 and C_3 protein lines (Figure 4.8). These results show the Nasca highland values to be in-between a C_3 and C_4 pathways, which suggests a mixed plant protein diet.

In addition, a more comprehensive multivariate carbon/nitrogen model was generated using the discriminant function established in Froehle et al. (2012) (Figure 4.9).

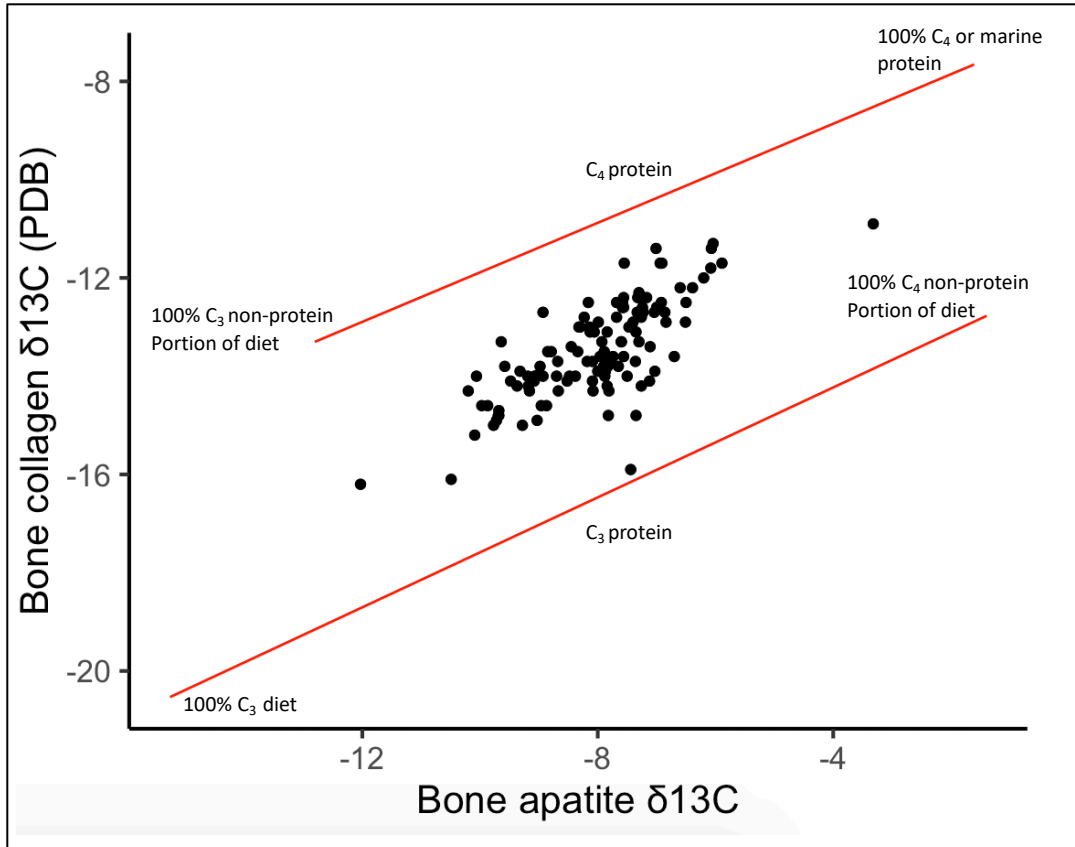


Figure 4.8. A simple carbon model using the LIP data and experimentally derived regression lines (see Somerville et al. 2013).

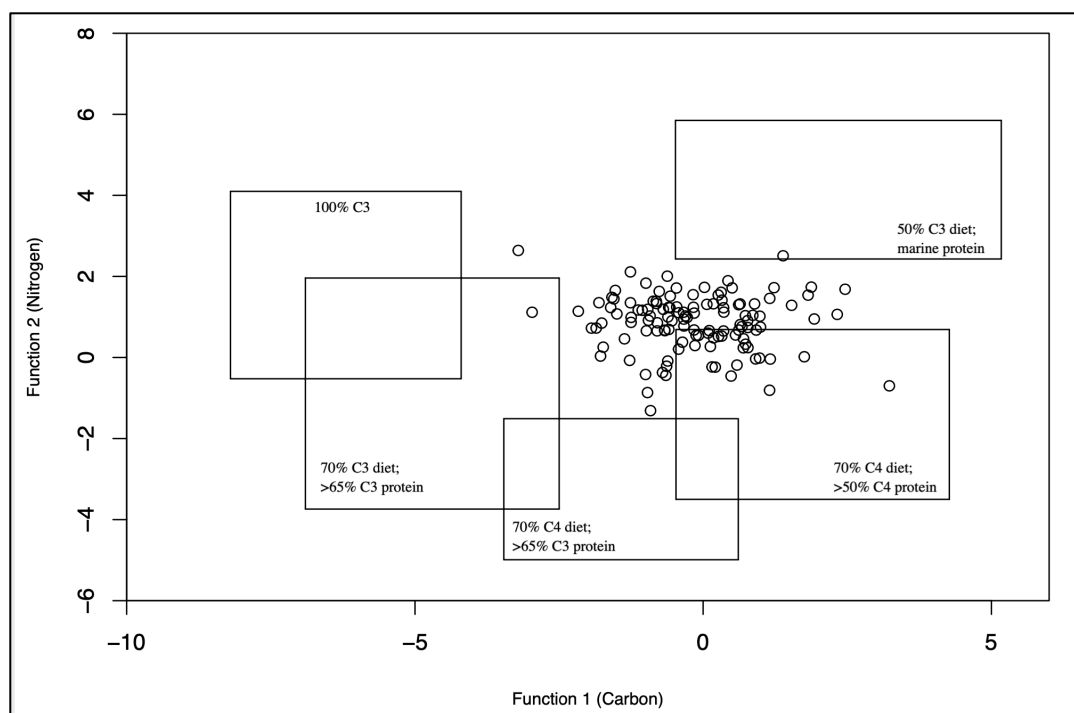


Figure 4.9. A multivariate carbon and nitrogen isotope model using the LIP data.

The results of the multivariate C/N model show the Nasca population to be in-between established dietary clusters. The cluster of values show that C₄ plants (maize) constituted the staple of the plant diet while the spread of values on the horizontal axis show a mixed reliance on C₃ and C₄ crops for dietary plant protein. Nevertheless, the trend towards the C₄ protein box suggests the consumption of protein-rich plants such as amaranth. The model also suggests little reliance on marine resources, meaning the high $\delta^{15}\text{N}$ values are likely due to an alternative pathway.

To assess the effect of dietary plant protein, which is primarily reflected by $\delta^{13}\text{C}_{\text{collagen}}$, on $\delta^{15}\text{N}$ values a General Additive Model (GAM) was employed. Results show a non-significant positive relationship between $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}$ ($R^2 = 0.02$, $p = 0.071$), suggesting the high $\delta^{15}\text{N}$ values cannot alone be explained by dietary plant protein. When broken down by LIP phase results are mixed, with Phase I exhibiting a significant positive relationship ($R^2 = 0.40$, $p =$

0.005), Phase II exhibiting a very weak relationship ($R^2 = 0.052$, $p = 0.137$) and a weak negative relationship during Phase III ($R^2 = 0.052$, $p = 0.026$). Overall, these results show an inconsistent relationship between $\delta^{13}\text{C}_{\text{collagen}}$ and $\delta^{15}\text{N}$.

3. Dietary Stress Results

The percentage of orbital lesions increases significantly from the MH (8.2%) (Kellner 2002) to the LIP (21.6%, $p = 0.008$), as does the prevalence of more extreme expressions of orbital lesions ($p = 0.034$). The percentage of vault lesions increases significantly from the MH (5.2%) (Kellner 2002) to the LIP (21.3%, $p = 0.000$) as does the severity of porous vault lesions ($p = 0.021$). Diachronic results show significant changes in morbidity and mortality. Cribriform orbitalia increased to 10% at the onset of the LIP during Phase I, declines during Phase II to 3.8%, and significantly increases during Phase III to 22% ($p = 0.028$). Porotic hyperostosis rises to 22% in Phase I, increases to 25% in Phase II and reaches its peak in Phase III at 30%, although these changes are not significant. Severity patterns parallel frequency results, with cribriform severity low in Phase II and higher in Phases I and III, and porotic severity increasing linearly through time. Overall, 36.1% of the LIP sample exhibits cribriform orbitalia, porotic hyperostosis, or both.

4. Relationship Between Diet and Pathology/Trauma

To assess the relationships between phenotypic quality and subsistence strategy, we utilized binomial GAMs to compare stable isotope values with the presence/absence of cribriform orbitalia and porotic hyperostosis. Results are weak and mixed. $\delta^{15}\text{N}$ has a trending but non-significant relationship with cribriform orbitalia ($p = 0.113$) and porotic hyperostosis ($p = 0.216$). These two trends are in opposite directions, with increased $\delta^{15}\text{N}$ values associated with decreased cribriform orbitalia and increased porotic hyperostosis. $\delta^{13}\text{C}_{\text{collagen}}$ has a non-significant relationship

with cribra orbitalia ($p = 0.694$) and a trending relationship with porotic hyperostosis ($p = 0.082$). In both instances increased pathology is associated with C₄ focused diets. $\delta^{13}\text{C}_{\text{apatite}}$ has a non-significant relationship with cribra orbitalia ($p = 0.577$) and porotic hyperostosis ($p = 0.24$).

To evaluate the relationship between dietary diversity and variability in violence we conducted binomial GAMs comparing isotope values with our four measures of violent trauma. Results show mixed, weak relationships. $\delta^{15}\text{N}$ has a trending relationship with peri-mortem ($p = 0.137$), overkill ($p = 0.130$), and sum of traumas ($p = 0.145$), in addition to a non-significant relationship with critical trauma ($p = 0.215$). In each case, $\delta^{15}\text{N}$ has a positive though weak relationship with violence. $\delta^{13}\text{C}_{\text{collagen}}$ has a trending relationship with peri-mortem ($p = 0.072$), a significant relationship with critical trauma ($p = 0.022$) and non-significant relationships with overkill ($p = 0.446$) and sum of traumas ($p = 0.269$). In each test, increased violence is associated with a C₃ focused diet. $\delta^{13}\text{C}_{\text{apatite}}$ has no relationship to violence.

F. Discussion and Conclusion

1. $\delta^{15}\text{N}$ Results

The most notable result is the $\delta^{15}\text{N}$ values of the Nasca highland population. The average $\delta^{15}\text{N}$ value of 13.2‰, $\sigma = 0.94$ is unusually high for the Andean highlands and is typically only observed among populations dependent on marine resource (e.g. Slovak and Paytan 2011). This may, at first glance, suggest that herding was actually expanded during the LIP. However, $\delta^{15}\text{N}$ values of this order cannot be achieved by hunting and herding alone and most likely point to a mosaic of subsistence transformations.

We present five non-mutually exclusive pathways by which a population can exhibit $\delta^{15}\text{N}$ enrichment to the observed values. Breast-feeding is not included, as the study sample excluded

infants in order to focus on adult subsistence strategies. We report these pathways as hypotheses that we test using isotopic and statistical analysis.

The first and most widely observed pathway is a dietary reliance on marine resources. Marine taxa exhibit higher $\delta^{15}\text{N}$ values relative to terrestrial flora and fauna (Schoeninger and DeNiro 1984). Indeed, the zooplankton at the bottom of the marine food pyramid exhibit $\delta^{15}\text{N}$ values that average $\sim 10\%$, a value equivalent to top terrestrial predators (Knudson and Frink 2011). If the Nasca highland population were able to procure a regular supply of marine resources this may account for the observed values. However, the marine resources most easily distributed to inland regions would be the bivalves, anchovies, and sardines that dominate the offshore Humboldt current (Gutierrez et al. 2007). These near-shore and pelagic taxa are relatively low in the marine food chain and exhibit lower $\delta^{15}\text{N}$ values relative to marine predators such as tuna, seals, or sealion (Knudson and Frink 2011). As a result, the Nasca highlanders would need to consume an inordinate amount of pelagic fish or bivalves relative to other dietary inputs to achieve the observed $\delta^{15}\text{N}$ enrichment. An alternative would be the transportation of large marine taxa (e.g. Pinnipeds), which are higher in $\delta^{15}\text{N}$ values. However, a steady reliance on marine resources is unlikely given that the Nasca Highlands are 100 km from and 3,000 meters above the sea. While other inland regions have been shown to exhibit high $\delta^{15}\text{N}$ values (e.g., Santata-Sagredo et al. 2019), these inland regions have long histories of interactions with marine-focused coastal populations. The Nasca lowland region has a consistent history of terrestrial-focused diets and a notably paucity of dietary marine resource going back thousands of years (Kellner and Schoeninger 2008; Webb et al. 2013). Additionally, the results of the multivariate C/N model show that the Nasca highland samples are not centered on the marine

protein cluster (Figure 4.9), suggesting these resources were not a major component of the diet. The results of upcoming Sulphur isotope analysis will further test this hypothesis.

The second pathway is a mixed diet of C₄ plant protein, terrestrial meat protein (Camelids, Guinea pig), and locally available freshwater fish. Archaeological populations from Ontario are known to have relied on maize agriculture, terrestrial game, waterfowl and aquatic resources, and these populations exhibit $\delta^{15}\text{N}$ values within the same range (10-15‰) as the Nasca highlands population (Froehle et al. 2012). While the abundance of freshwater fish was sure to be limited during the dry season desiccation of rivers and the lack of permanent water bodies, fish may have provided a minor dietary supplement during the wet season when river flow is high. However, experimental and field studies of stable isotopic values of Brook, Brown, and Rainbow trout across varied ecological settings produce $\delta^{15}\text{N}$ values ranging from 5.4 - 12‰ with an average value of 8.05‰ (Beltran et al. 2009; Cucherousset et al. 2007; Doucett et al. 1999; France and Steedman 1996) questioning whether the seasonal consumption freshwater fish could account for the elevated values. The absence of large abundances of waterfowl or alternative freshwater game in the region rule out these resources as a consistent pathways to elevated $\delta^{15}\text{N}$ values.

The notable enrichment in the four camelids sampled for $\delta^{15}\text{N}$ (Figure 4.5) suggests the high $\delta^{15}\text{N}$ values in humans may be the result of consuming enriched camelid meat. Nevertheless, this interpretation warrants caution as our camelid sample size is small ($n = 4$) and two of these individuals are subadults and may be enriched due to breastfeeding. Interestingly, the $\delta^{13}\text{C}_{\text{collagen}}$ signature of the camelids parallels human values, and trend towards a C₄ (maize) based plant diet. The bunch grasses abundant on the Pampa Galeras are C₃, suggesting the camelids subsisted largely on domestic C₄ crops rather than wild grasses. The observed camelid

values suggest camelids were corralled away from the Pampa Galeras and allowed to fodder in post-harvest agricultural fields or directly fed crop resources. The enrichment of the camelids themselves may be the result of dung fertilizing practices discussed below.

The third pathway is the repeated use of camelid dung as fertilizer combined with the practice of allowing domestic camelids to forage in agricultural fields after harvest. Experimental as well as field studies have shown that the use of manure or guano to fertilize cultivated fields results in a $\delta^{15}\text{N}$ enrichment of the surrounding soils and plants (Szpak et al. 2012). Szpak et al.'s (2012) experimental study shows that maize grain $\delta^{15}\text{N}$ values are enriched an average of 1.8‰ while maize stems are enriched an average of 2.3‰ when grown with camelid dung fertilizers. The authors note the possibility that repeated use of dung fertilizers in fields over generations will lead to further $\delta^{15}\text{N}$ fractionation. If camelids are able to consume the enriched plant stalks or grains the camelid $\delta^{15}\text{N}$ values may increase to 8-11‰ (Szpak et al. 2012). If humans consumed the enriched camelids the resulting $\delta^{15}\text{N}$ values would be 11-14‰, which are in-line with the observed human values. This process may explain much of $\delta^{15}\text{N}$ values in the Nasca highland population but does not account the upper 50% of the distribution with $\delta^{15}\text{N}$ values 14-16‰ (Figure 4.5). The possibility that bird guano led to additional enrichment is falsified when the multivariate carbon/nitrogen model results are examined (Figure 4.9), which show no evidence of a marine enrichment signature. Further, the lack of a linear relationship between $\delta^{13}\text{C}$ from bone collagen and $\delta^{15}\text{N}$ ($R^2 = 0.029$, $p = 0.058$) suggests that plant consumption does not directly affect human $\delta^{15}\text{N}$ values, reducing the likelihood that $\delta^{15}\text{N}$ enrichment was the result of consuming domesticates enriched with camelid manure fertilizers (Finucane 2007).

A potential issue with the fertilizer hypothesis is the uniqueness of the Nasca highlands $\delta^{15}\text{N}$ signature. For fertilizer enrichment to have been responsible for the inordinately high

values one would have to assume that dung fertilizing was a relatively rare practice in the prehispanic highlands. If dung fertilizing was a common strategy one would expect the Nasca highland $\delta^{15}\text{N}$ values to be the normal baseline, rather than an outlier. Human ecology research in the Altiplano has shown dung fertilizer to be a crucial component of normative agricultural practice in the high Andes (Winterhalder et al. 1974; Winterhalder and Thomas 1978; Thomas 1973). The research conducted by Winterhalder and Thomas in the Altiplano demonstrated that fallow fields are not sufficiently fertile to grow domestic potatoes without the application of dung fertilizers. This is due to the soil's paucity of nitrogen, phosphorus, and organic materials along with poor water retention. Winterhalder and Thomas (1978) do however note that dung was not used as a fertilizer for cereal crops. These results imply that dung fertilizing would have been required for agriculture throughout much of the Andean Altiplano and would therefore be representative of the average $\delta^{15}\text{N}$ values in high elevation agricultural populations. It also implies that dung fertilizers are used more infrequently in regions dependent on cereal crops. Nonetheless, Szpak et al. (2012) suggest that additional $\delta^{15}\text{N}$ enrichment can occur with intensive and repeated use of dung fertilizers as a strategy of agricultural intensification. Thus, the Nasca highland signature may be partially driven by increasingly intensive fertilizer enrichment as an agricultural intensification strategy. All things considered; it is unlikely that fertilizer enrichment can alone account for the observed $\delta^{15}\text{N}$ values, in particular the upper half of the nitrogen distribution.

As a useful set of $\delta^{15}\text{N}$ comparisons, the MH population living 30 km down valley in the Nasca lowlands exhibit an average $\delta^{15}\text{N}$ value of 8.8‰ (Kellner and Schoeninger 2008), the MH population living to the east in Ayacucho exhibit average $\delta^{15}\text{N}$ values of 10.7‰ (Finucane et al. 2006) and MH population to the south in the Majes valley average 10.8‰ (Tung and Knudson

2017). The nitrogen enrichment in the Ayacucho sample is argued to be the result of herding practices and the use of dung fertilizer (Finucane 2009), while the elevated values in the Majes valley are argued to be a result of freshwater and marine dietary resources (Tung and Knudson 2017). These data show that agropastoral groups in the central and southern Andes exhibit normative $\delta^{15}\text{N}$ values ranging from 8.8-10.8‰ even when non-terrestrial resources are consumed, or dung fertilizer is used. These comparative data make suggest that the previously mentioned pathways cannot alone account for the Nasca highland values.

The fourth pathway is starvation-induced catabolism. Prolonged protein deficiency can result in the breakdown of tissues and fats to serve as amino acid pools in order to maintain critical bodily functions (Orten and Neuhaus 1982). This process, known as catabolism, has been shown to enrich $\delta^{15}\text{N}$ values during the period of starvation (Beaumont and Montgomery 2016; Doi et al. 2017; Walter 2017). Most studies that have successfully identified the isotopic effects of catabolism were able to do so by comparing cemetery samples with known starvation subgroups against those who were less likely to have experienced extended protein deficiency (e.g. Beaumont and Montgomery 2016; Walter 2017). Without comparative starving/non-starving populations it is difficult to parse out starvation-induced effects, as the $\delta^{15}\text{N}$ enrichment caused by catabolism is only relative to one's diet. Further, most population-wide starvation is episodic or acute rather than chronic. Subsequently, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values will average over the period during which the sampled bone remodels and will inevitably yield a signature that aggregates the starving and non-starving diet. If bones with relatively long turnover rates (e.g., long bones) are sampled the resulting isotopic analysis may not capture catabolism induced enrichment if the period of starvation is restricted to a short interval. The cranial bones sampled for this study (vomer and nasal concha) have rapid turnover rates on the order of 2-4 years (Sealy

et al. 1995), making it more likely that our isotopic measures will capture episodic periods of dietary stress.

Experimental feeding studies on domestic pigs have shown that reduced growth can lead to $\delta^{15}\text{N}$ enrichment of a full trophic level (Warinner and Tuross 2010), suggesting more general resource stress can produce elevated nitrogen values even when starvation is absent.

Comparing the LIP nitrogen values to the MH sample and neighboring populations renders starvation—or at the very least dietary stress—induced nitrogen enrichment a potentially viable pathway. Compared to the MH nitrogen average of 8.8‰ the LIP average of 13.2‰ exhibits an enrichment of 4.4‰. Neighboring populations with dietary practices utilizing terrestrial meat protein and dung fertilizer exhibit average nitrogen values well below the LIP sample (e.g. Finucane 2007). Indeed, populations known to subsist of a mix of terrestrial and marine resources exhibit values well below those of the Nasca highland sample (e.g. Tung and Knudson 2017). The Nasca highland population's nitrogen enrichment one-to-two trophic levels above the neighboring populations suggests some degree of stress-induced catabolysis. This is especially true for the upper 50% of the Nasca highland nitrogen distribution, which exhibits values ranging from 14‰ to 16‰, which are unlikely to be achieved by standard practices of hunting, herding, and manuring fertilizing.

The fifth pathway is a sustained strategy of anthropophagy. The consumption of human body tissues, known colloquially as cannibalism, has been observed throughout historic and prehistoric times (Cole 2017; Billman et al. 2000; Defleur et al. 1999; Jones et al. 2015; Turner and Turner 1999). While anthropophagy has only rarely been shown to be a consistent dietary strategy among humans, some case studies support the idea that anthropophagy is utilized as a last resort when resources are scarce (Cole 2017; Fernandez-Jalvo et al. 1999; Saladié et al.

2012; Saladié and Rodríguez-Hidalgo 2017) and occasionally as a form of ritual (Bellow et al. 2017; Vayda 1974). The consumption of human tissues leads to $\delta^{15}\text{N}$ enrichment that could be consistent with observed values. The consumption of human tissues with baseline values averaging 8.8-10.8‰ (see comparison data above) would result in a trophic shift somewhere in the order of 2-4‰, resulting in values of $\delta^{15}\text{N}$ 10-15‰. For these elevated $\delta^{15}\text{N}$ values to be maintained over the period of bone remodeling, anthropophagy would need to be a very consistent dietary strategy. Given the exceedingly high nitrogen values of the Nasca highlanders, we cannot rule out this strategy, although the sheer amount of anthropophagy that would have to occur to produce such consistently high nitrogen values render this pathway somewhat unlikely. Nonetheless, the Nasca highland nitrogen values are statistically similar to values from a LIP Ayacucho skeletal sample where osteological evidence shows indisputable evidence for anthropophagy in the form of butchery marks, cooking, and marrow processing (Tung et al. 2017). While further osteological analysis is needed to test this hypothesis in the Nasca highlands, cannibalism may be a partial pathway to the observed nitrogen values.

2. Stable $\delta^{13}\text{C}$ Signatures

The change during the LIP to include more C_3 plants in the diet, and in particular a mixed C_3 and C_4 plant protein diet, can be explained by the need to increase economic diversity in the challenging climatic and social environment. If the Nasca population constrained herding and general mobility, the result would have been elevated economic risk. A commonly observed risk-mitigating strategy in the Andes is intra-field crop diversification (Goland 1993; Marston 2011), which required farms to plant a mosaic of crops within each field. The move towards a mixed C_3/C_4 plant diet may indicate a strategy of crop diversification.

3. An Explanatory Model

We present a probable explanatory model that works to clarify the complicated isotopic data and link the results to our model predictions. We argue that the most parsimonious explanation of the dietary data appears to be that Nasca highland subsistence was driven by low-mobility, high-intensification strategies that were seasonally variable and prone to recurrent bouts of dietary stress and possibly starvation. Further, we hypothesize that localized protein shortages may have forced individuals into a strategy of anthropophagy, similar to LIP patterns seen in the neighboring Ayacucho region (Tung et al. 2017). These outcomes were likely the result of reduced access to macronutrients either through malnutrition, malabsorption, or both.

Stable $\delta^{15}\text{N}$ values and our analytical results suggest that camelid dung fertilizers were used to enhance the soil productivity, intensify agricultural regimes, and permit domestic camelids to forage in agricultural fields after harvests, thereby taking advantage of local fodder to reduce mobility. This practice was likely augmented by the use of domestic guinea pigs that can be raised indoors on food scraps (Kurin 2016). However, even if these strategies were practiced in-concert, they cannot account for the extremely high nitrogen values nor their temporal and demographic consistency. High nitrogen values are likely a result of multivariate processes, but strongly suggest the consumption of enriched camelids combined with seasonal catabolism that was a physiological response to recurrent food shortfalls. The dry season was most likely a time of increased raiding and violent activities, owing to the lack of agricultural-based activities such as planting, field maintenance, or harvesting. If the Nasca highland populace hunkered down during this season, any shortfalls in stored harvests could lead to acute starvation for both people and domestic camelids. So long as the period of food shortage was relatively brief and predictable, the population could have maintained this system indefinitely, and could explain the aberrantly high nitrogen values as well as their consistency. This strategy

would limit mobility by curtailing the seasonal round of camelid herding on the Pampa Galeras and allow individuals to remain in the confines of fortified hilltop settlements. We argue that this strategy would provide an adaptive trade-off between the risk of death due to starvation versus interpersonal violence.

The trend towards a more mixed C₃/C₄ diet during the LIP relative to the Middle Horizon may suggest a wider mosaic of plant dietary resources, perhaps through the risk-minimizing tactic of intra-field crop diversification (Goland 1993). This would have worked to decrease economic risk and provide a wider array of plant based macro- and micro-nutrients. Nonetheless, the population show a consistent trend towards C₄ plants, which were likely maize.

To summarize, we argue that LIP farmers implemented a subsistence system that reduced mobility when possible to avoid violence encounters, resulting in chronic dietary stress, starvation, and possible anthropophagy. Thus, individuals sought to trade-off the two risks, but could not effectively eliminate both the risk of resource stress and the risk of violence and would have had to make difficult decisions with potentially disastrous outcomes.

4. Variability in Risk-Preference

The lack of major differences in isotopic values between the sexes and age cohorts makes it difficult to discern how diversity in diet structures variability in violence. The sustained similarity in $\delta^{15}\text{N}$ values between the sexes suggests that diets, and perhaps severity of food shortfalls, were similar. As such, it is not clear with the current data whether the variation in violent trauma is a result of differences in subsistence risk-preference.

Finally, the lack of defined relationships between isotope values and pathology/trauma suggest the stable isotope values are not sufficiently clear and/or differentiated to assess how they relate to variability in pathology or violence.

5. Conclusion

Isotopic results suggest initial support for model predictions, whereby the Nasca highland population reduced mobility by intensifying agricultural regimes and permitting camelids to consume domestic plant resources thereby eliminating the need to travel to distant herding patches. Nevertheless, results remain ambiguous, require further testing, and show mixed support for our predictions pertaining to variability in risk-preferences. Nonetheless, we contend the model is useful for a number of contexts and can provide explicit predictions regarding population-level and individual variability in risk-preference. The model proposed here attempts to move beyond descriptive studies of human responses to warfare by acknowledging that human subsistence behavior will be a function of the costs and benefits of alternative strategies, and therefore should be patterned and mediated by optimality logic. Future research will seek data that can provide a more robust test of model predictions and more fully explore the isotope results presented here.

V. Dissertation Summary and Conclusions

This dissertation research sought to address two main questions: 1) what conditions promote conflict? 2) how do people cope with conflict? Here, we outline four main points that summarize the results of dissertation research as well as the intellectual merits.

First, this research develops formal expectations regarding the characteristics of prehistoric violence, which can provide a framework for osteologists to build more informed hypotheses concerning the causes and consequences of violence. Results show compelling evidence for intense, internecine warfare in the study region and a pattern of social substitutability, whereby all members of the population were viable targets of lethal killings.

Second, this research provides a novel approach for dealing with the issues of the osteological paradox and does so within a complicated cemetery context, which are typically avoided by paleopathologists seeking to engage with the osteological paradox. Results show a deterioration in health during the study period via an increase in pathologies indicative of dietary stress and increasing mortality as revealed by hazard models. Our findings also show substantial heterogeneity in frailty in the risk of death, particularly by sex, whereby females are more likely to exhibit pathology and have lower life expectancy at birth.

Third, our evaluation of the drivers of warfare led us to develop general predictive models that can explain variability in warfare across time and space. Hypothesis tests included interactions between independent variables, going beyond monocausal explanations of conflict. By developing and testing predictive models using case studies we will be better able to predict whether similar conditions will favor conflict in the future (Burke et al. 2015; Hsiang et al. 2013; Zhang et al. 2007b). Results show resource scarcity to be the major driving factor both with the

initiation of conflict in the region, and its variability throughout the 500-year study period. These findings are in-line with our evolutionary derived hypotheses.

Fourth, our risk-sensitive subsistence model provides a means for moving beyond descriptive studies of human responses to warfare by acknowledging that human subsistence behavior will be a function of the costs and benefits of alternative strategies, and therefore should be patterned and mediated by optimality logic. Results suggest an environmentally mediated tradeoff that promotes risk-averse behavior whereby mobility was reduced through a combination of agricultural intensification and an emphasis on maintaining camelid herds locally using domestic crops as fodder.

In all, this dissertation provides a novel avenue for exploring the character, causes, and consequences of warfare by providing robust methodological procedures and predictive models that tie deductive theory-driven hypotheses to high-resolution datasets.

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