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Stable Isotope Ecology and Human-Animal Interactions in Northern Peru

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A thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Anthropology

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STABLE ISOTOPE ECOLOGY AND HUMAN-ANIMAL INTERACTIONS IN NORTHERN PERU

(Thesis format: Integrated Article)

by

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Graduate Program in Anthropology

A thesis submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

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Abstract

This dissertation addresses several issues related to isotopic ecology in northern Peru. The first portion of the dissertation focuses on baseline carbon and nitrogen isotopic variability in plants for comparison with paleodietary data. The second portion applies these data to assess animal management practices (camelids) in the Virú Valley on the north coast of Peru using isotopic analysis of bone collagen and serially sampled hair.

A detailed survey of plants from the Moche River Valley region demonstrates significant east-west variation in plant carbon and nitrogen isotopic compositions, following changes in altitude from the Pacific coast to the highlands. A growth chamber study and a field experiment show the potential for Andean fertilizers (seabird guano and camelid dung) to increase the δ^{15}N values of plant tissues (by +11 to +45 ‰ for seabird guano and by +2 to +4 ‰ for camelid dung). These findings have important implications for the reconstruction of diet in the Andean region, potentially confounding the interpretation of bulk isotopic data (from bone collagen or hair keratin), with camelid dung fertilized plants appearing isotopically similar to terrestrial animal meat, and guano fertilizer maize appearing isotopically similar to high trophic level marine organisms.

Carbon and nitrogen isotopic compositions from camelid bone collagen and hair keratin from two sites (Huaca Gallinazo and Huaca Santa Clara) in the Virú Valley (Peru) are highly variable, with an overall tendency towards higher δ^{13}C and δ^{15}N values relative to modern animals raised in highland environments, suggesting that at least some of these animals were raised locally. The high amount of isotopic variability between individuals, inconsistent amount of within-individual variation, and no consistent shift in isotopic compositions leading up to the time of death is consistent with small-scale camelid husbandry on the north coast of Peru, with small groups of camelids being managed by individual families or other small social units. The isotopic analysis of zooarchaeological material derived from livestock has great potential with respect to better understanding animal husbandry practices, and human-animal interactions in the broadest sense.

Keywords

Carbon isotopes, nitrogen isotopes, isotopic baselines, plant physiology, fertilizers, guano, dung, paleodiet, Peru, Andes, camelid, llama, alpaca, animal management, animal husbandry, human-animal interactions, Virú Valley, isotopic variation

Co-Authorship Statement

Chapter 2 was co-authored by Christine D. White, Fred J. Longstaffe, Jean-François Millaire, and Victor F. Vásquez Sánchez. FJL, JFM, CDW provided funding for the project, contributed to the experimental design, and edited the manuscript. VFVS collected and identified samples. This is a modified version of a published paper:

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Chapter 3 was co-authored by Fred J. Longstaffe, Jean-François Millaire, and Christine D. White. FJL, CDW provided funding for the project, FJL, JFM contributed to the experimental design, JFM assisted with the growth chamber experiment, and FJL, JFM, CDW edited the manuscript. This is a modified version of a published paper:

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Chapter 4 was co-authored by Jean-François Millaire, Christine D. White, and Fred J. Longstaffe. FJL, JFM, CDW provided funding for the project, JFM contributed to the experimental design and facilitated its execution in Peru, and FJL, JFM, CDW edited the manuscript. This is a modified version of a published paper:

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Dedication

This work is dedicated to the memory of my father.

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Chapter 1

1 Introduction and Overview

1.1 Introduction

Over the last thirty years, stable isotope analysis has transitioned from a labor-intensive, expensive methodology practiced in a limited number of laboratories to a nearly standard part of the archaeological toolkit (Figure 1.1). This is because of the significantly reduced costs of most types of analyses, the proliferation of stable isotope laboratories, and the training of anthropologists and archaeologists in isotopic techniques beginning in the 1980s. Isotopic analysis has provided great insight into a variety of issues in archaeology and paleontology, to name but a few areas of study: foraging ecology of extinct species (e.g. Corbett et al., 2008; Hobson and Montevecchi, 1991; Noe-Nygaard et al., 2005), large-scale shifts in ecosystems due to natural and anthropogenic processes (e.g. Burton et al., 2001; Emslie and Patterson, 2007; Newsome et al., 2007b; Szpak et al., 2013a), issues surrounding animal domestication and management (e.g. Barton et al., 2009; Germonpré et al., 2009; Minagawa et al., 2005; Rawlings and Driver, 2010; White et al., 2001), weaning practices in past populations (e.g. Dupras et al., 2001; Katzenberg et al., 1996; Pearson et al., 2010; Richards et al., 2002), and (perhaps most commonly) the diet of prehistoric human populations (e.g. Ambrose et al., 2003; Bocherens and Drucker, 2006; Knudson et al., 2007; Newsome et al., 2004; Richards et al., 1998; Schwarcz et al., 1985; Watts et al., 2011; White and Schwarcz, 1989; White et al., 2009). While the number of studies being conducted has increased rapidly (Figure 1.1), two areas that have lagged behind considerably are: (1) the development of detailed isotopic baselines at a regional or local level, and (2) the refinement of quantitative methodologies used in the interpretation of isotopic data. This dissertation attempts to address several of these issues in one particular region of the world (the northern Peruvian Andes) and apply them to a case study involving the management of a class of domestic animal (South American camelids) in the region. Ultimately, these data aid in the understanding of the ways in which humans interacted with their environment.

1.2 Isotopic Analysis in Archaeology: A Brief Introduction

1.2.1 *Stable Isotopes*

Isotopes are forms of the same chemical element that differ in terms of their atomic mass (specifically the number of neutrons). Stable isotopes are those that do not undergo measurable radioactive decay and are therefore stable. For instance, carbon has three isotopes: carbon-14, carbon-13, and carbon-12. Carbon-14 is radioactive, decaying to ^{14}N at a known rate, while carbon-13 and carbon-12 are stable. While stable isotopes do not change over time, the relative proportions of isotopes in biological systems undergo characteristic changes (fractionation) because the lighter isotope reacts more rapidly than the heavier isotope (Fry, 2006). Some of these reactions are associated with chemical, biological, or geological processes that are functionally significant. For example, terrestrial vascular plants are characterized primarily by two photosynthetic pathways: C_3 (Calvin-Benson Cycle) and C_4 (Hatch-Slack Pathway). Each of these pathways comprise a different set of reactions, which leads to differences in the relative distribution of carbon isotopes in the tissues of these two types of plants (Bender et al., 1981; Smith and Epstein, 1971). In absolute terms, these differences are very small, and therefore relative abundances of stable isotopes are expressed as a ratio of heavy to light isotopes multiplied by 10^3 relative to an international reference standard:

Equation 1.1 $$\delta^{H}X = [(R_{sample}/R_{standard}) - 1]$$

This nomenclature is known as δ notation and is reported in parts per thousand (per mil, ‰). In the above equation X represents an element (e.g. O, C, N), H represents the heavy isotope of that element (e.g. 18, 13, 15), and R represents the ratio of heavy to light isotopes in the sample or standard respectively (e.g. $^{18}O/^{16}O$, $^{13}C/^{12}C$, $^{15}N/^{14}N$).

1.2.2 *Natural Variation in Carbon and Nitrogen Isotopic Compositions*

There are a number of processes that occur in the biosphere that lead to characteristic patterns of isotopic variation at multiple scales. These processes, particularly as they relate to plant-soil systems, are reviewed in greater detail in Chapters 2, 3, and 4, and therefore are only treated in brief here.

The carbon and nitrogen isotopic compositions of an animal's tissues are representative of the weighted average of the carbon and nitrogen isotopic compositions of the foods consumed (DeNiro and Epstein, 1978, 1981; Schoeninger et al., 1983; Schoeninger and DeNiro, 1984). The breakdown of foodstuffs in the digestive system and eventual incorporation of macronutrients into body tissues are associated with offsets (often called trophic level discrimination or trophic level fractionation), which vary between different tissues; these offsets are denoted by capital delta (Δ) and in some cases a subscript that denotes the tissue being measured (e.g. $\Delta^{13}C_{\text{feather−diet}}$ or $\Delta^{15}N_{\text{hair keratin−diet}}$). Generally, body tissues tend to be relatively enriched in ^{15}N by ca. 3 to 4 ‰ compared to the diet (Hobson and Welch, 1992; Minagawa and Wada, 1984); this is fairly consistent between different tissue types, although there is some variation (Caut et al., 2009). This allows for the approximation of trophic position in animals that may either forage at multiple trophic levels (Hobson et al., 2000; Jacoby et al., 1999; Jones et al., 2006; Newsome et al., 2009; Smith et al., 2010; Szpak et al., 2012c), or in extinct species wherein the trophic level and foraging ecology of the animal are unknown (Bocherens et al., 2011; Corbett et al., 2008; Fernandez-Mosquera et al., 2001; Gröcke, 1997; Nelson et al., 1998; Richards et al., 2008). Body tissues also tend to be enriched in ^{13}C relative to food, but the difference is much more variable. For most tissues the diet-tissue fractionation is relatively small (<2 ‰) (Caut et al., 2009; Miller et al., 2008; Rau et al., 1983), with the notable exception of bone collagen. For bone collagen, $\Delta^{13}C$ values >5 ‰ are not unusual (Jim et al., 2004; Sullivan and Krueger, 1981; Vogel, 1978b), although a mean value for controlled and field studies (3.7±1.6 ‰) is lower (Szpak et al., 2012c). On these bases, the carbon and nitrogen isotopic compositions of a consumer can be informative with respect to the types of foods that are consumed, as well as the types of habitats that are utilized (Kelly, 2000; Newsome et al., 2007c; Newsome et al., 2010; Schwarcz et al., 2010). Within the context of terrestrial herbivores, it is especially crucial to understand the isotopic ecology of plant-soil systems, since it is at this level that the variations in animal isotopic compositions are driven (Hartman, 2011; Murphy and Bowman, 2006).

Terrestrial plants obtain carbon primarily through two photosynthetic processes: the Calvin Cycle (in C_3 plants) and the Hatch-Slack Pathway (in C_4 plants). C_4 plants are predominantly tropical grasses, while C_3 plants include most other terrestrial vascular plants, including some grasses (O'Leary, 1981; Sage and Pearcy, 2004). C_3 plants tend to have carbon isotopic compositions around −27 ‰, while C_4 plants tend to have carbon isotopic compositions around −12.5 ‰ (Bender, 1968; Kohn, 2010; O'Leary, 1988; Smith and Epstein, 1971). Within the context of archaeology, certain cultigens utilize the C_4 photosynthetic pathway (most notably maize, but also millet, amaranth, sorghum, and sugar cane), and this has served as the basis for a great number of studies that have attempted to quantify the relative contribution of these plants to human diets (Ambrose et al., 2003; Barton et al., 2009; Bender et al., 1981; Buikstra and Milner, 1991; Burger and van der Merwe, 1990; Hu et al., 2006; Schwarcz et al., 1985; Staller et al., 2006; White et al., 1993). Aside from these two groups of plants, many species of succulents and cacti in arid environments utilize a distinct photosynthetic pathway, Crassulacean acid metabolism (Ting, 1985), and have highly variable carbon isotopic compositions that are intermediate between those of C_3 and C_4 plants (Bender et al., 1973; Hietz et al., 1999; Szarek and Troughton, 1976; Winter, 1979).

Aside from the differences in plant photosynthetic pathways, a number of environmental factors can also impact plant carbon isotopic compositions. Plants growing in dense understory environments tend to have $\delta^{13}C$ values that are lower by as much as 5 ‰ relative to canopy plants, or plants growing in open environments (Heaton, 1999). This is referred to as the ‘canopy effect’ and has primarily been observed in tropical rain forest environments (Cerling et al., 2004; Martinelli et al., 1998; van der Merwe and Medina, 1989, 1991), but it has also been suggested that this effect occurs in more temperate settings (Barberena et al., 2011; Drucker et al., 2008; Drucker et al., 2010). This effect is large enough to manifest itself as a significance difference in the carbon isotopic compositions of animals using predominantly open versus closed habitats (Drucker et al., 2008; Drucker et al., 2010; Forbes et al., 2010; MacFadden and Higgins, 2004; Nelson, 2007; Secord et al., 2008; Voigt, 2010).

Both soil salinity and water availability have been demonstrated to affect plant carbon isotopic compositions in similar ways. C_3 plants growing under conditions of low water availability tend to have less negative $\delta^{13}C$ values than those plants growing under conditions of higher water availability (Austin and Vitousek, 1998; Condon et al., 1992; Damesin et al., 1997; Lajtha and Getz, 1993; Lopes and Araus, 2006; Miller et al., 2001; Murphy and Bowman, 2009; Panek and Waring, 1997; Peri et al., 2012; Scartazza et al., 1998; Scartazza et al., 2004; Stewart et al., 1995; Swap et al., 2004; Syvertsen et al., 1997; Weiguo et al., 2005; Welker et al., 1993). Similarly, plants growing under saline conditions tend to have comparatively less negative $\delta^{13}C$ values relative to those growing under normal conditions (Brugnoli and Lauteri, 1991; Choi et al., 2005b; Farquhar et al., 1982b; Guy et al., 1980; Isla et al., 1998; Neales et al., 1983; van Groenigen and van Kessel, 2002). Both highly saline and arid conditions are thought to influence plant $\delta^{13}C$ values by altering the degree of stomatal closure. Specifically, under these conditions, stomatal closure increases, resulting in less discrimination against ^{13}C during diffusion of CO_2 into leaf cells (Farquhar et al., 1982a). These effects tend not to be clearly manifested in the carbon isotopic compositions of consumer tissues because they are often overshadowed by the relative contribution of C_3 and C_4 plants. In environments that are entirely composed of C_3 plants, these effects may be apparent, but are of fairly small magnitude (Britton et al., 2008).

Altitude, which significantly varies in the Andean region of South America, has also been demonstrated to influence C_3 plant $\delta^{13}C$ values, with higher $\delta^{13}C$ values associated with higher altitudes (Cordell et al., 1998; Hultine and Marshall, 2000; Kogami et al., 2001; Körner et al., 1988; Lajtha and Getz, 1993; Marshall and Zhang, 1994; Qiang et al., 2003; Sah and Brumme, 2003; Sparks and Ehleringer, 1997; Szpak et al., 2013b; Vitousek et al., 1990; Yi and Yang, 2006). This variation is most likely driven by a number of factors including differences in carboxylation efficiency and leaf morphology, both influencing ^{13}C discrimination (Körner et al., 1991). Aside from differences in $\delta^{13}C$ values with altitude, the relative distribution of C_3 and C_4 plants is also influenced by altitude, with relatively few C_4 plants occurring at high elevations (Bird et al., 1994; Cabido et al., 1997; Cavagnaro, 1988; Szpak et al., 2013b; Tieszen et al., 1979). Altitudinal effects on animal tissue $\delta^{13}C$ values have been observed in some studies (Chang et al., 2011; Graves et al., 2002; Graves and Romanek, 2009; Hobson et al., 2003), but not in others (Chang et al., 2011; Yi and Yang, 2006). The majority of the altitudinal variation in consumer tissue $\delta^{13}C$ values is, however, driven by variation in the relative distribution of C_3 and C_4 plants, rather than the direct effects of altitude on C_3 plants themselves.

Most plants acquire nitrogen primarily through uptake of mineralized nitrogen (NO_3^- and NH_4^+) in the soil. Processes associated with the nitrogen cycle (nitrification, denitrification, ammonification, ammonia volatilization) are associated with, in some cases, substantial fractionations, and therefore the relative importance of these processes, and the reliance of plants on particular N species can have a significant impact on plant nitrogen isotopic compositions. The addition of exogenous N species to soil systems can also lead to substantial changes in soil and plant $\delta^{15}N$ values. In particular, the application of fertilizers of animal origin has received some attention in the last ten years within the context of archaeology (Bogaard et al., 2007; Fraser et al., 2011; Kanstrup et al., 2011), soil science (Choi et al., 2006; Choi et al., 2002; Choi et al., 2004; Lim et al., 2007; Nakano et al., 2003) and food chemistry (Bateman et al., 2005; Bateman et al., 2007; Camin et al., 2007; Camin et al., 2011; Flores et al., 2007; Flores et al., 2011; Rapisarda et al., 2005; Rapisarda et al., 2010; Rogers, 2008; Šturm et al., 2011; Verenitch and Mazumder, 2012; Yuan et al., 2012). Generally, a pattern of higher $\delta^{15}N$ in plants treated with animal fertilizers has been observed relative to untreated plants, although the magnitude of this difference varies considerably. The vast majority of work conducted to date has focused on the most economically significant organic fertilizers today (those derived from cattle and pigs); studies considering archaeological implications have also focused exclusively on cattle manure. Chapters 3 and 4 address these issues in the Andean region of South America, examining the potential isotopic effects of the two most widely discussed fertilizers (based on ethnohistoric and ethnographic texts): seabird guano and camelid dung.

The effects of fertilizers on plant $\delta^{15}N$ values can largely be categorized as ‘source’ effects since the most significant difference is the addition of a new source of N with a (potentially) distinct nitrogen isotopic composition. Other aspects of the N cycle may also be influenced by a number of environmental parameters and these may also impact fractionations of N species in the soil and ultimately plant δ^{15}N. In general, plants and soils in hot, arid environments tend to have higher δ^{15}N values than plants growing in cold, moist environments. This is because hot and arid environments tend to be more prone to loss of N and cool and moist environments tend to conserve and recycle N (Handley et al., 1999a). The loss of N, through processes such as ammonia volatilization, strongly concentrates the remaining substrate (in this case the soil NH_4^+) in ^{15}N (Mizutani et al., 1985b; Mizutani et al., 1986), leading to an overall higher δ^{15}N value for that ecosystem. Aside from the differences in reliance on C_3 and C_4 plants, these effects have been observed with the greatest consistency in animal species (Ambrose and DeNiro, 1986a, 1986b, 1987; Cormie and Schwarcz, 1996; Gröcke et al., 1997; Heaton et al., 1986; Murphy and Bowman, 2006; Pate and Anson, 2008; Schwarcz et al., 1999; Sealy et al., 1987; Vogel et al., 1990a; Vogel et al., 1990b).

Overall, there are a number of complex environmental factors that influence the carbon and nitrogen isotopic compositions of soils and plants. To understand the diet and ecology of archaeological or paleontological animals it is crucial that these factors be understood in as much detail as possible. It is not sufficient to rely only on general principles of stable isotope ecology, or on baseline isotopic data that are spatially or temporally inappropriate. Chapters 2, 3, and 4 of this dissertation are aimed at resolving these issues in the northern Peruvian Andes.

1.2.3 *Interpreting Isotopic Data*

Within the context of palaeodietary studies, stable isotopes of carbon and nitrogen are most commonly analyzed (as discussed above), with a much smaller number of studies including sulfur isotopic analysis (Craig et al., 2006; Nehlich et al., 2010; Privat et al., 2007; Richards et al., 2001). Accordingly, this discussion is limited to interpretations of carbon and nitrogen isotopic data. While there have been substantial changes in the manner and scale with which isotopic data are generated, the interpretive techniques employed by archaeologists and anthropologists have remained fairly consistent over the last twenty years. The types of questions that have been asked have generally been limited to, “what was the diet composition of population/group/individual *x*” and “how similar were the diets of groups *x* and *y*”. To answer the first of these questions requires relatively detailed knowledge on the range and variation of the isotopic compositions of the foods that may have contributed to the diet. This requires the analysis of modern flora/fauna, archaeological fauna, or a combination of these. Isotopic data derived from archaeological humans or animals (mixtures) are then interpreted using these baselines (sources) as a reference point using a range of qualitative and quantitative approaches, as outlined below.

1.2.3.1 Isotopic Mixing Basics and the *n*+1 Model

Understanding isotopic mixing is crucial to the interpretation of isotopic data in a wide range of contexts, including in paleodietary studies. Before exploring any particular method in great detail, it is first necessary to introduce some of the basic concepts of isotopic mixing. To do so, a basic linear mixing model (*n*+1 Model) will be discussed.

In isotopic mixing models, foods are often referred to as ‘sources’ and consumers are sometimes referred to as mixtures, but in this context are more frequently simply called ‘consumers’. As mentioned previously, the isotopic compositions of a consumer’s tissue represent an average of the isotopic composition of the foods (sources) consumed over a given period of time (depending on the tissue being analyzed). This relationship is summarized very simply in Figure 1.2. In this case, the consumer (solid dot) has a very similar isotopic composition to Source 2, which suggests this particular source (food) is prominent in the diet of this consumer. To make such comparisons, appropriate adjustments must be made to either the consumers or sources for trophic level fractionation. The interpretation of Source 2 being important can be made qualitatively by evaluating the proximity of the consumer to the source in bivariate (*x*, *y*) space. This relationship can also be expressed quantitatively: the contribution of a particular source to the diet of a consumer is inversely proportional to the line connecting the consumer and source. In other words, the shorter the line between the consumer and the source, the greater the contribution of that source to the diet/mixture. A series of equations can be performed in this case to determine the *exact* contributions of each source, as discussed by Schwarcz (1991).

Equation 1.2 $$\mathbf{X_1} + \mathbf{X_2} + \mathbf{X_3} = \mathbf{1}$$

Equation 1.3 $$(\mathbf{C_1})(\mathbf{X_1}) + (\mathbf{C_2})(\mathbf{X_2}) + (\mathbf{C_3})(\mathbf{X_3}) = \mathbf{C}_{\boldsymbol{M}}$$

Equation 1.4 $$(\mathbf{N_1})(\mathbf{X_1}) + (\mathbf{N_2})(\mathbf{X_2}) + (\mathbf{N_3})(\mathbf{X_3}) = \mathbf{N}_{\boldsymbol{M}}$$

X_1, X_2, and X_3 represent the % contribution of each of the three sources, C_x and N_x represent the carbon and nitrogen isotopic compositions of each of the sources, C_M and N_M represent the carbon and nitrogen isotopic compositions of the consumer/mixture. These three equations can be used to produce solutions for each source contribution. A related, but alternative approach is provided by Ben-David et al. (1997) that explicitly uses the Euclidean distance between the consumer and each source.

The limitation of both of these approaches is that calculations of source contributions are limited to *n*+1 sources, where *n* is the number of isotopes being measured (typically two); higher numbers of sources do not produce finite solutions. In most practical cases, this limits the number of sources being examined to two. This may be acceptable, for example, when only two distinct sources of primary production contribute to the diet of a consumer, as is sometimes the case in nearshore marine ecosystems (Bustamante and Branch, 1996; Duggins et al., 1989; Fredriksen, 2003; Hill and McQuaid, 2008; Kaehler et al., 2006; Kang et al., 2008; Schaal et al., 2009, 2010; Simenstad et al., 1993). In the case of more complex systems, as is often the case with humans, where food is consumed from multiple trophic levels and habitats, this approach has few practical applications. Nevertheless, it does illustrate the basic premises of isotopic mixing and paleodietary interpretation that form the basis of most other methods.

While the focus of the following section is not explicitly on reconstructing diet composition with mixing models, much more refined methods to do this have been developed in recent years, using computer-assisted iterative methods that are constrained to provide feasible solutions for larger numbers of sources (Newsome et al., 2004; Phillips and Gregg, 2001; Phillips and Koch, 2002; Phillips and Gregg, 2003; Phillips et al., 2005), and also methods that use a Bayesian framework to incorporate uncertainty in source isotopic compositions, trophic level fractionation estimates, and so on (Bond and

Diamond, 2010; Moore and Semmens, 2008; Parnell et al., 2010; Semmens et al., 2009; Ward et al., 2010). Nevertheless, what remains of the utmost importance in such models is that the variation in isotopic baselines (in this case food) be understood as completely as possible. Moreover, if Bayesian models are used, it is useful to know how much uncertainty to expect in the isotopic compositions of the sources. The remainder of this section focuses on data presentation and interpretation methods currently employed and introduces some new approaches that are later utilized in Chapter 5.

1.2.3.2 Box Model Method

This approach to interpreting isotopic data visualizes source isotopic compositions as boxes in bivariate space (Figure 1.3). The dimensions of the boxes may be determined by the range, or the mean and standard deviations of the isotopic compositions of one or several sources. Sources may be grouped together based on functional and/or isotopic similarity, although this is not specific to this particular approach. Carbon and nitrogen isotopic data from consumers are plotted alongside the source boxes, with either the boxes or the consumers being adjusted to account for trophic level fractionation. These data are interpreted qualitatively, although the mechanistic basis for the interpretation is essentially quantitative and based in Euclidean geometry. Generally, if a consumer falls within a given box, that individual is interpreted as having been largely reliant on that particular food source, or more likely group of foods. In some instances such an assessment is entirely reasonable. Taking the data presented in Figure 1.3 as an example, individuals that fall within the C_3 plant box (especially close to the bottom left of the box), the C_4 plant box (especially close to the bottom right), or the marine animals box (especially close to the top right) are likely to have consumed primarily these resources. For most of the individuals plotted in Figure 1.3, however, we could interpret marine plants as having been the primary food source. While this may be mathematically sensible, it is only *one* possible solution to this mixing problem. Alternatively, a mixture of some proportion of marine animals and C_3 plants can produce the same consumer isotopic signature. While this may be implicit for those who understand isotopic mixing, those reading such a figure with less knowledge of its mathematical basis may be prone to misinterpretation.

Additional problems come in the forms of the boxes themselves. Rarely are animal or plant isotopic compositions distributed evenly within the rectangular bivariate space of one of these boxes. This is especially problematic if the boxes are defined on the basis of source ranges. If boxes are defined on the basis of means and standard deviations this better conveys the density of a particular source, but problems arise when collapsing multiple sources into one box. Finally, the actual distribution of carbon and nitrogen isotopic data within bivariate space is rarely even, and in many cases these variables may be correlated (this is explored in the following section). Again, the right angle boxes used in this approach do not adequately capture these aspects of typical isotopic data.

The Box Model Method is a very straightforward and somewhat attractive means of displaying the relationship between sources and consumers; it tends to be less cluttered than similar plots that utilize a mean and standard deviation for individual food sources (Beasley et al., 2013; Kinaston et al., 2013; Kusaka et al., 2010; Szpak et al., 2009; Szpak et al., 2012c). Problematic as this Box Model Method may be, it is still superior to presenting consumer isotopic data absent of any baseline information.

1.2.3.3 Polygons and the Convex Hull

The areas formed by isotopic data in bivariate space are significant in ways beyond the generation of mixing polygons as discussed previously. The basis for the Box Model Method, as well as many other qualitative interpretive approaches to bivariate isotopic plots, is that they rely on the spatial relationships (proximity of A to B, area of A relative to B) of the data. These spatial relationships are significant because the variation in isotopic compositions is associated with larger biological, chemical, or geological significance. The methods discussed in this section make use of the spatial nature of isotopic data and provide a number of ways that these data can be compared in a more quantitative approach. This understanding of bivariate data underpins the approaches used in Chapter 5. The crucial point here is that we are moving away from an approach that is primarily concerned with reconstructing diet *composition* to one that is instead focused on diet *variation*. While reconstructing diet composition has become a much more refined art with the introduction of more involved linear models (Newsome et al., 2004; Phillips and Gregg, 2001; Phillips and Koch, 2002; Phillips and Gregg, 2003;

Phillips et al., 2005), and the incorporation of more complex Bayesian statistics (Bond and Diamond, 2010; Moore and Semmens, 2008; Parnell et al., 2010; Semmens et al., 2009; Ward et al., 2010), the uncertainty associated with these estimates remains problematic. Even under ideal conditions in modern contexts where prey species can be re-sampled in a much more unrestrictive manner and the temporal span is both known and extremely limited, these issues of uncertainty are still significant. In archaeological contexts this is taken to the extreme where source isotopic compositions will necessarily be even more uncertain. While it is certainly not a futile task to attempt these diet composition assessments, a more productive approach (either as an alternative, *or* as a complement) can be to focus on the variability in isotopic data.

Consider the three groups of isotopic data presented in Figure 1.4A for Holocene humans from central California (Beasley et al., 2013). Expressing these data as means and standard deviations (Figure 1.4B) does not adequately capture the distribution of the data, largely because there is clearly a correlation between $\delta^{13}C$ and $\delta^{15}N$. Moreover, as a descriptive tool, Figure 1.4B does a poor job of conveying the spatial distribution of the isotopic variation around the means. If, as discussed previously, the isotopic variation is meaningful, this is particularly problematic. Two alternative approaches to displaying the variation in bivariate isotopic datasets have been proposed. The first is the convex hull area (or total area), which is simply the minimum area polygon that encloses all of the individual data in bivariate space (Figure 1.4C) (Layman et al., 2007a). The area occupied by this polygon can be used as a comparative metric in discussing the amount of isotopic variation ($\delta^{13}C$ and $\delta^{15}N$ *together*, rather than separately) in a given dataset. The convex hull matches the distribution of the data faithfully, but it does not convey any information about the density or packing of the isotopic data in space. In Figure 1.4C, for example, one polygon is much larger than the other two, which is caused by the three individuals with low $\delta^{13}C$ and $\delta^{15}N$ values. The convex hull is therefore very sensitive to extreme values, and a single outlier or small number of outliers can drastically alter the calculated value. The circumvention of this problem, the standard ellipse, has recently become a popular tool for analyzing bivariate isotopic variation (Figure 1.4D). The standard ellipse is the bivariate equivalent of the univariate mean and standard deviation

(Batschelet, 1981), and much like the convex hull, a numeric area can be computed that can be used to compare isotopic variation between groups (Jackson et al., 2011). Unlike the convex hull, however, the standard ellipse is much less sensitive to extreme values, and does account for the density or packing of data within bivariate space. Additionally, calculations can be employed to account for variations in sample size and large numbers of calculations of estimated standard ellipse areas can be generated using a Bayesian framework, both allowing for fairly robust comparison between groups (Jackson et al., 2011). These methods are outlined in greater detail in Chapter 5.

Aside from quantifying variation, the convex hull and standard ellipse allow several important questions about bivariate isotopic data (and in turn diet and ecology) to be addressed. For instance, two groups of bivariate isotopic data may be compared on the basis of their mean δ^{13}C and δ^{15}N values, respectively using an ANOVA, t-test, or similar approach to assess whether or not the means differ from one another (how similar is the diet of population A to population B?). This approach has some utility, but it does treat bivariate data as two unrelated sets of univariate data. The standard ellipse approach allows for a direct comparison of bivariate data, and similar questions can be asked by examining the extent of overlap between the two ellipses (how similar is the diet of population A to population B?). In cases of small sample size, robust estimates can be performed using an iterative re-sampling approach that generates a large number of areas for comparative purposes. Similarly, we can use these metrics to address whether one group is characterized by a greater amount of variability than another (is the diet of population A more variable than that of population B?). Therefore, we can ask the same questions using this approach, but we can do so in a way that is more appropriate for these types of data.

1.3 Setting: The Central Peruvian Andes

1.3.1 *The Environment*

The Andean region of Peru is one of marked environmental diversity, which is largely influenced by the east-west altitudinal gradient formed by the mountain range. Within the larger region, three subdivisions are generally recognized: Northern Andes (Venezuela south to northernmost Peru), Central Andes (northern Peru to northern Chile), and Southern Andes (southernmost extent of range from northern Chile) (Molina and Little, 1981). Physical setting has figured prominently in archaeological, geographical, and ecological studies of the region, and as such, the local environmental context has been addressed at length by a number of authors (Brush, 1982; Molina and Little, 1981; Moseley, 2001; Pulgar Vidal, 1987; Sandweiss and Richardson, 2008; Troll, 1968; Winterhalder and Thomas, 1978). Overall, the environment is extremely complex, with numerous microenvironments distributed unevenly throughout the region (Molina and Little, 1981). The brief overview given here is necessarily an oversimplification of the great environmental diversity of the region.

Among the more widely-utilized organizations of Andean geographic zones are those introduced by Pulgar Vidal (1987). These zones, which are organized longitudinally from the Pacific coast (Table 1.1), take into account both climatic variation and elements of human ecology and land use. Alternatively, Tosi (1960) has proposed a classification of wild vegetation, which is similarly largely structured by differences in altitude (Table 1.2). These classifications are further simplified into three zones (coast, sierra, *puna*) for the purposes of the discussion that follows.

1.3.1.1 Coast (0 to 1,000 masl)

In this case, the coast can loosely be defined as the region including the immediate Pacific coast and offshore guano islands up to approximately 1,000 masl. The climate of this zone is extremely arid, but relatively temperate due largely to the influence of the cool Peruvian Current (Humboldt Current), which flows north. Precipitation occurs only during El Niño years when warm, nutrient-poor surface waters off the north coast of Peru displace the usually nutrient-rich cool waters, which has deleterious effects on the marine environment (Arntz and Tarazona, 1990; Barber and Chavez, 1983; Jaksic, 2001). On the coast, precipitation occurs, in some cases in the form of violent storms that cause flooding (Block and Richter, 2000; Dillon, 1985). This precipitation can also markedly increase the productivity of terrestrial vegetation in the coastal zones (Catenazzi and Donnelly, 2007; Dillon, 1985; Holmgren et al., 2001; Holmgren et al., 2006a; Holmgren et al., 2006b). Due to the hyperarid conditions, wild vegetation is sparse, consisting of small trees and shrubs, grasses, sand-associated epiphytes (*Tillandsia* sp.), succulents, and nitrogen-fixing trees (*Prosopis* sp. and *Acacia macracantha*) (Rundel et al., 1991; Towle, 1961). Vegetation is generally concentrated in and around coastal river valleys, which occur every 20 to 50 km and cut through the desert. The river valleys are generally relatively narrow in the upper stretches of the coastal desert, widening into an alluvial plain close to the Pacific (Parsons, 1970). Productive agricultural fields are facilitated by these river valleys (and associated irrigation networks) and a great diversity of crops were grown in the region in prehispanic times, including maize, various types of beans, chili peppers, several types of gourds, peanuts, avocado, lúcuma (eggfruit), pacay (ice-cream bean), and cotton (Table 1.3).

Within this coastal zone, rising topography creates conditions where a seasonal (December to May) fog zone forms, typically between 600 and 900 masl, although in some valleys the fog zone may begin at 250 masl (Weir and Dering, 1986). Where this fog zone meets land, ephemeral plant communities, known as *lomas* or fog oases, grow. These *lomas* may be characterized by a number of different vegetation types depending on local topography and climate with various species of herbs, shrubs, epiphytes, and cacti being abundant at particular altitudinal ranges within the fog zone (Ono, 1982). These *lomas* formations are sparsely distributed on the landscape, often several hundred kilometers apart (Ono, 1986a). Moreover, their extent varies from one year to the next, depending on local environmental conditions (water availability in particular); they may expand greatly during times of extensive precipitation, as occurs during El Nino years (Dillon, 1985; Ono, 1986a).

The marine environment off the coast of Peru is among the most productive on the planet, supporting the largest fish biomass relative to all other upwelling systems (Bakun and Broad, 2003). This environment has been and continues to be extensively exploited by people inhabiting the coastal region. The extremely productive coastal upwelling supports an abundant marine community of fish, shellfish, macroalgae, marine mammals, and marine birds, many of which figured prominently in prehistoric subsistence economies (Creamer et al., 2011; Marcus et al., 1999; Masuda, 1985; Pozorski and Pozorski, 1979a; Reitz, 1979, 1988a, 1988b, 2001; Reitz and Sandweiss, 2001; Reitz, 2003; Reitz et al., 2008; Roselló et al., 2001; Sandweiss, 1988; Sandweiss et al., 1989; Sandweiss, 1992, 1996, 2008). Particularly noteworthy within the context of this dissertation are the massive numbers of seabirds that nest on nearshore islands off the coast of Peru (Tovar et al., 1987). The droppings (guano) produced by these seabirds were recorded as an important fertilizer in ethnohistoric texts (Julien, 1985; Netherly, 1977) and were quickly overexploited during a short-lived guano boom in the nineteenth century prior to the development of chemical fertilizers (Cushman, 2013). There is archaeological evidence of visitation of prehistoric peoples to these guano islands dating back to at least 600 years prior to the time of the Inka (Kubler, 1948), but it is unclear whether or not the guano was exploited as a fertilizer. This problem is central to the work reported on in Chapters 3 and 4.

1.3.1.2 Sierra (1,000 to 3,800 masl)

For the purposes of this discussion, sierra refers to the area immediately above (in elevation) the coastal region (ca. 1,000 masl) to the upper limit of maize cultivation (ca. 3,500 masl), but not including the grasslands associated with the *puna* (ca. 3,800 masl). Essentially, this zone aggregates Pulgar Vidal’s (1987) *suni* and *quechua* zones, or alternatively combines the low (ca. 1,000 to 2,500 masl) and high (ca. 2,500 to 3,800 masl) sierra zones discussed by several other authors (Kuznar, 1991b; Kuznar, 1989; Tomka, 2001). While the environments of the low and high ends differ greatly, the area as a whole serves as an intermediate point between the traditional camelid-raising areas of the *puna*, and the arid coastal region.

The lower stretches of this zone are somewhat similar to the coastal region, with dry hills and slopes characterized by limited wild vegetation. Again, river valleys create patches of richer riparian vegetation. This environment is typical up to about 2,500 masl. Above this altitude, seasonal rainfall (November to April) occurs in sufficient amounts (200 to 800 mm/year) that enables more abundant vegetation to thrive, even outside of the areas immediately surrounding watercourses. This vegetation consists largely of herbs, shrubs, and bunchgrasses, and although they are more abundant than in the coastal zone, still produce poor pasture relative to the *puna* (Brush, 1982).

The upper portion of the sierra is characterized by smooth slopes rising above valleys, which provide some of the best land for agriculture in the Andes (Sandweiss and Richardson, 2008). This prime land (ca. 2,500 to 3,500 masl) sees the cultivation of maize, beans, and squash, among other crops. Moving above 3,500 masl and beyond the extent of maize cultivation, the terrain becomes much steeper, with fewer areas being suitable for agriculture; tubers become more important (potatoes, oca, olluco), as well as chenopods (quinoa and cañihua) and legumes (fava bean and Andean lupin) (Sandweiss and Richardson, 2008). The upper sierra sees higher amounts of seasonal rainfall than the lower sierra, allowing for a much richer diversity of flora, with numerous species of grasses, herbs, shrubs, and some cacti (Kuznar, 1991b; Kuznar, 1990). The vegetation present is sufficient to allow for the raising of domestic animals, which today consist primarily of goats, sheep, and cows (Kuznar, 1991b).

1.3.1.3 *Puna* (3,800 to 4,800 masl)

The *puna* is the highest zone that is permanently habitable by humans. It is a cold region, with strong daily fluctuations in temperature. Mean annual precipitation ranges between 500 and 1,000 mm (Baied and Wheeler, 1993). The *puna* is not distributed continuously throughout the Andes, with a latitudinal range between 7º and 27º south (Baied and Wheeler, 1993). Additionally, there is latitudinal variation in the type of *puna* that occurs owing to differences in water availability, with moist *puna* predominating in the north and east, and dry *puna* being more common in the south and west (Cabrera, 1968).

Limited agriculture occurs in the *puna*, with the potato being the most important cultigen, although chenopods are also grown in some regions (Sandweiss and Richardson, 2008). The topography is generally characterized by low relief, with fairly abundant vegetation in the form of grasslands consisting of tundra and alpine meadow-like vegetation that occurs on plateaus and intermontane drainage basins (Brush, 1982). The most common species are bunch grasses (*Stipa*, *Calamagrostis*, and *Festuca*), which may occur in great density or be unevenly distributed (in bunches) depending on local hydrological conditions (Orlove, 1977b). Significantly, these are the plants most commonly consumed by camelids living in the *puna* (Bryant and Farfan, 1984; Franklin, 1982; Genin et al., 1994; Pfister et al., 1989; Reiner and Bryant, 1986; Reiner et al., 1987; San Martin, 1987;

San Martin and Bryant, 1989). It is generally believed that the *puna* is the habitat best suited to the camelids, particularly the alpaca and vicuña. Within the *puna*, significant features called *bofedales* form where the water table is underlain by clay or hardpan and the surface retains significant moisture throughout the year (Orlove, 1977b). These areas are characterized by a dense, marsh-like formation of plants (mostly *Distichia muscoides*) (Kuznar, 1990; Rodríguez and Quispe, 2007). The *bofedales* are known to be utilized or preferred by camelids (especially in the dry season), particularly alpacas (Browman, 1990b; Franklin, 1982; Kuznar, 1990; Orlove, 1977b; Reiner and Bryant, 1986).

1.3.2 *Archaeological Context*

This dissertation is concerned primarily with the north coast of Peru, which can be defined as the coastal region between the Chira and Huarme river valleys. Specifically, archaeological materials analyzed are derived from the Virú Valley, and as such this particular area, as well as the neighbouring Moche Valley, is of greatest significance. While there are substantial differences in the cultural developments throughout the Andean region, the periods outlined in Figure 1.5 are widely used by Andeanists. This dissertation focuses on the Early Intermediate Period and Middle Horizon.

The north coast of Peru has a long and rich cultural history, with the development of several large, prominent polities beginning during the Early Intermediate Period, and quite possibility the *in situ* development of societies with the political organization characteristic of archaic states (Millaire, 2010b). Our understanding of cultural developments in the region continues to develop. Many previously held assertions about the nature of north coast political organization and state expansions are now being called into question (as discussed below), and a more complex picture with an important role assigned to localized development is being emphasized. To understand the developments in the Virú Valley during the Early Intermediate Period, particularly from a historical perspective, it is first necessary to briefly outline some aspects of the Moche culture tradition (ca. AD 100 to 800), and its political organization.

‘Moche’ largely refers to a material culture tradition that flourished on the north coast of Peru during the Early Intermediate Period, and was widely distributed throughout the region. According to many, Moche represents a state, with its capital at Huacas de Moche in the Moche Valley. This assignation is made on the basis of craft specialization, monumental public architecture, hierarchical settlement organization, and the considerable power (ideological, military, economic) of Moche rulers (Billman, 2002; Chapdelaine, 2009). Ultimately, however, Moche is defined largely on the basis of ceramics (Quilter, 2002). Initially, Moche was believed to have been a wide-ranging state, incorporating many of the valleys on the north coast (Proulx, 1982; Topic, 1982). Within this context, the ruling polity in the neighboring Virú Valley during the Early Intermediate Period was conquered by the Moche and brought under its influence sometime between AD 350 and 550 (Donnan, 1973; Willey, 1953; Wilson, 1988). Recent excavations, and reexaminations of ceramic traditions and chronologies have cast doubt on this view of Moche political organization. At the very least, most scholars now suggest the Moche realm was divided into northern and southern spheres that were autonomous, at least to some extent (Billman, 2002; Shimada et al., 2008). Moreover, there has been an increased emphasis on localized developments within the traditional Moche area, and questions regarding the extent to which Moche may have influenced local elites (Bourget, 2010; Millaire, 2010a). These suggestions are more in line with Bawden’s (1995:259-260) reckoning of Moche, which he sees as “a symbolic manifestation of an influential political ideology that was differentially adopted by local groups.” At the very least, Moche political organization and the nature of its presence in other valleys on the north coast are complex, variable, and only beginning to be understood (Castillo and Quilter, 2010).

The Virú Valley is characterized by a complex history of development. A large body of archaeological research, conducted primarily in the 1940s, was able to document several important features of the region, particularly as they relate to cultural developments during the Early Intermediate Period (Bennett, 1939; Bennett, 1950; Collier, 1955; Ford, 1949; Strong and Evans, 1952; Willey, 1953). This work (primarily in the form of surface collection) documented the hierarchical settlement pattern in the valley and established a ceramic chronology for the region (although this chronology is considered to be highly problematic today). Willey (1953) suggested that the Gallinazo culture had formed a valley-wide polity during the Early Intermediate Period, with its capital at the Gallinazo

Group. The intrusion of Moche ceramics led Willey to conclude that the valley was later conquered by the Moche, a view that was supported by the work of Strong and Evans (1952) at Huaca de la Cruz. More recently, this work has been challenged in light of new excavations, radiocarbon dating programs, and reevaluations of ceramics. Most significantly, the picture of a large political entity associated with Gallinazo plainware ceramics that is later supplanted by the Moche appears untenable. The Virú Valley does see the development of a large, complex polity (quite possibly an archaic state) during the Early Intermediate Period with its capital at the Gallinazo Group. The material manifestation of this polity is a subset of the larger ceramic package originally classified as Gallinazo (Virú Negative), but does not include the Gallinazo plainware (Millaire and Morlion, 2009; Millaire, 2010a, 2010b; Millaire and Eastaugh, 2011). Importantly, there is no evidence that suggests a violent takeover in Virú by the Moche, and it is unclear what, if any, influence the Moche tradition may have had on local ruling elites (Bourget, 2010; Millaire, 2010a).

1.3.3 *South American Camelids*

There are four species of South American camelid (Camelidae), two domestic (llama [*Lama glama*] and alpaca [*Vicugna pacos*, previously *Lama pacos*]) and two wild (guanaco [*Lama guanicoe*] and vicuña [*Vicugna vicugna*]). The llama and guanaco have fairly wide ranges and are more amenable to a wide variety habitats relative to the vicuña and alpaca, which are today largely restricted to the high altitude *puna* (Franklin, 1982). After the Spanish conquest in the sixteenth century, the camelid population (both wild and domestic) was negatively impacted to a great degree due to competition with European domesticates, diseases, and unregulated slaughter (Flores-Ochoa, 1982; Shimada and Shimada, 1985; Wheeler, 1995). In addition to precipitous population declines, the ranges of these species were also reduced; again, this applies to both wild and domestic camelids (Bonavia, 2008; Weinstock et al., 2009; Wheeler et al., 1995). Additional species, subspecies, or hybrids may also have existed prior to the arrival of the Spanish (Wheeler et al., 1995).

Several important physical differences exist between the llama and alpaca. First, llamas are much larger than alpacas, the former typically weighing between 130 and 155 kg and the latter between 55 and 65 kg (Franklin, 1982). It is important to point out, however, that these figures are based on modern llama and alpaca populations, which may not faithfully capture the variation that may have characterized the greater diversity of pre-conquest breeds (Wheeler et al., 1995). Both llamas and alpacas may be utilized for the fleece that they produce, although there is a marked difference in the quality of the fiber between the two species. Llamas produce a much coarser fiber relative to alpacas and they are therefore less desirable in fine textile production, but nevertheless, produce valuable wool (Antonini, 2010; Iñiguez et al., 1998; Lupton et al., 2006; Valbonesi et al., 2010).

The evolutionary history and genetic relationships of these species are complex (Wheeler, 1995), but recent studies strongly suggest the llama is the descendant of the guanaco and the alpaca is the descendent of the vicuña (Kadwell et al., 2001). The timing of the domestication of either species is widely debated and is much less clear. The process may have begun in earnest through intensified hunting beginning about 8,500 BP that was prevalent throughout much of the Andes (Kent, 1987; Moore, 1988, 1989; Wheeler, 1984). Domestication of the alpaca occurred by about 6,000 BP in the central Andes; domestication of the llama took place approximately 1,500 years later further south (Mengoni Goñalons, 2008).

Camelids served numerous functions in Andean societies, playing important roles in the economic, social, political, and ritual spheres. Because of the much larger size of the llama, it was a more important source of dietary protein than the alpaca, although both were consumed (Hesse, 1982; Kent, 1982; Lynch, 1983; Miller and Burger, 1995; Vallières, 2012). Textiles manufactured from camelid wool served as important markers of identity and status (Ackerman, 1991; Boytner, 1998a, 1998b, 2004; Costin, 1998; Dumais, 2004; Millaire, 2009; Plunger, 2009; Rodman and Fernandez Lopez, 2005; Splitstoser, 2009), and in some cases were traded extensively (Murra, 1980; Stanish et al., 2010). While alpacas may have played more significant roles as fiber producers, the more robust llamas were utilized as pack animals (Dillehay and Núñez, 1988; Lynch, 1983; Marcus et al., 1999; Nielsen, 2001), being crucial in long distance exchange networks (Browman, 1975, 1990a; Stanish et al., 2010; Tripcevich, 2007). Camelid dung is also known to have been an important source of fuel (Arnold, 1993; Arnold, 1988; Bruno, 2008; Chávez, 1984-1985; Deere, 1990; Franke, 1992; Hastorf and Wright, 1998; Johannessen and Hastorf, 1990; Sillar, 2000a, 2000b) and fertilizer (Bruno, 2008; Mitchell, 1991) in the highlands, and may have played a key role in agricultural intensification in some regions (Chepstow-Lusty, 2011). In addition to these economic aspects of camelids, they were also very prominent in the ritual activities of many prehispanic cultures. For instance, among the Moche on the north coast, camelid skeletal elements represent the most common funerary offerings in burials (Goepfert, 2012).

As mentioned previously, the llama and alpaca are both primarily associated with high altitude habitats in most archaeological and ethnohistoric literature. This is because camelid pastoralism was and continues to be an important part of the economies of many groups living in the *puna*, while reliance on domestic camelids at lower altitudes is typically minimal; this is true today even throughout most of the sierra. Accordingly, most first-hand accounts of camelid husbandry are of seasonally mobile pastoralists living in fairly small settlements dispersed throughout the *puna* (Browman, 1983, 1990b; Flannery et al., 1989; Flores-Ochoa, 1979; Kuznar, 1991a; McCorkle, 1987; McGreevy, 1984; Murra, 1965, 1980; Orlove, 1977b; Tomka, 1992; Tomoeda, 1985; Webster, 1973). Many authors have explicitly stated that camelids were never capable of acclimating to the conditions outside of this highland environment and on the coast specifically (Bushnell, 1963; Flannery et al., 1989; Gilmore, 1950; Menzel, 1977; Troll, 1958; Tschudi, 1854, 1918). Others, however, have suggested the husbandry of camelids in coastal and low altitude regions (Goepfert, 2012; Goepfert et al., 2013; Horkheimer, 1961; Lanning, 1967; Pozorski, 1976; Rostworowski, 1981, 1988; Shimada and Shimada, 1981, 1985; Thornton et al., 2011). Of these, none have suggested the maintenance of alpaca herds on the coast, but have focused on llamas, which are more adaptable to a wide range of habitats; Franklin (1982) cites the range of the alpaca and llama to be 4,400 to 4,800 masl and 2,300 to 4,000 masl respectively. While a growing body of zooarchaeological evidence has documented the occurrence of camelid skeletal elementals at low altitude and coastal sites, these data are often insufficient to document the herding of animals. Except in the case of very young individuals, the presence of camelids may be explained by the inclusion of animals involved in caravan trade, or the trade in dried camelid meat (*charki*) from high altitude locations. Isotopic analysis is particularly promising both for assessing whether or not animals were indeed raised on the coast, and what the nature of this coastal husbandry may have been. These issues are explored in greater detail in Chapter 5.

1.4 Organization of the Dissertation

The dissertation is divided into four main chapters, excluding the introductory and concluding chapters. The first three of these four main chapters are largely concerned with the development of isotopic baselines for paleodietary and paleoecological studies in the Peruvian Andes.

Chapter 2 reports the carbon and nitrogen isotopic compositions from wild plants sampled along an altitudinal transect in northern Peru (Moche River valley area), as well as cultivated plants sampled from local markets in the central Andean highlands. As discussed above, these baseline data are necessary for accurate interpretations of isotopic data derived from archaeological contexts, and have to date been lacking in this region.

Chapter 3 presents results from a growth-chamber study examining the effects of seabird guano fertilization on maize. This is the first study to examine the isotopic effects of guano fertilization and has important implications in food chemistry, soil science, plant physiology, and in archaeology. Fitting Chapter 2's theme of developing baseline data for the region, Chapter 3 demonstrates the potentially large effects of guano fertilization on crops, which must be accounted for when interpreting isotopic data from the region.

Building on the findings of Chapter 3, Chapter 4 summarizes a controlled field-scale study conducted in the Virú Valley with seabird guano and camelid dung fertilizers. This study confirms the results of the growth chamber study and also demonstrates the potential impact of camelid dung fertilization on plant nitrogen isotopic compositions. Taken together, the data accumulated in these first three chapters provide a step forward in the area of isotopic baseline development.

Chapter 5 puts these data into practice. It presents carbon and nitrogen isotopic analysis of a large group of camelids from two sites in the Virú Valley of northern Peru. This chapter addresses the nature of human-animal interactions as these sites within their larger social and political contexts. From a methodological perspective, this chapter also suggests some novel means of approaching isotopic data, which may have great potential in the broadest sense.

Table 1.1. Geographic zones of the western Andean slope according to Pulgar Vidal (1987) arranged west to east.

Zone	Altitude (masl)	Summary
Chala	0 to 500	Mostly desert (temperate), interrupted by river valleys running east-west
Yunga	500 to 2,300	Dry slopes with sparse xerophytic vegetation, seasonal *lomas* formations
Quechua	2,300 to 3,500	Gentle hills, greater rainfall, cooler temperatures, upper limit of maize cultivation
Suni	3,500 to 4,000	Steep terrain, cool climate, less suitable for agriculture than *quechua*
Puna	4,000 to 4,800	Low relief grasslands, cold climate, extensive tuber cultivation, camelid pastoralism
Janca	>4,800	Glaciers and snowcapped peaks, not continuously habitable

Table 1.2. Ecological classifications of the western Andean slope from Tosi (1960).

Zone	Altitude (masl)
Coastal desert	0 – 500
Premontane desert scrub	500 – 1,800
Premontane thorny steppe	1,800 – 2,800
Montane moist pasture	2,800 – 3,700
Montane wet pasture	3,700 – 4,200

Table 1.3. Cultivated plants of the northern coastal valleys of Peru.

Taxonomic Name	Common name	Local name
Annona muricata	Soursop	*Guanábana*
Arachis hypogaea	Peanut	*Maní*
Bunchosia armeniaca	Peanut butter fruit	*Cansaboca*
Capiscum sp.	Pepper	*Aji*
Cucurbita sp.	Squash	*Calabaza*
Cyclanthera pedata	Slipper gourd	*Caigua*
Gossypium barbadense	Cotton	*Algondón*
Inga feuillei	Ice cream bean	*Pacae*
Ipomoea batatas	Sweet potato	*Camote*
Lagenaria siceraria	Calabash	*Mate*
Lucuma obovata	Eggfruit	*Lúcuma*
Persea americana	Avocado	*Palta*
Phaseolus lunatus	Lima bean	*Pallar*
Phaseolus vulgaris	Common bean	*Frijol*
Psidium guajava	Guava	*Guayaba*
Zea mays	Maize	*Maíz*

Data from compiled from Pozorski (1979; 1982, 1983) and Pozorski and Pozorski (1979b).

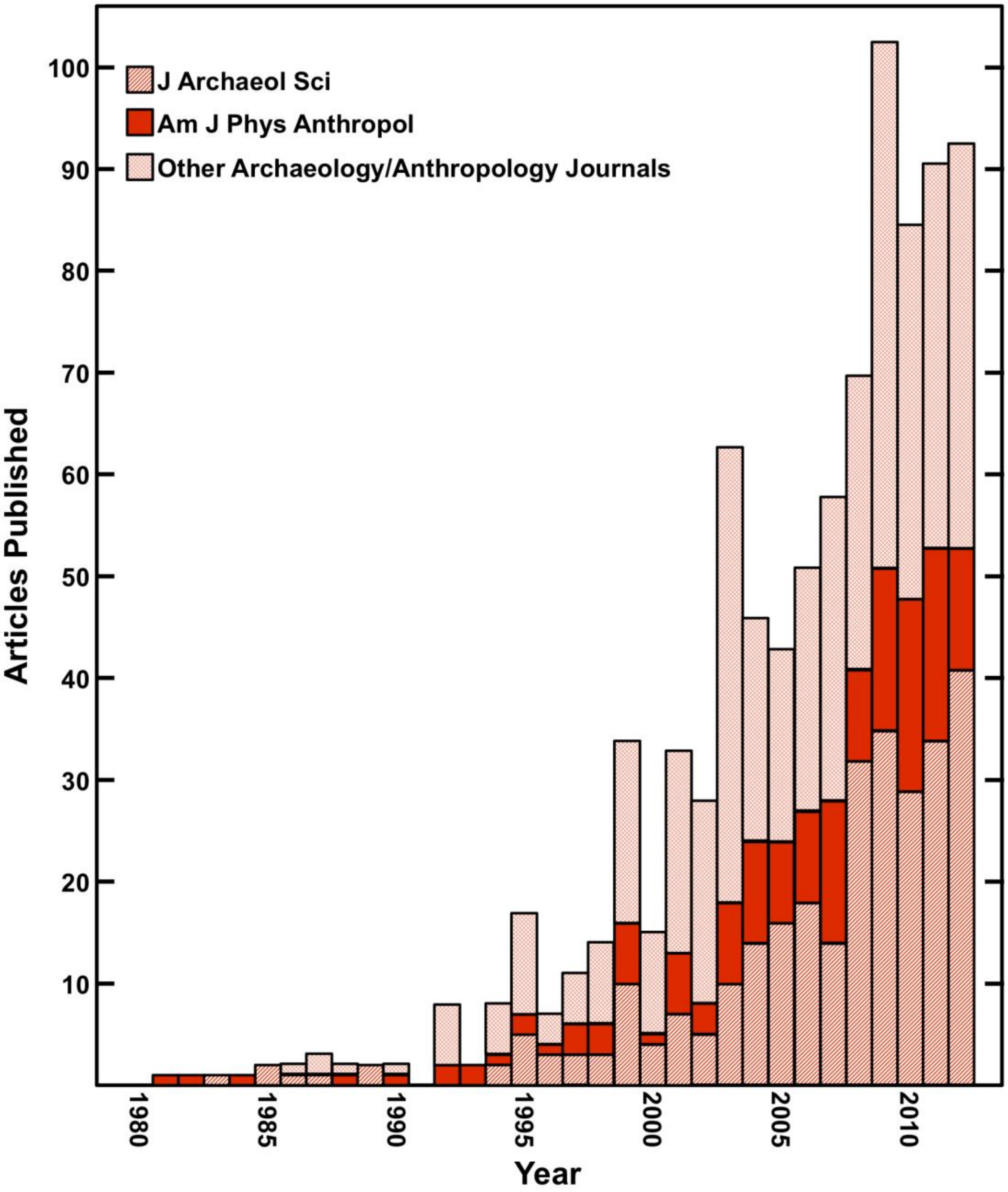

Figure 1.1. Number of papers published between 1980 and 2012 with "stable isotope" listed among keywords or in the abstract (determined using ISI Web of Knowledge v.5.10). "Other Journals" includes only archaeology or anthropology journals.

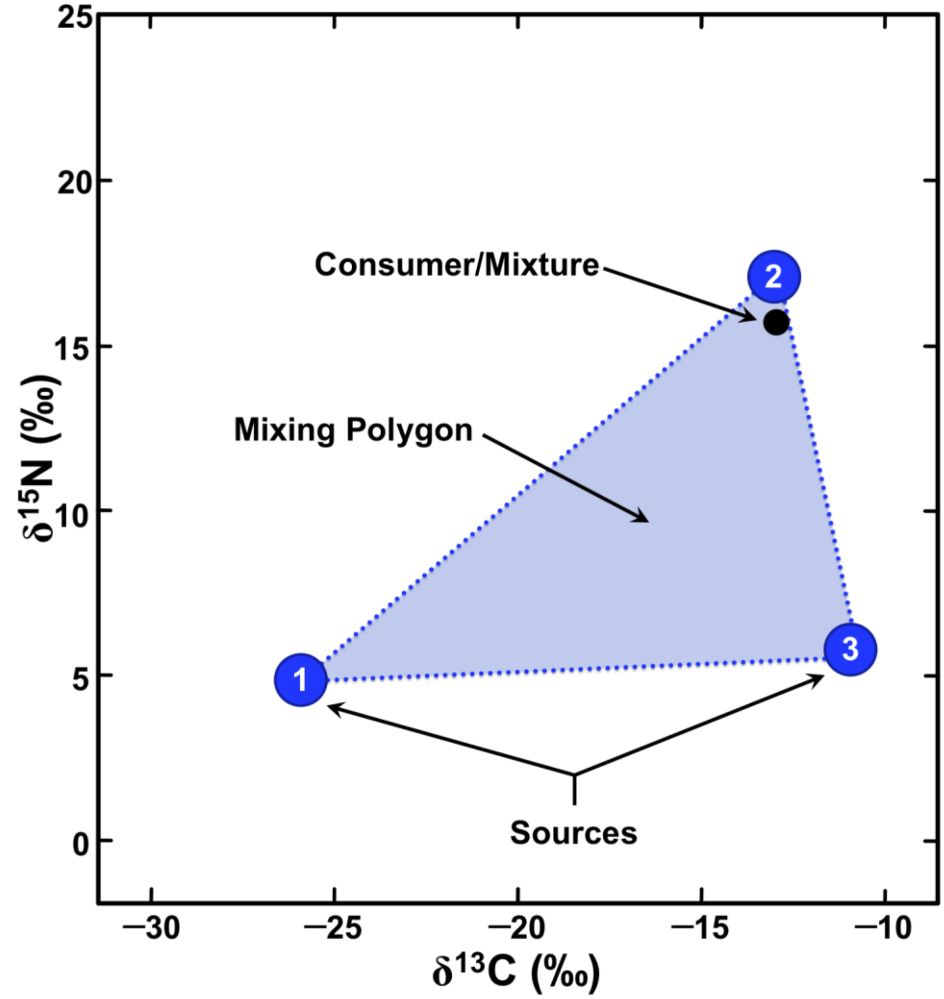

Figure 1.2. Depiction of basic n+1 mixing model for three sources (labeled 1,2,3) and one consumer.

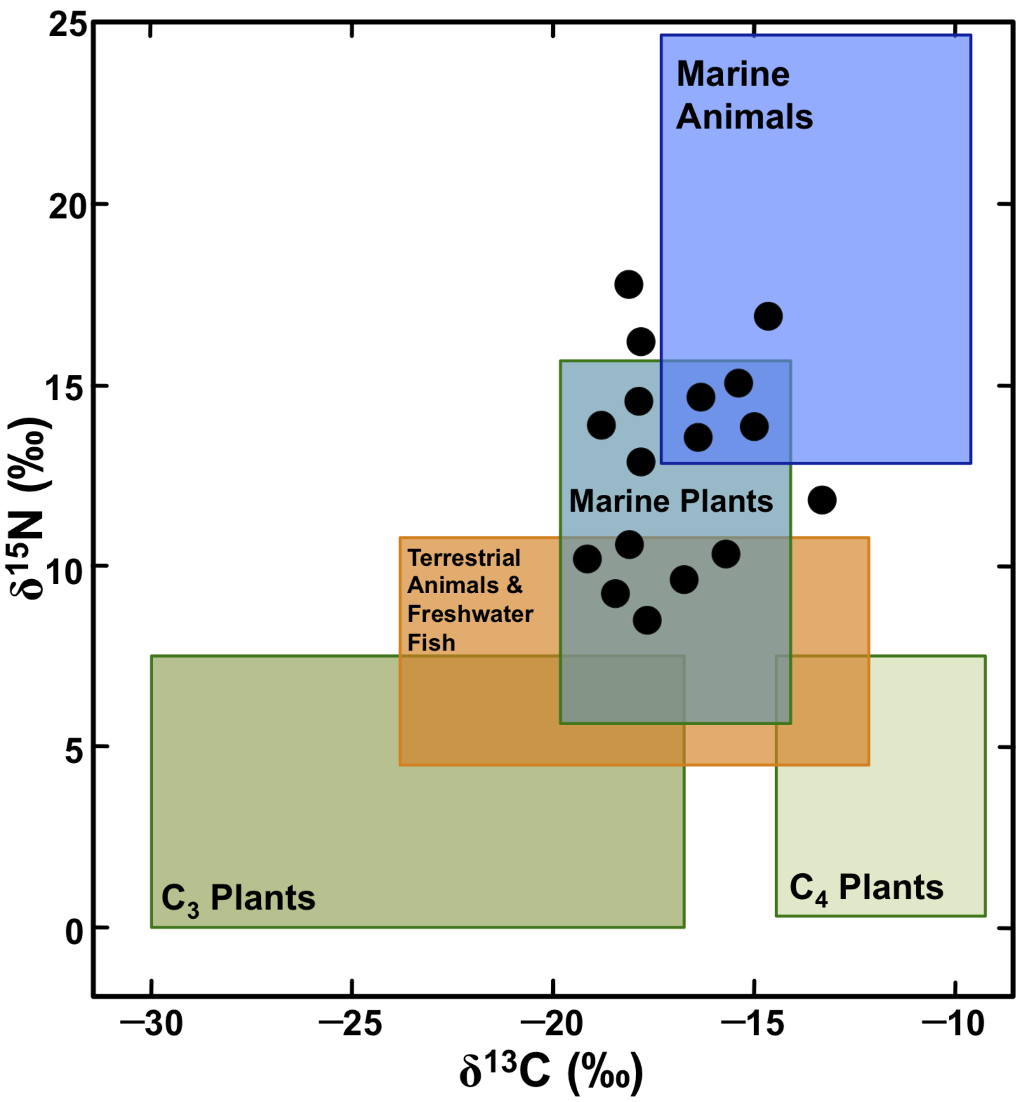

Figure 1.3. Example of a ‘box model’ method for interpreting isotopic data. Boxes represent food sources and circles represent consumers. This particular box model was constructed for southern Peru and is redrawn from Tomczak (2003), although this approach is fairly common (Thornton et al., 2011; White et al., 2009; Williams and Katzenberg, 2012). The consumer data (solid dots) are hypothetical.

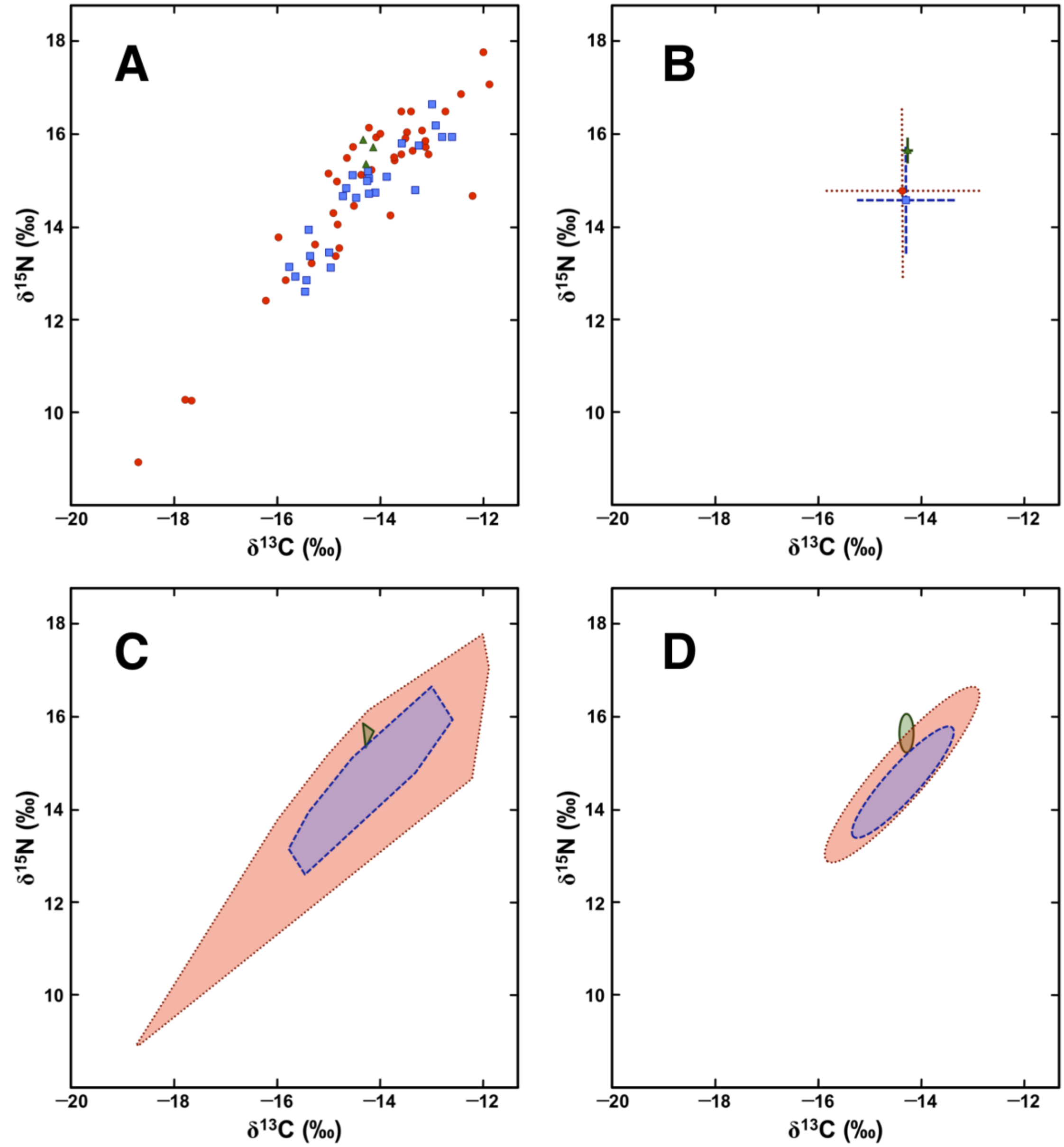

Figure 1.4. Four methods of displaying bivariate isotopic data graphically: (A) individual isotopic compositions, (B) mean and standard deviations, (C) convex hull area, (D) standard ellipse area. Data are taken from three human groups from Holocene northern California (Beasley et al., 2013).

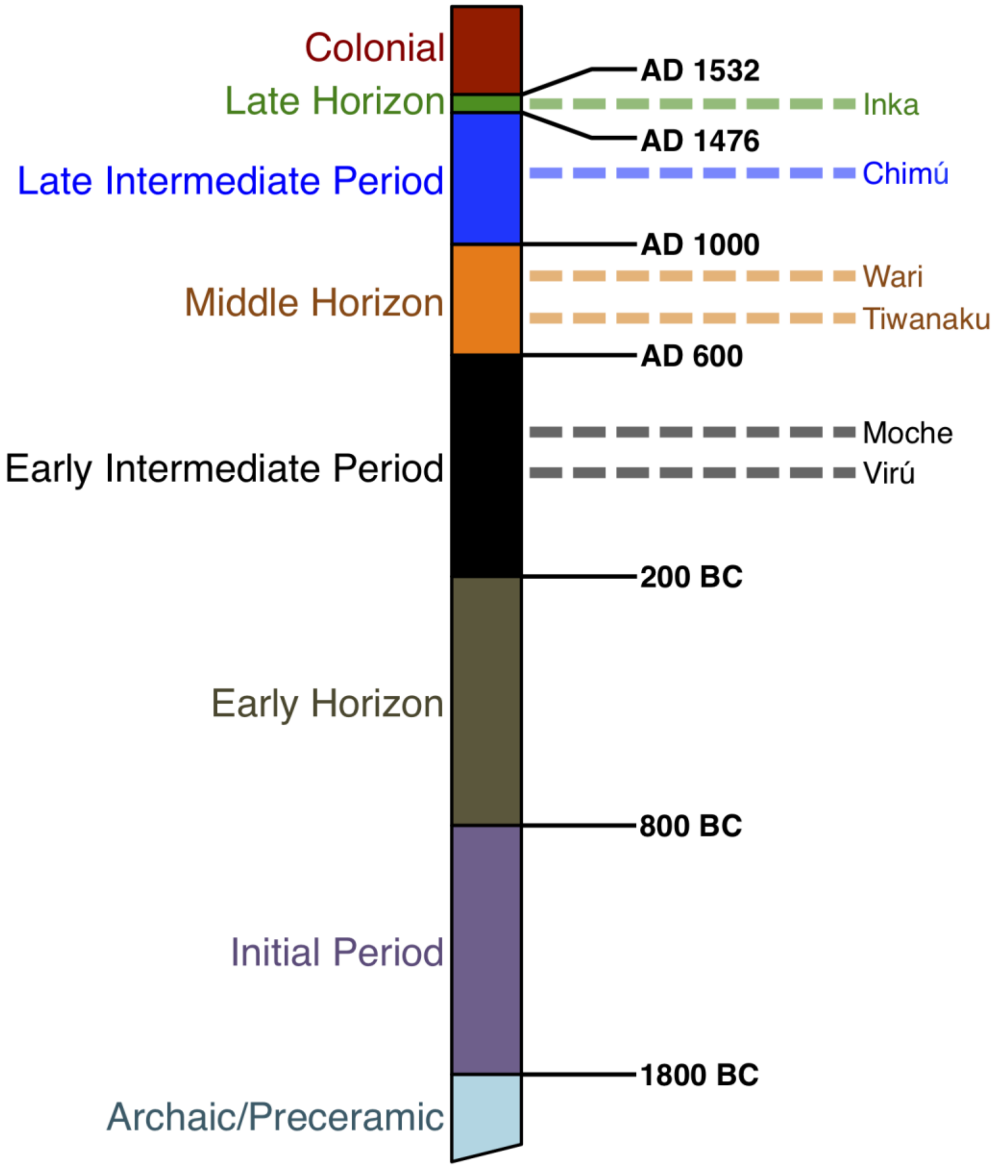

Figure 1.5. Generalized chronology for Peru with approximate ages for some widely known cultures.

Chapter 2

2 Carbon and Nitrogen Isotopic Survey of Northern Peruvian Plants: Baselines for Paleodietary and Paleoecological Studies

The development of isotopic baselines for comparison with paleodietary data is crucial, but often overlooked. We review the factors affecting the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic compositions of plants, with a special focus on the carbon and nitrogen isotopic compositions of twelve different species of cultivated plants (*n*=91) and 139 wild plant species collected in northern Peru. The cultivated plants were collected from nineteen local markets. The mean $\delta^{13}C$ value for maize (grain) was −11.8±0.4 ‰ (*n*=27). Leguminous cultigens (beans, Andean lupin) were characterized by significantly lower $\delta^{15}N$ values and significantly higher %N than non-leguminous cultigens. Wild plants from thirteen sites were collected in the Moche River Valley area between sea level and ~4,000 meters above sea level (masl). These sites were associated with mean annual precipitation ranging from 0 to 710 mm. Plants growing at low altitude sites receiving low amounts of precipitation were characterized by higher $\delta^{15}N$ values than plants growing at higher altitudes and receiving higher amounts of precipitation, although this trend dissipated when altitude was >2,000 masl and MAP was >400 mm. For C_3 plants, foliar $\delta^{13}C$ was positively correlated with altitude and precipitation. This suggests that the influence of altitude may overshadow the influence of water availability on foliar $\delta^{13}C$ values at this scale.

2.1 Introduction

Stable isotope analysis is an important tool for reconstructing the diet, local environmental conditions, migration, and health of prehistoric human and animal populations. This method is useful because the carbon and nitrogen isotopic compositions of consumer tissues are directly related to the carbon and nitrogen isotopic compositions of the foods consumed (DeNiro and Epstein, 1978, 1981), after accounting for the trophic level enrichments of ^{13}C and ^{15}N for any particular tissue (Caut et al., 2009; Szpak et al., 2012c).

In all cases, interpretations of isotopic data depend on a thorough understanding of the range and variation in isotopic compositions of source materials (Casey and Post, 2011). For instance, studies of animal migrations using oxygen and hydrogen isotopic analyses require a thorough understanding of the spatial variation in surface water and precipitation isotopic compositions (Bowen, 2010; Hobson, 1999), and in that avenue of research, there has generally been an emphasis on establishing good baselines. With respect to diet and local environmental conditions, the interpretation of isotopic data (typically the carbon and nitrogen isotopic composition of bone or tooth collagen) depends upon a thorough knowledge of the range and variation in isotopic compositions of foods that may have been consumed. Although several authors have attempted to develop such isotopic baselines for dietary reconstruction (Borić et al., 2004; Bösl et al., 2006; Choy and Richards, 2009; Eriksson, 2004; Eriksson et al., 2008; Fischer et al., 2007; Fornander et al., 2008; Grupe et al., 2003; Grupe et al., 2009; Katzenberg and Weber, 1999; Kusaka et al., 2010; Müldner and Richards, 2005, 2007; Szpak et al., 2009), these studies have typically focused on vertebrate fauna.

Despite the fact that plants are known to be characterized by extremely variable carbon and nitrogen isotopic compositions (Craine et al., 2009; Kohn, 2010), few studies have attempted to systematically document this variability in floral resources at a regional scale using an intensive sampling program, although there are exceptions (Codron et al., 2005; Hartman and Danin, 2010; Tieszen and Chapman, 1992). This is problematic, particularly in light of the development and refinement of new techniques (e.g. isotopic analysis of individual amino acids), which will increase the resolution with which isotopic data can be interpreted. If isotopic baselines continue to be given marginal status, the power of new methodological advancements will never be fully realized.

With respect to the Andean region of South America, the isotopic composition of plants is very poorly studied, both from ecological and paleodietary perspectives. The most comprehensive study of the latter type was conducted by Tieszen and Chapman (1992) who analyzed the carbon and nitrogen isotopic compositions of plants collected along an altitudinal transect (~0 to 4,400 masl) following the Lluta River in northern Chile. Ehleringer et al. (1998) presented δ^{13}C values for plants along a more limited altitudinal transect in Chile (Atacama Desert). Recently, Cadwallader et al. (Cadwallader et al., 2012) have provided δ^{13}C values for a number of wild and domestic taxa from southern Peru. A number of other studies have provided isotopic data on a much more limited scale from various sites in Argentina (Gil et al., 2006; Gil et al., 2009; Izeta et al., 2009; Martínez et al., 2009; Panarello and Fernández, 2002), Chile (Falabella et al., 2007; Latorre et al., 2011; Rundel et al., 2002), Bolivia (Ehleringer et al., 1999; Miller et al., 2010), Ecuador (Ehleringer et al., 1999), Colombia (Ehleringer et al., 1999), and Peru (Catenazzi and Donnelly, 2007; DeNiro and Hastorf, 1985; Ehleringer et al., 1999; Townsend-Small et al., 2005; Turner et al., 2010a).

The number of carbon and nitrogen isotopic studies in the Andean region has increased dramatically in the last ten years, facilitated by outstanding organic preservation in many areas. The majority of these studies have been conducted in Peru (Burger and van der Merwe, 1990; Coutts et al., 2011; Ericson et al., 1989; Finucane et al., 2006; Finucane, 2007, 2008, 2009; Kellner and Schoeninger, 2008; Knudson et al., 2007; Slovak and Paytan, 2011; Thornton et al., 2011; Tomczak, 2003; Turner et al., 2010a; Tykot et al., 2006; White et al., 2009; Williams and Katzenberg, 2012) and Argentina (Berón et al., 2009; Calo and Cortés, 2009; Fernández et al., 1999; Gil et al., 2006; Gil et al., 2009; Gil et al., 2011; Izeta et al., 2009; Laguens et al., 2009; Loponte and Corriale, 2013; Martínez et al., 2009; Panarello and Fernández, 2002; Panarello et al., 2003; Politis et al., 2009; Tessone et al., 2009; Yacobaccio et al., 2009). With respect to northern Peru in particular, a comparatively small number of isotopic data have been published (Ericson et al., 1989; Verano and DeNiro, 1993; White et al., 2009), although this will certainly rise in coming years as biological materials from several understudied polities (e.g. Virú, Moche, Chimú) in the region are subjected to isotopic analysis.

The purpose of this study is to systematically examine the carbon and nitrogen isotopic compositions of plants from the Moche River Valley in northern Peru collected at various altitudes from the coast to the highlands. These data provide a robust baseline for paleodietary, paleoecological, and related investigations in northern Peru that will utilize the carbon and nitrogen isotopic compositions of consumer tissues.

2.2 Study Area

The Andes are an area of marked environmental complexity and diversity. This diversity is driven largely by variation in altitude (Figure 2.1). As one proceeds from the Pacific coast to the upper limits of the Andes, mean daily temperature declines, typically by ~5°C per 1,000 m (Bush et al., 2005), and mean annual precipitation increases (Figure 2.2). The eastern slope of the Andes, which connects to the Amazon basin, is environmentally very different from the western slope. Because this study deals exclusively with the western slope, the eastern slope is not discussed further. Many authors have addressed the environment of the central Andes and Peru in particular (Brush, 1982; Koepcke, 1961; Koepcke, 1954; Rundel et al., 1991; Sandweiss and Richardson, 2008; Tosi, 1960; Troll, 1968; Winterhalder and Thomas, 1978); hence only a brief review is necessary here.

The coastal region of Peru is dominated by the hyper-arid Peruvian desert. Cool sea-surface temperatures created by the northward flowing Peruvian Current, combined with a subtropical anticyclone, create remarkably stable and relatively mild temperatures along the roughly 2,000 km north-south extent of the Peruvian desert (Rundel et al., 1991). The phytogeography of the coastal region of Peru is fairly homogenous, although the composition of the vegetation varies in accordance with local topography (de Mera et al., 1997). Except in El Niño years, precipitation is extremely low or non-existent along much of the Peruvian coast, but in areas where topography is steep close to the coast, a fog zone forms (typically between 600 and 900 masl), which allows for the development of ephemeral plant communities (*lomas*) (Engel, 1973; Masuda, 1985; Oka and Ogawa, 1984; Ono, 1986b; Péfaur, 1982; Weir and Dering, 1986). Aside from these *lomas*, riparian vegetation grows in the relatively lush river valleys that cut into the Andes, although the vast majority of this land is cultivated. Thickets of the leguminous algarroba tree regularly occur at low altitudes, and it is generally believed that much more extensive forests of these trees existed in the past (Beresford-Jones, 2005; Beresford-Jones et al., 2011; Beresford-Jones et al., 2009; West, 1971). The coastal zone usually ends where the oceanic influence becomes minimal, typically about 1,000 masl (Koepcke, 1954).

Immediately above the area of oceanic influence and up to an altitude of ~1,800 m, the environment is cooler, although generally similar, in comparison to the coastal zone. Although mean annual precipitation increases, this zone can still be characterized as dry, with most locations receiving less than 400 mm of annual precipitation. In some circumstances, *lomas* may form within this zone (Sandweiss and Richardson, 2008), although this is not common. In the Moche River Valley of northern Peru, the vegetation is dominated by xerophytic scrub vegetation from 500 to 1,800 masl, and transitions to thorny steppe vegetation between 1,800 and 2,800 masl. Again, the area is still characterized by relatively low annual precipitation, although water availability is greater close to major water courses and other ground water sources.

Ascending further, mean annual precipitation increases, and average daily temperature decreases. Night frost begins to occur. Vegetation is largely dominated by low-growing shrubs, herbs, and grasses, as well as open stands of some tree species (*Acacia*, *Polylepis*) (Winterhalder and Thomas, 1978). Pastures dominated by dense bunchgrasses occur in moister areas.

2.3 Natural Variation in Plant Carbon Isotopic Composition

2.3.1 *Photosynthetic Pathway and Taxonomy*

The most salient mechanism influencing the carbon isotopic composition ($\delta^{13}C$) of terrestrial plants is the photosynthetic pathway utilized. Plants that fix carbon using the C_3 pathway (Calvin cycle) are characterized by lower $\delta^{13}C$ values (ca. −26 ‰) than plants utilizing the C_4 (Hatch-Slack) pathway (ca. −12 ‰) (O'Leary, 1981; Smith and Epstein, 1971). This is because carbon isotope discrimination ($\Delta^{13}C$) is smaller in C_4 plants than in C_3 plants. In other words, C_3 plants discriminate more strongly against the heavier isotope (^{13}C) than C_4 plants. The vast majority of C_4 plants are tropical grasses, the most significant of which in New World archaeological contexts is maize (*Zea mays*), but also amaranth (*Amaranthus caudatus*). With respect to human diet, most wild C_4

plants are not significant, and thus a large body of research has focused on assessing and quantifying the contribution of C_4 cultigens (mostly maize, but also millet) to the diet (Schwarcz, 2006). Some desert plants and succulents exhibit carbon isotopic compositions that are intermediate between C_3 and C_4 plants (Earnshaw et al., 1987; Szarek and Troughton, 1976; Winter, 1979; Winter et al., 1983). Referred to as CAM (Crassulacean acid metabolism) plants, these species fix carbon in a manner analogous to C_4 plants overnight, but utilize the C_3 photosynthetic pathway during the afternoon (O'Leary, 1988).

Additional plant groups that are not readily assigned into the aforementioned categories include mosses and lichens. Mosses, which are non-vascular plants, utilize the C_3 photosynthetic pathway (Rice, 2000; Rundel et al., 1979), but are distinct from vascular plants in that they lack stomata and CO_2 availability is influenced primarily by the thickness of the water film accumulated on the leaves. Lichens are composite organisms, consisting of two parts: a mycobiont (fungi) and photobiont or phycobiont (algae). The carbon isotopic composition of lichens is determined largely by the type of photobiont involved. Lichens with green algae as the photobiont exhibit a wide range of carbon isotopic compositions (−35 to −17 ‰), while lichens with cyanobacteria as the photobiont tend to have higher, and a more restricted range of carbon isotopic compositions (−23 to −14 ‰) (Cipro et al., 2011; Fogel et al., 2008; Huiskes et al., 2006; Lange et al., 1988; Lee et al., 2009).

2.3.2 *Environmental Factors Affecting Plant $\delta^{13}C$*

Aside from the differences in carbon isotopic composition resulting from variable carbon fixation, a number of environmental factors have also been demonstrated to influence the carbon isotopic composition of plant tissues. For example, low-growing plants under dense forest cover tend to exhibit lower $\delta^{13}C$ values relative to canopy plants and plants growing in more open environments. Often referred to as the 'canopy effect', this is attributed to relatively ^{13}C-depleted CO_2 in the understory due to the utilization of recycled CO_2 (Medina et al., 1991; Sonesson et al., 1992; van der Merwe and Medina, 1989, 1991; Vogel, 1978a), and/or lower irradiance and higher $[CO_2]$ relative to the canopy (Broadmeadow and Griffiths, 1993; Buchmann et al., 1997). The magnitude of differences in plant carbon isotopic composition observed due to the canopy effect typically range between 2 and 5 ‰ (Heaton, 1999). It has been posited that the canopy effect significantly impacts the carbon isotopic composition of consumer tissues and thus reflects the use of closed and open habitats (Drucker et al., 2008; Drucker et al., 2010; Schoeninger et al., 1997; Voigt, 2010). None of the sites sampled in this study were characterized by sufficiently dense forest for a canopy effect to have been significant.

Water availability has been observed to be negatively correlated with the carbon isotopic composition of plants (Austin and Vitousek, 1998; Condon et al., 1992; Damesin et al., 1997; Lajtha and Getz, 1993; Lamont et al., 2002; Lopes and Araus, 2006; Ma et al., 2005; Ma et al., 2012; Miller et al., 2001; Murphy and Bowman, 2009; Panek and Waring, 1997; Peri et al., 2012; Scartazza et al., 1998; Scartazza et al., 2004; Stewart et al., 1995; Sun et al., 2003; Swap et al., 2004; Syvertsen et al., 1997; Weiguo et al., 2005; Welker et al., 1993). In most instances, these effects are limited to C_3 plants, with most studies finding little or no correlation between rainfall and/or water availability and plant $\delta^{13}C$ for C_4 plants (Schulze et al., 1996; Swap et al., 2004). Murphy and Bowman (2009) found a positive correlation between rainfall and C_4 plant $\delta^{13}C$ over a continental (Australia) rainfall gradient, although this relationship is atypical. It is believed that the relationship between aridity and plant $\delta^{13}C$ is caused by increased stomatal closure when water availability is low, which is accompanied by decreased discrimination against ^{13}C during photosynthesis and, in turn, comparatively less negative $\delta^{13}C$ values (Farquhar et al., 1982a; Farquhar and Richards, 1984).

Soil salinity has also been demonstrated to influence plant $\delta^{13}C$ values. In a manner somewhat analogous to drought stress, salt stress induces increased stomatal closure, and therefore reduces discrimination against ^{13}C by the plant (Farquhar et al., 1989). A number of studies have observed this relationship, which occurs in both halophytic (salt-tolerant) (Choi et al., 2005b; Farquhar et al., 1982b; Guy et al., 1980; Neales et al., 1983) and non-halophytic species (Brugnoli and Lauteri, 1991; Isla et al., 1998; van Groenigen and van Kessel, 2002).

A number of studies have found elevational gradients in plant carbon isotopic composition. Generally, foliar $\delta^{13}C$ values have been found to increase with increasing altitude (Cordell et al., 1998; Cordell et al., 1999; Hultine and Marshall, 2000; Körner et al., 1988; Lajtha and Getz, 1993; Sah and Brumme, 2003; Sparks and Ehleringer, 1997; Vitousek et al., 1990). It is important to point out, however, that the majority of these studies have examined the isotopic composition of a single species or a small number of species over an elevational gradient of ~1,000 m. The exact mechanism responsible for the relationship between plant $\delta^{13}C$ and altitude is not entirely clear. Some have suggested exceptionally high carboxylation rates relative to stomatal conductance (Friend et al., 1989; Körner and Diemer, 1987) and/or high carboxylation efficiency (Körner et al., 1991) for plants growing at high altitudes, resulting in decreased discrimination against ^{13}C. A very strong positive correlation has been observed between altitude and leaf mass per unit area (Cordell et al., 1999; Geeske et al., 1994; Hultine and Marshall, 2000; van de Weg et al., 2009; Vitousek et al., 1990), which is thought to be instrumental in increasing carboxylation capacity.

Irradiance has also been shown to influence foliar $\delta^{13}C$ values, with higher irradiance being associated with less negative $\delta^{13}C$ values in leaves. Such variation can occur within a single plant (usually trees), and even along a single branch, with leaves growing in interior, shaded areas having lower $\delta^{13}C$ values than leaves growing in exterior, exposed areas (Duursma and Marshall, 2006; Ehleringer et al., 1986; Hanba et al., 1997; Le Roux et al., 2001; Lockheart et al., 1998; Zimmerman and Ehleringer, 1990). These differences in $\delta^{13}C$ associated with irradiance have been attributed to differences in intercellular CO_2 concentration (Farquhar et al., 1982a).

2.3.3 *Intra-plant and Temporal Variation in Plant $\delta^{13}C$*

Carbon isotopic composition is not necessarily equal among different plant parts. Numerous studies have observed variation in the $\delta^{13}C$ values of leaves, stems, roots, and other tissues (Badeck et al., 2005; Cernusak et al., 2009; Hobbie and Werner, 2004). The vast majority of studies examining the carbon isotopic compositions of multiple plant tissues have found that leaves are slightly depleted of ^{13}C relative to non-photosynthetic tissues, typically by 2 to 4 ‰ (Cernusak et al., 2005; Cernusak et al., 2007; Damesin and Lelarge, 2003; Francey et al., 1985; Gebauer and Schulze, 1991; Guehl et al., 1998; Handley et al., 1993; Hobbie and Colpaert, 2004; Hobbie and Werner, 2004; Ineson et al., 1995; Leavitt and Long, 1982, 1986; Martinelli et al., 1998; Medina et al., 1991; Miller et al., 2001; Park and Epstein, 1960; Pate and Arthur, 1998; Scartazza et al., 1998; Schleser, 1992; Syvertsen et al., 1997; Yoder et al., 1994; Yoneyama and Ohtani, 1983). These differences are only consistent among C_3 plants, with C_4 plants often showing little variation between leaves and non-photosynthetic tissues, or leaves with relatively high $\delta^{13}C$ values in some cases (Badeck et al., 2005; Hobbie and Werner, 2004). There are several potential variables contributing to intraplant variation in tissue $\delta^{13}C$. First, different tissues may contain variable proportions of molecules that are relatively enriched or depleted of ^{13}C compared to total organic matter. Most notably, lipids (DeNiro and Epstein, 1977) and lignin (Benner et al., 1987) are known to be characterized by relatively low $\delta^{13}C$ values, while the opposite is true for cellulose, sugars, and starches (Gleixner et al., 1993). Because some studies have found significant differences in the $\delta^{13}C$ of specific compounds (e.g. cellulose, sucrose) between different plant parts (Damesin and Lelarge, 2003; Francey et al., 1985; Leavitt and Long, 1982), it is thought that additional mechanisms are responsible for the observed patterns in intraplant $\delta^{13}C$ variation. Damesin and Lelarge (2003) suggest that some discrimination occurs during the translocation of sugars, particularly when certain plasma membrane proteins are involved in phloem transport. Potential mechanisms causing intraplant variation in $\delta^{13}C$ are treated at length by Cernusak et al. (2009).

In addition to variation among plant parts, a number of studies have found variation in $\delta^{13}C$ within plant parts, over time. Specifically, emerging leaves, which are not yet photosynthetic and therefore more closely resemble other non-photosynthetic or heterotrophic plants parts, tend to have less negative $\delta^{13}C$ values (by about 1 to 3 ‰) relative to fully emerged, photosynthetic leaves (Damesin et al., 1997, 1998; Damesin and Lelarge, 2003; Eglin et al., 2009; Holtum and Winter, 2005; Jäggi et al., 2002; Leavitt and Long, 1982, 1985; Li et al., 2007; Lowdon and Dyck, 1974; Stokes et al., 2010; Terwilliger, 1997; Terwilliger et al., 2001a, 2001b). Products assimilated via photosynthesis will tend to have lower $\delta^{13}C$ values than those acquired heterotrophically, and this is likely partly responsible for the decrease in leaf $\delta^{13}C$ over time (Terwilliger and Huang, 1996).

2.3.4 *Marine Plants*

For the purpose of this paper, 'marine plants' refers specifically to macroalgae, or plants that are typically classified as kelps, seaweeds, and seagrasses. One of the most commonly reported distinctions in carbon isotopic composition is that marine animals tend to have higher $\delta^{13}C$ values than terrestrial animals, except in cases where C_4 plants dominate the diet of the latter. While this distinction holds in the vast majority of circumstances (Ambrose et al., 1997; Schoeninger and DeNiro, 1984; Szpak et al., 2009), the same relationship is not necessarily true for marine and terrestrial plants.

Marine plants are characterized by a high degree of variability in carbon isotopic composition. Figure 2.3 presents the carbon isotopic compositions for the four major classes of marine macroalgae (data are taken from published literature: Bode et al., 2006; Corbisier et al., 2004; Filgueira and Castro, 2011; Fredriksen, 2003; Gillies et al., 2012; Golléty et al., 2010; Grall et al., 2006; Kang et al., 2008; Mayr et al., 2011; Nadon and Himmelman, 2010; Olsen et al., 2011; Raven et al., 2002; Riera et al., 2009; Schaal et al., 2009, 2010; Schaal et al., 2012; Vizzini and Mazzola, 2003; Wang and Yeh, 2003).

In general, marine plants are characterized by carbon isotopic compositions that are intermediate in comparison to terrestrial C_3 and C_4 plants, with two notable exceptions. Seagrasses (*Zostera* sp.), have extremely high $\delta^{13}C$ values, typically higher than most terrestrial C_4 plants (Figure 2.3d). There is evidence to suggest C_4 photosynthetic activity in a few species of marine algae (Xu et al., 2012), but the comparatively high $\delta^{13}C$ values observed in many species, including seagrasses, cannot typically be explained in this way (Raven et al., 2002). The variable use of dissolved $CO_{2(aq)}$ and $HCO_3^-{}_{(aq)}$ is a significant factor, as $\delta^{13}C$ of $HCO_3^-{}_{(aq)}$ is ~9 ‰ less negative than that of $CO_{2(aq)}$ (Kroopnick, 1985). Moreover, for intertidal plants, which are exposed to the atmosphere for a portion of the day, the utilization of atmospheric CO_2 further complicates matters (Raven et al., 2002). The thickness of the diffusive boundary layer is also a potentially important factor with respect to $\Delta^{13}C$ as it may differ due to variable water velocity (France, 1995; Osmond et al., 1981). Other environmental factors have also been demonstrated to influence aquatic plant $\delta^{13}C$ values, such as: salinity (Cornelisen et al., 2007), extracellular CO_2 concentration (Burkhardt et al., 1999; Kopczyńska et al., 1995), light intensity (Cornelisen et al., 2007), algal growth rate (Laws et al., 1995), water velocity (Osmond et al., 1981), and water temperature (Wiencke and Fischer, 1990).

Some red algae (Floridiophyceae) are characterized by consistently very low $\delta^{13}C$ values (<−30 ‰). In general, the brown algae (kelps) have been noted to contribute significantly to nearshore ecosystems in terms of secondary production, with numerous studies examining the relative contributions of offshore phytoplankton and nearshore macroalgae (Miller and Page, 2012).

2.4 Natural Variation in Plant Nitrogen Isotopic Composition

2.4.1 *Nitrogen Source*

Unlike carbon, which is obtained by plants as atmospheric CO_2, nitrogen is actively taken up from the soil in the vast majority of cases. The two most important nitrogenous species utilized by plants are nitrate (NO_3^-) and ammonium (NH_4^+). In general, nitrate is the most abundant form of mineralized nitrogen available to plants, but in some instances, such as waterlogged or acidic soils, ammonium may predominate (Pilbeam, 2010; Yoneyama et al., 2003). Additionally, some plants rely, at least to some extent, on atmospheric nitrogen (N_2), which is obtained by symbiotic bacteria residing in root nodules (rhizobia) (Vitousek et al., 2002). Plants may also take up organic nitrogen (e.g. free amino acids) from the soil (Henry and Jefferies, 2003; Kielland, 1994; Kielland et al., 2006; Persson and Näsholm, 2001; Persson et al., 2003), although the relative importance of such processes is not well understood and relatively poorly documented (Jones et al., 2005; Näsholm et al., 2009). The extent to which plants rely on these N sources is significant because they may have distinct nitrogen isotopic compositions due to fractionations associated with different steps in the nitrogen cycle (e.g. ammonification, nitrification, denitrification), as well as the uptake and eventual incorporation of mineralized N into organic N (Evans, 2001; Högberg, 1997; Robinson, 2001).

There are two important aspects of variation in N source pertinent to the present study. The first relates to N_2-fixation by plants (mostly members of Fabaceae), which are common in both wild and domestic contexts in many parts of the central Andes. Plants that utilize significant amounts of atmospheric N_2 are characterized by comparatively low $\delta^{15}N$ values, typically ~0 ‰ (Belane and Dakora, 2010; Delwiche and Steyn, 1970; Delwiche et al., 1979; DeNiro and Hastorf, 1985; Gathumbi et al., 2002; Kohl and Shearer, 1980; Mariotti et al., 1980; Shearer et al., 1983; Shearer and Kohl, 1986; Sprent et al., 1996; Spriggs et al., 2003; Steele et al., 1983; Virginia and Delwiche, 1982; Yoneyama et al., 1986; Yoneyama et al., 1993b). These plants acquire such compositions because the $\delta^{15}N$ of atmospheric N_2 is ~0 ‰ (Mariotti, 1983) and the assimilation of N from N_2-fixation is not associated with significant fractionation of ^{15}N (Delwiche and Steyn, 1970; Mariotti et al., 1980; Shearer and Kohl, 1986). By comparison, soil NO_3^- and NH_4^+ tend to have $\delta^{15}N$ values >0 ‰ (Shearer et al., 1978), and non N_2-fixing plants have $\delta^{15}N$ values that tend to be >0 ‰, although these are highly variable for a number of reasons as discussed in more detail below.

The second potentially significant source-related cause of plant $\delta^{15}N$ variation is the uptake of fertilizer-derived N by plants. Animal fertilizers are characterized by extremely variable $\delta^{15}N$ values depending on the relative proportions of N-bearing species in the fertilizer (e.g. urea, uric acid, ammonium, organic matter) (Szpak et al., 2012a). Manures consisting primarily of solid waste derived from terrestrial herbivores tend to have $\delta^{15}N$ values between 2 and 8 ‰ (Bateman and Kelly, 2007; Dijkstra et al., 2006; Kerley and Jarvis, 1996; Rapisarda et al., 2010; Rogers, 2008; Steele and Daniel, 1978), while those that contain a mix of solid and liquid waste (slurry fertilizers) tend to have higher $\delta^{15}N$ values, often between 6 and 15 ‰ (Choi et al., 2002; Choi et al., 2003; Lim et al., 2007; Rogers, 2008; Yun et al., 2006; Yun et al., 2011). The highest $\delta^{15}N$ values for animal fertilizers (>25 ‰) have been recorded for seabird guano (Szpak et al., 2012a; Szpak et al., 2012b), which consists primarily of uric acid and is subject to significant NH_4^+

volatilization. The addition of animal fertilizer N to the soil therefore adds an N source with an isotopic composition that is usually enriched in ^{15}N relative to endogenous soil N. This results in higher δ^{15}N values for plants growing in soils fertilized with animal waste than those plants growing in unfertilized soil or soils fertilized with chemical fertilizers (Bogaard et al., 2007; Choi et al., 2006; Choi et al., 2002; Choi et al., 2003; del Amor et al., 2008; Flores et al., 2007; Fraser et al., 2011; Lim et al., 2007; Nakano et al., 2003; Nakano and Uehara, 2007; Rapisarda et al., 2005; Rapisarda et al., 2010; Senbayram et al., 2008; Szpak et al., 2012a; Szpak et al., 2012b; Yun et al., 2006; Yun and Ro, 2009; Yun et al., 2011).

Animal-derived N may be delivered to plants by means other than purposeful application of manures. Several studies have documented that the addition of N from animal carcasses (salmon in particular) provide substantial quantities of N taken up by plants. These plants tend to be characterized by relatively high δ^{15}N values (Ben-David et al., 1998; Bilby et al., 2003; Helfield and Naiman, 2001; Hilderbrand et al., 1999). Increased grazing intensity has also been suggested to influence plant δ^{15}N values due to the concentrated addition of animal waste, but studies have produced conflicting results, with some finding grazing to: increase plant δ^{15}N values (Coetsee et al., 2011; Li et al., 2010; Schulze et al., 1998), decrease plant δ^{15}N values (Frank and Evans, 1997; Golluscio et al., 2009), have little or no impact on plant δ^{15}N values (Cook, 2001; Han et al., 2008; Neilson et al., 1998; Wittmer et al., 2011; Xu et al., 2010), or increase δ^{15}N in plant roots, but decrease δ^{15}N in shoots (Frank et al., 2004).

2.4.2 *Taxonomic Variation*

Strong distinctions in plant δ^{15}N have been related to mycorrhizal (fungal) associations (Craine et al., 2009; Emmerton et al., 2001; Handley et al., 1999b; Hobbie et al., 2000; Högberg, 1990; Michelsen et al., 1998). In some ecosystems, particularly those at high latitudes characterized by soils with low N content, this facilitates the distinction between plant functional types – trees, shrubs, and grasses (Högberg et al., 1996; Michelsen et al., 1996; Schulze et al., 1994). In a global survey of foliar δ^{15}N values, Craine et al. (2009) found significant differences in plant δ^{15}N on the basis of mycorrhizal associations, with the following patterns (numbers in parentheses are differences relative to non-mycorrhizal plants): ericoid (−2 ‰), ectomycorrhizal (−3.2 ‰), arbuscular (−5.9 ‰). The comparatively low $\delta^{15}N$ values of plants with mycorrhizal associations has been attributed to a fractionation of 8 to 10 ‰ against ^{15}N during the transfer of N from fungi to plants (Hobbie et al., 2005; Hobbie et al., 1999), with the lowest values indicating higher retention of N in the fungi compared to the plant (Hobbie and Colpaert, 2003).

2.4.3 *Intra-plant and Temporal Variation in Plant $\delta^{15}N$*

There are three main reasons that plants exhibit intraplant and temporal variation in their tissue $\delta^{15}N$ values: (1) fractionations associated with NO_3^- assimilation in the root vs. shoot, (2) movement of nitrogenous compounds between nitrogen sources and sinks, (3) reliance on isotopically variable N sources as tissue forms over time.

Both NO_3^- and NH_4^+ are taken up by plant roots. NO_3^- can be immediately assimilated into organic N in the root, or it may be routed to the shoot and assimilated there. The assimilation of NO_3^- into organic N is associated with a fractionation of ^{15}N of up to −20 ‰ (Ledgard et al., 1985; Robinson, 2001). Therefore, the NO_3^- that is moved to the shoot has already been exposed to some fractionation associated with assimilation and is enriched in ^{15}N compared to the NO_3^- that was assimilated in the root. On this basis, it is expected that shoots will have higher $\delta^{15}N$ values than roots in plants fed with NO_3^- (Evans et al., 1996). Because NH_4^+ is assimilated only in the root, plants with NH_4^+ as their primary N source are not expected to have significant root/shoot variation in $\delta^{15}N$ (Evans, 2001).

As plants grow they accumulate N in certain tissues (sources) and, over time, move this N to other tissues (sinks). In many species, annuals in particular, large portions of the plant's resources are allocated to grain production or flowering. In these cases, significant portions of leaf and/or stem N is mobilized and allocated to the fruits, grains, or flowers (Bausenwein et al., 2001a; Bausenwein et al., 2001b; Crawford et al., 1982; Mae and Ohira, 1981). When stored proteins are hydrolyzed, moved, and synthesized, isotopic fractionations occur (Bada et al., 1989; Silfer et al., 1992). Theoretically, nitrogen sources (leaves, stems) should be comparatively enriched in ^{15}N in relation to sinks (grains, flowers), which has been observed in several studies (Choi et al., 2002; Choi et al., 2005a; Gebauer et al., 1994; Näsholm, 1994; Szpak et al., 2012a; Szpak et al., 2012b).

In agricultural settings, the variation within a plant over time may become particularly complex due to the application of nitrogenous fertilizers. The availability of different N-bearing species from the fertilizer (NH_4^+, NO_3^-) and the nitrogen isotopic composition of fertilizer-derived N changes over time as various soil processes (e.g. ammonification, nitrification) occur. The nature of this variation is complex and will depend on the type of fertilizer applied (Szpak et al., 2012b).

2.4.4 *Environmental Factors Affecting Plant $\delta^{15}N$*

Plant nitrogen isotopic compositions are strongly influenced by a series of environmental factors. The environmental variation in plant $\delta^{15}N$ can be passed on to consumers and cause significant spatial variation in animal isotopic compositions at regional and continental scales (Ambrose and DeNiro, 1986a, 1986b, 1987; Cormie and Schwarcz, 1996; Gröcke et al., 1997; Heaton et al., 1986; Murphy and Bowman, 2006; Schwarcz et al., 1999; Sealy et al., 1987; Szpak et al., 2010; Vogel et al., 1990a; Vogel et al., 1990b).

Plant $\delta^{15}N$ values have been observed to be positively correlated with mean annual temperature (MAT) (Amundson et al., 2003; Martinelli et al., 1999), although this relationship appears to be absent in areas where MAT ≤ −0.5°C (Craine et al., 2009). A large number of studies have found a negative correlation between plant $\delta^{15}N$ values and local precipitation and/or water availability. These effects have been demonstrated at regional or continental (Aranibar et al., 2004; Austin and Vitousek, 1998; Austin and Sala, 1999; Hartman and Danin, 2010; Heaton, 1987; Murphy and Bowman, 2006, 2009; Peri et al., 2012; Schulze et al., 1999; Schuur and Matson, 2001; Swap et al., 2004), and global (Amundson et al., 2003; Craine et al., 2009; Handley et al., 1999a) scales. Several authors have hypothesized that relatively high $\delta^{15}N$ values in herbivore tissues may be the product of physiological processes within the animal related to drought stress (Ambrose and DeNiro, 1986a; Gröcke et al., 1997; Sealy et al., 1987), although controlled experiments have failed to provide any evidence supporting this hypothesis (Ambrose, 2000). More recent research has demonstrated a clear link between herbivore tissue $\delta^{15}N$ values and plant $\delta^{15}N$ values, while providing no support for the ‘physiological stress hypothesis’ (Hartman, 2011; Murphy and Bowman, 2006).

The nature of the relationship between rainfall and plant $\delta^{15}N$ values appears to be extremely complex, with numerous variables contributing to the pattern. Several authors, including Handley et al. (1999a), have attributed this pattern to the relative ‘openness’ of the nitrogen cycle. In comparison to hot and dry systems, which are prone to losses of excess N, colder and wetter systems more efficiently conserve and recycle mineral N (Amundson et al., 2003) and are thus considered less open. With respect to ecosystem $\delta^{15}N$, ^{15}N enrichment will be favored for any process that increases the flux of organic matter to mineral N, or decreases the flux of mineral N into organic matter (Aranibar et al., 2004). For instance, low microbial activity, or high NH_3 volatilization would cause an overall enrichment in ^{15}N of the soil-plant system.

2.4.5 *Marine Plants*

In comparison to terrestrial plants, the factors affecting the nitrogen isotopic composition of marine plants have not been investigated intensively other than the influence of anthropogenic nitrogen. As is the case with terrestrial plants, marine plant $\delta^{15}N$ values are strongly influenced by the forms and isotopic composition of available N (Ostrom et al., 1997; Waser et al., 1998). Specifically, the relative reliance on upwelled NO_3^- relative to recycled NH_4^+ will strongly influence the $\delta^{15}N$ of marine producers, including macroalgae. Systems that are nutrient poor (oligotrophic) tend to be more dependent on recycled NH_4^+, and systems that are nutrient rich (eutrophic) tend to be more dependent on upwelled NO_3^-. This results in nutrient-rich, upwelling systems being enriched in ^{15}N relative to oligotrophic systems (Wu et al., 1997).

2.5 Materials and Methods

2.5.1 *Sample Collection*

Wild plants were collected between 2011/07/18 and 2011/08/03. We used regional ecological classifications defined by Tosi (1960), which are summarized in Table 2.1. In each of these five zones, two sites were selected that typified the composition of local vegetation. Sampling locations were chosen to minimize the possibility of significant anthropogenic inputs; in particular, areas close to agricultural fields and disturbed areas were avoided. Sampling locations were fairly open and did not have significant canopy cover. At each sampling location, all plant taxa within a 10 m radius were sampled. Wherever possible, three individuals of each species were sampled and were later homogenized into a single sample for isotopic analysis. Images for eight of the wild plant sampling locations are presented in Figure 2.4.

Cultigens (edible portions) were collected from local markets between 2008/10/08 and 2008/11/09 (Table 2.2). Plants introduced to the Americas were not collected (e.g. peas, barley), even though these species were common. Entire large cultigens (e.g. tubers) were selected and subsequently, a thin (ca. 0.5 cm) slice was sampled. For smaller cultigens (e.g. maize, beans, quinoa) one handful of material was sampled.

For both wild plants and cultigens, geospatial data were recorded using a Garmin® Oregon® 450 portable GPS unit (Garmin®, Olathe, KS, USA). After collection, plants were air-dried on site. Prior to shipping, plants were dried with a Salton® DH−1171 food dehydrator (Salton Canada, Dollard-des-Ormeaux, QC, Canada). Plants were separated according to tissue (leaf, stem, seed, flower). For grasses, all aboveground tissues were considered to be leaf except where significant stem development was present, in which case, leaf and stem were differentiated. All geospatial data associated with these sampling sites are available as a Google Earth .kmz file in the Supporting Information (http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0053763#s6).

Plants were not sampled from privately-held land or from protected areas. Endangered or protected species were not sampled. Plant materials were imported under permit #2011−03853 from the Canadian Food Inspection Agency. No additional specific permissions were required for these activities.

2.5.2 *Sample Preparation*

Samples were prepared according to Szpak et al. (2012a) with minor modifications. As described above, plant material was dried prior to arrival in the laboratory. Whole plant samples were first homogenized using a Magic Bullet® compact blender (Homeland Housewares, Los Angeles, CA, USA). Ground material was then sieved, with the <180 μm material retained for analysis in glass vials. If insufficient material was produced after sieving, the remaining material was further ground using a Wig-L-Bug mechanical shaker (Crescent, Lyons, IL, USA) and retained for analysis in glass vials. Glass vials containing the ground material were dried at 90°C for at least 48 h under normal atmosphere.

2.5.3 *Stable Isotope Analysis*

Isotopic (δ^{13}C and δ^{15}N) and elemental compositions (%C and %N) were determined using a Delta V isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany) coupled to an elemental analyzer (Costech Analytical Technologies, Valencia, CA, USA), located in the Laboratory for Stable Isotope Science (LSIS) at the University of Western Ontario (London, ON, Canada). For samples with <2% N, nitrogen isotopic compositions were determined separately, with excess CO_2 being removed with a Carbo-Sorb trap (Elemental Microanalysis, Okehampton, Devon, UK) prior to isotopic analysis.

Sample δ^{13}C and δ^{15}N values were calibrated to VPDB and AIR, respectively, with USGS40 (accepted values: δ^{13}C = −26.39 ‰, δ^{15}N = −4.52 ‰) and USGS41 (accepted values: δ^{13}C = 37.63 ‰, δ^{15}N = 47.6 ‰). In addition to USGS40 and USGS41, internal (keratin) and international (IAEA-CH-6, IAEA-N-2) standard reference materials were analyzed to monitor analytical precision and accuracy. A δ^{13}C value of −24.03±0.14 ‰ was obtained for 81 analyses of the internal keratin standard, which compared well with its average value of −24.04 ‰. A δ^{13}C value of −10.46±0.09 ‰ was obtained for 46 analyses of IAEA-CH-6, which compared well with its accepted value of −10.45 ‰. Sample reproducibility was ±0.10 ‰ for δ^{13}C and ±0.50 % for %C (50 replicates). A δ^{15}N value of 6.37±0.13 ‰ was obtained for 172 analyses of an internal keratin standard, which compared well with its average value of 6.36 ‰. A δ^{15}N value of 20.3±0.4 ‰ was obtained for 76 analyses of IAEA-N-2, which compared well with its accepted value of 20.3 ‰. Sample reproducibility was ±0.14 ‰ for δ^{15}N and ±0.10 % for %N (84 replicates).

2.5.4 *Data Treatment and Statistical Analyses*

Plants were grouped into the following major functional categories for analysis: herb/shrub, tree, grass/sedge, vine. Plants that are invasive and/or introduced species were included in the calculation of means for particular sites since their isotopic compositions should still be impacted by the same environmental factors as other plants. For all statistical analyses of carbon isotopic composition, grass/sedge and herb/shrub were further separated into C_3 and C_4 categories. For comparisons among plant functional types, and sampling sites, foliar tissue was used since other tissues were not as extensively sampled.

Correlations between foliar isotopic compositions and environmental parameters (altitude, mean annual precipitation) were assessed using Spearman's rank correlation coefficient (ρ). One-way analysis of variance (ANOVA) followed by either a Tukey's HSD test (if variance was homoscedastic) or a Dunnett's T3 test (if variance was not homoscedastic) was used to compare means. All statistical analyses and regressions were performed in SPSS 16 for Windows.

2.6 Results

2.6.1 *Cultigens*

The carbon and nitrogen isotopic compositions were analyzed for a total of 85 cultigen samples from eleven species. Carbon and nitrogen isotopic compositions for cultigens are presented in Figure 2.5. Mean δ^{13}C and δ^{15}N values for cultigens are presented in Table 2.3. Isotopic and elemental data, as well as corresponding geospatial data for individual cultigens are presented in Table 2.4. All isotopic and elemental compositions for cultigens are for consumable portions of the plant, with one exception (maize leaves), which is excluded from Table 2.3 and Figure 2.5. Mean δ^{13}C values for C_3 cultigens ranged from −29.8±0.9 ‰ (coca) to −25.6±1.9 ‰ (mashua). The mean δ^{13}C value for maize, which was the only C_4 plant examined, was −11.8±0.4 ‰. Mean δ^{15}N values for cultigens were typically more variable than δ^{13}C values, ranging from −0.2±0.4 ‰ (*Phaseolus lunatus*) to 7.9±1.3 ‰ (quinoa).

When maize is excluded, there were no significant differences in δ^{13}C among cultigens ($F_{[7,49]}$=0.3, p=0.93), but there were for δ^{15}N (maize included) ($F_{[8,73]}$=9.7, p<0.001). Results of post-hoc Dunnett's T3 test for δ^{15}N differences among individual cultigen species are presented in Table 2.5. The three leguminous species were generally characterized by significantly lower δ^{15}N values than non-leguminous species (Table 2.5); collectively, legumes were characterized by significantly lower δ^{15}N values than non-legumes (Figure 2.6; $F_{[1,80]}$=51.8, p<0.001).

Cultigen N content is presented in Table 2.3 and Figure 2.7. Mean %N for cultigens ranged from 1.2±0.2% (maize) to 6.8±1.3% (Andean lupin). Results of post-hoc Dunnett's T3 test for differences between individual cultigen species in N content are presented in Table 2.6. The three leguminous species were characterized by significantly higher N contents than non-leguminous species (Table 2.6); collectively, legumes were characterized by significantly higher %N values than non-legumes (Figure 2.7; $F_{[1,80]}$=116.0, p<0.001).

2.6.2 *Wild Plants*

A total of 139 species were sampled primarily from ten sites distributed along an altitudinal transect from 10 to 4,070 masl. The number of taxa sampled and environmental variables for each of the sampling locations are presented in Table 2.7. The number of C_4 plant taxa was generally higher at lower altitude sites receiving low amounts of rainfall. This fits with what is known about the global distribution of C_4 plants (Sage and Pearcy, 2004).

The carbon and nitrogen isotopic compositions were measured for all 139 species. Foliar tissue was analyzed from all species, and additional tissues analyzed included: 112 stems, 28 roots, 51 flowers, and 62 seeds. Carbon and nitrogen isotopic compositions for wild plants are presented in Table 2.8 according to plant part. Foliar δ^{13}C values for C_3 plants ranged from −31.9 to −22.5 ‰, with a mean value of −27.6±1.9 ‰ (n=122). Foliar δ^{13}C values for C_4 plants ranged from −15.6 to −11.6 ‰, with a mean value of −13.5±1.0 ‰ (n=17). Foliar δ^{15}N values for C_3 plants ranged from −4.1 to 13.0‰, with a mean value of 3.7±4.0 ‰. Foliar $\delta^{15}N$ values for C_4 plants ranged from −3.2 to 15.0 ‰, with a mean value of 5.5±5.7 ‰. The single lichen analyzed (*Usnea andina*) was characterized by a $\delta^{13}C$ value intermediate between C_3 and C_4 plants (−20.5 ‰) and a very low $\delta^{15}N$ value (−6.5 ‰), consistent with previously reported results for lichens (Huiskes et al., 2006; Lange et al., 1988; Lee et al., 2009).

There were no significant differences in foliar $\delta^{15}N$ among plant functional groups ($F_{[3,132]}=1.8$, $p=0.15$). Foliar $\delta^{13}C$ differed significantly among plant functional groups ($F_{[5,130]}=195.0$, $p<0.001$), although this was driven by differences between C_3 and C_4 groups; there were no significant differences in foliar $\delta^{13}C$ between plant functional groups within C_3 and C_4 groups (Table 2.9).

There was no clear pattern of intraplant variation in $\delta^{15}N$ (Figure 2.8) with differences in $\delta^{15}N$ between tissues ($\Delta^{15}N$) being highly variable: $\Delta^{15}N_{stem-leaf}$ = −0.3±2.3 ‰, $\Delta^{15}N_{root-leaf}$ = 0.4±3.1 ‰, $\Delta^{15}N_{flower-leaf}$ = 0.5±1.4 ‰, $\Delta^{15}N_{seed-leaf}$ = 0.5±1.7 ‰. Conversely, foliar tissue was typically characterized by lower $\delta^{13}C$ values than all other tissues analyzed (Figure 2.9), and intraplant variation was generally smaller: $\Delta^{13}C_{stem-leaf}$ = 0.5±0.9 ‰, $\Delta^{13}C_{root-leaf}$ = 0.4±0.8 ‰, $\Delta^{13}C_{flower-leaf}$ = 0.6±1.0 ‰, $\Delta^{13}C_{seed-leaf}$ = 0.5±1.7 ‰. For C_4 plants ($n=17$), there was no clear pattern of intraplant variation in $\delta^{13}C$: $\Delta^{13}C_{stem-leaf}$ = 0.0±0.8 ‰, $\Delta^{13}C_{root-leaf}$ = 0.5±0.7 ‰, $\Delta^{13}C_{flower-leaf}$ = −0.3±0.6 ‰, $\Delta^{13}C_{seed-leaf}$ = −0.2±1.3 ‰.

Foliar nitrogen isotopic compositions for wild legumes (Fabaceae) were highly variable, ranging from −1.4 to 9.6 ‰. Among *Acacia* trees and shrubs alone, foliar $\delta^{15}N$ values ranged from −1.0 to 9.6 ‰, suggesting that some species are not engaged in active N_2-fixation. While wild legumes were characterized by lower foliar $\delta^{15}N$ values relative to non-legumes (4.1±4.4 ‰, n = 119 for non-legumes; 2.7±3.4 ‰, n = 17 for legumes), this difference was not statistically significant ($F_{[1,134]}=1.8$, $p=0.18$).

Mean wild C_3 plant foliar $\delta^{13}C$ and $\delta^{15}N$ values for sampling locations with ≥5 species sampled are presented in Table 2.10. Mean foliar carbon and nitrogen isotopic compositions for these sites are plotted against altitude in Figure 2.10 and estimated mean annual precipitation in Figure 2.11. Mean foliar δ^{15}N values at low altitude sites were 2 to 8 ‰ higher than mean foliar δ^{15}N values at high altitude sites. Foliar δ^{15}N was negatively correlated with mean annual precipitation (Spearman's $\rho=-0.770$, $p=0.009$) and altitude (Spearman's $\rho=-0.782$, $p=0.008$). Foliar δ^{13}C was positively correlated with mean annual precipitation (Spearman's $\rho=0.879$, $p=0.001$) and altitude (Spearman's $\rho=0.903$, $p<0.001$). For comparative purposes, mean plant δ^{13}C values for sites sampled along an altitudinal transect in northern Chile are presented in Figure 2.12 (Tieszen and Chapman, 1992).

2.6.3 *Marine Plants*

The carbon and nitrogen isotopic compositions were determined for a total of 25 marine plant samples from five species. Mean δ^{13}C and δ^{15}N values for marine plants are presented in Table 2.11. Mean δ^{13}C values for marine plants ranged from −18.7±0.7 ‰ (*Gymnogongrus furcellatus*) to −14.2±1.2 ‰ (*Grateloupia doryphora*). Mean δ^{15}N values for marine plants ranged from 2.5±0.9 ‰ (*Gymnogongrus furcellatus*) to 7.8±0.1 ‰ (*Cryptopleura cryptoneuron*). Overall, marine plants were characterized by δ^{13}C values that were intermediate between C_3 and C_4 plant isotopic compositions, although more similar to the latter. In comparison to wild plants growing at the three sites located closest to the coast, marine plants were not characterized by significantly higher δ^{15}N values when the plants from the three terrestrial sites are treated separately ($F_{[3,39]}=0.5$, $p=0.71$) or grouped together ($F_{[1,41]}<0.1$, $p=0.91$).

2.7 Discussion

2.7.1 *Cultigens*

The carbon isotopic composition of maize was ~2 ‰ more enriched in ^{13}C than wild C_4 plants (all tissues), similar to previously determined values for other parts of the world (Tieszen and Fagre, 1993; Warinner et al., 2013). This suggests that a δ^{13}C value of −10.3 ‰ (adjusted by +1.5 ‰ for the Suess Effect (Keeling, 1979; Yakir, 2011)) would be appropriate for paleodietary models in the central Andes. There may, however, be some small-scale environmental effects on maize $\delta^{13}C$ values along an altitudinal gradient as discussed in more detail below.

For the most part, the $\delta^{15}N$ values of the modern cultigens presented in this study should be interpreted cautiously with respect to paleodietary studies. The primary factor influencing the nitrogen isotopic composition of plant tissues is the N source, and it cannot be assumed that modern N sources are directly analogous to those used in antiquity. The nitrogen isotopic composition of locally grown produce sold in Andean markets today may be influenced by chemical fertilizers (which cause plants to have relatively low nitrogen isotopic compositions) or by animal manures (e.g. sheep, cow, pig) that would not have been available in the region prior to the arrival of the Spanish. The same is true for nitrogen isotopic data obtained from modern agricultural plants globally, and as a general rule, the limitations of these data must be recognized. Nevertheless, some patterns are likely to be broadly applicable.

In contrast to the vast majority of published literature (Belane and Dakora, 2010; Delwiche and Steyn, 1970; Delwiche et al., 1979; DeNiro and Hastorf, 1985; Gathumbi et al., 2002; Kohl and Shearer, 1980; Mariotti et al., 1980; Shearer et al., 1983; Shearer and Kohl, 1986; Sprent et al., 1996; Spriggs et al., 2003; Steele et al., 1983; Virginia and Delwiche, 1982; Yoneyama et al., 1986; Yoneyama et al., 1993b), Warinner et al. (2013) showed very little distinction between the nitrogen isotopic composition of Mesoamerican legumes and non-legumes, suggesting that the assumption of lower $\delta^{15}N$ values in legumes in that region is tenuous. Where the potential effects of nitrogenous fertilizers on legume $\delta^{15}N$ values are unknown (as is the case for the data presented by Warinner et al. (2013)), the interpretation of $\delta^{15}N$ values in legumes and non-legumes is not straightforward. While there was some overlap in $\delta^{15}N$ values between legumes and non-legumes in this study, leguminous cultigens had significantly higher N contents (Figure 2.7; Table 2.6) and significantly lower $\delta^{15}N$ values (Figure 2.6; Table 2.5) than non-legumes.

Aside from the differences in $\delta^{15}N$ between legumes and non-legumes, it is very difficult to generalize the $\delta^{15}N$ values for cultigens in this study. Nitrogen isotopic compositions were highly variable, particularly for potato, which most likely reflected variable local growing conditions (soil fertility, type of manure used) rather than any biochemical or physiological process specific to any particular plant species. Ultimately, the best source of baseline isotopic data for paleodietary studies may be from archaeobotanical remains (Aguilera et al., 2008; DeNiro and Hastorf, 1985; Fiorentino et al., 2012; Lightfoot and Stevens, 2012), provided that preservation of original carbon and nitrogen isotopic compositions can be demonstrated. Considerable work has been done in this regard for the isotopic composition of bone collagen (Ambrose, 1990; DeNiro, 1985; Nehlich and Richards, 2009; Szpak, 2011; van Klinken, 1999) and to a lesser extent hair keratin (O'Connell et al., 2001), but a solid set of parameters for detecting preservation versus alteration of original plant carbon and nitrogen isotopic compositions have not yet been determined. The excellent organic preservation at many archaeological sites on the coasts of Peru and Chile provides the potential for such analyses to be conducted on botanical remains.

2.7.2 *Wild Plants*

2.7.2.1 Plant Functional Group

There were no clear distinctions between different plant functional groups (grass, herb, shrub, tree, vine) with respect to either carbon or nitrogen isotopic compositions. While some systematic variation may be expected due to variable nitrogen acquisition strategies (e.g. rooting depth) or differential distribution of biomolecules with distinct isotopic compositions, the diverse range of environmental conditions from which plants were sampled likely served to blur any isotopic distinctions between functional groups. Moreover, the sample sizes for different plant functional groups within any one site were too small for meaningful comparisons to be made.

There was no consistent pattern in plant $\delta^{15}N$ with respect to leguminous trees and shrubs, with some species having foliar $\delta^{15}N$ values close to 0 ‰, and others having relatively high $\delta^{15}N$ values. Previous studies have similarly found conflicting patterns of relatively high and low $\delta^{15}N$ values in leguminous trees. Codron et al. (2005) found no clear distinction between leguminous and non-leguminous trees at a regional scale in

South Africa. Aranibar et al. (2004) did not observe significant amounts of N_2-fixation among leguminous trees in an arid region of southern Africa, with trees growing at the most arid sites showing no evidence of N_2-fixation. Fruit-bearing trees of the genus *Prosopsis* (often called huarango or algarrobo) are suggested to have been an important food source for various groups in the Andean region (Beresford-Jones et al., 2009; Towle, 1961). Catenazzi and Donnelly (2007) found $\delta^{15}N$ values typical of N_2-fixing trees (ca. 0 ‰) in *Prosopis pallida* from the Sechura Desert of northern Peru. Conversely, on the basis of the isotopic data recorded in this study for leguminous trees in the Moche River Valley, the assumption that *Prosopis* would be characterized by significantly lower $\delta^{15}N$ values relative to other plants is tenuous. Given the potential importance of these foods in the diet, a more extensive study of the nitrogen isotopic composition of central Andean leguminous trees would be beneficial.

2.7.2.2 Intra-plant Variation in Carbon and Nitrogen Isotopic Composition

Plant nitrogen isotopic composition did not systematically vary between different tissues sampled. On the basis of hydroponic studies, significant intraplant variation (between roots and shoots) is only expected when plants are fed with NO_3^- as the N source (Evans et al., 1996). Additionally, plant $\delta^{15}N$ may vary considerably among tissues due to biochemical processes associated with growth and senescence over time (Choi et al., 2005a; Kolb and Evans, 2002; Näsholm, 1994; Szpak et al., 2012a). The lack of any clear pattern of intraplant variation in $\delta^{15}N$ likely relates to a number of factors, including: variable reliance on different N sources (nitrate, ammonium, organic N) by different plant taxa and between sampling locations, differences in plant life cycles between different taxa, and spatial variation in the influence of environmental factors on the isotopic composition of source N.

Foliar tissues tended to be more depleted of ^{13}C than other tissues (Figure 2.9). The magnitude of this difference was typically ≤1 ‰, but was absent for C_4 plants. This fits with previously described data for other plants. The small difference in $\delta^{13}C$ among plant tissues is not likely to be significant with respect to the interpretation of isotopic data in the context of paleodietary studies.

2.7.2.3 Geographic Variation in Carbon and Nitrogen Isotopic Compositions

There were strong relationships between sampling site and foliar carbon and nitrogen isotopic compositions. Foliar $\delta^{15}N$ was negatively correlated with altitude (Figure 2.10a) and mean annual precipitation (Figure 2.11a), although based on the large number of studies finding a strong relationship between rainfall amount and soil, plant, and animal $\delta^{15}N$ (Amundson et al., 2003; Aranibar et al., 2004; Austin and Vitousek, 1998; Craine et al., 2009; Handley et al., 1999a; Hartman and Danin, 2010; Martinelli et al., 1999; Murphy and Bowman, 2006, 2009; Swap et al., 2004), this relationship is likely driven by rainfall. This suggests that arid sites are characterized by a fairly open nitrogen cycle, as described in previous studies (Handley et al., 1999a). It is unclear to what extent these processes would act on agricultural plants growing in relatively arid versus wet sites. Even on the hyper-arid coast where rainfall is negligible, agriculture is made possible by substantial irrigation networks. Hence, water availability in agricultural contexts is markedly higher than in non-irrigated areas. Agricultural products grown in coastal regions of the central Andes may therefore not be characterized by higher $\delta^{15}N$ values relative to those growing at wetter, higher altitude sites. For instance, maize grown as part of a controlled experiment (no fertilization) located ~6 km from the coast, had grain $\delta^{15}N$ values of 6.3±0.3 ‰ (Szpak et al., 2012b), comparable to results for maize growing at higher altitudes in this study (6.4±2.2 ‰). Aside from issues of irrigation, agricultural plants analyzed in this study were sampled along a relatively limited altitudinal transect (2233 to 3588 masl) where effects on tissue $\delta^{15}N$ values would be expected to be more limited (Figure 2.10a).

The positive relationship found between rainfall and foliar $\delta^{13}C$ in C_3 plants contrasts with most other studies, which have typically found a negative relationship between rainfall and foliar $\delta^{13}C$. The majority of these studies, however, sampled plants along a large rainfall gradient (>1,000 mm), but with little difference in elevation between sites. Conversely, we sampled along a more restricted rainfall gradient (~700 mm), but a very large altitudinal gradient (~4,000 m). Increased altitude and increased rainfall have opposing effects on foliar $\delta^{13}C$ values, and the results of this study suggest the predominance of altitudinal effects on foliar carbon isotopic compositions in northern Peru. A similar pattern was observed along a comparable altitudinal gradient in northern Chile (Figure 2.12). This pattern is most likely related to high carboxylation rates relative to stomatal conductance at high altitudes resulting in lower ^{13}C discrimination. Such effects should be equally apparent in cultivated plants, although they were not observed in this study because of the limited altitudinal range from which cultigens were sampled (Table 2.2).

Variation in plant isotopic compositions along environmental gradients is particularly important with respect to the reconstruction of the diet of humans and animals using isotopic data. While the majority of wild plants analyzed in this study would not have been consumed by humans, the results are very relevant to the reconstruction of animal management practices. There is considerable debate in the Andean region with respect to the herding practices of South American camelids (llama and alpaca), and whether or not animals recovered from coastal sites were raised locally, or imported from elsewhere (Shimada and Shimada, 1985). The results of this study suggest that animals feeding on wild plants at drier, low altitude sites would be characterized by higher tissue $\delta^{15}N$ values than animals feeding on wild plants at wetter, high altitude sites. The magnitude of this difference could easily be 4 to 6 ‰, although the consumption of agricultural plants dependent on irrigation at lower altitudes could serve to obscure this difference (as discussed above).

The potential consequences of altitudinal variation in plant $\delta^{13}C$ values are more difficult to evaluate. While the positive linear relationship between altitude and foliar $\delta^{13}C$ is strong, the relative distribution of C_3 and C_4 plants would serve to counter these effects. Because there will be proportionately more C_4 plants at dry, low altitude sites relative to moister, high altitude sites, the average $\delta^{13}C$ value of available forage would still be higher at low altitude sites. Thus, markedly higher $\delta^{13}C$ and $\delta^{15}N$ values observed in some camelids from low altitude sites (DeNiro, 1988; Thornton et al., 2011) can be satisfactorily explained by the consumption of local terrestrial vegetation.

2.7.3 *Marine Plants*

Marine algae are known to have been an important dietary resource for many groups of people in the coastal regions of Peru and Chile (Masuda, 1985), but the lack of preservation of marine algae in all but the most exceptional archaeological contexts makes evaluating the potential importance of marine algae in the diet extremely difficult. Marine plants were characterized by δ^{13}C values intermediate between C_3 and C_4 plants, with δ^{15}N values comparable to terrestrial plants growing on the coast. DeNiro (1988) has suggested that consumption of marine algae may have been responsible for relatively high δ^{13}C and δ^{15}N values in coastal Peruvian camelids. While the number of macroalgal species sampled in this study is not extensive, the isotopic data presented here are not consistent with this explanation. With the exception of instances in which marine plants grow in areas of exceptionally high influence of marine bird and/or mammalian excreta (Wainright et al., 1998), there is no reason to expect marine algal δ^{15}N values to be higher than the δ^{15}N values of plants growing along the arid coast of Peru.

2.8 Conclusion

Maize from the study area has a mean δ^{13}C value of −11.8±0.4‰, which suggests that a δ^{13}C value (adjusted for the Suess Effect) of ca. −10.3 ‰ would be appropriate for paleodietary models in the region. Leguminous cultigens were characterized by significantly lower δ^{15}N values and higher N contents than non-leguminous cultigens; this distinction was not as clear for wild legumes. Marine plants were characterized by δ^{13}C values intermediate between wild terrestrial C_3 and C_4 vegetation and δ^{15}N values that were very similar to terrestrial plants growing at low altitudes. C_4 plants were generally more abundant at lower altitude sites. Carbon and nitrogen isotopic compositions of wild plants were strongly influenced by local environmental factors. Foliar δ^{13}C was positively correlated with altitude and negatively correlated with mean annual precipitation. Foliar δ^{15}N was negatively correlated with altitude and mean annual precipitation.

While the last twenty years have seen a proliferation of studies utilizing the isotopic analysis of archaeological materials for the purpose of reconstructing diet, the development of isotopic baselines for interpreting such data has lagged behind these investigations. This hampers our ability to realize the full potential of isotopic data. This study begins to fill part of that gap by providing an initial understanding of the baseline isotopic variation in plants from northern Peru. Further studies of this nature are required to better understand baseline isotopic variation in other regions.

Table 2.1. Ecological zones used for sampling in this study.

Zone	**Altitude (masl)**
Coastal desert	0 – 500
Premontane desert scrub	500 – 1,800
Premontane thorny steppe	1,800 – 2,800
Montane moist pasture	2,800 – 3,700
Montane wet pasture	3,700 – 4,200

Ecological classifications are adapted from Tosi (1960).

Table 2.2. Environmental data for market plant sampling sites.

Site ID	Site Name	Latitude	Longitude	Altitude (masl)
C1	Caraz	−9.0554	−77.8101	2233
C2	Yungay	−9.1394	−77.7481	2468
C3	Jesus	−7.2448	−78.3797	2530
C4	Jesus II	−7.2474	−78.3821	2573
C5	Ampu	−9.2757	−77.6558	2613
C6	Shuto	−7.2568	−78.3807	2629
C7	Carhuaz	−9.2844	−77.6422	2685
C8	Yamobamba	−7.8432	−78.0956	3176
C9	Huamachuco	−7.7846	−77.9748	3196
C10	Curgos	−7.8599	−77.9475	3220
C11	Poc Poc	−7.9651	−77.8964	3355
C12	Recuay	−9.7225	−77.4531	3400
C13	Olleros	−9.6667	−77.4657	3437
C14	Hierba Buena	−7.0683	−78.5959	3453
C15	Mirador II	−9.7220	−77.4601	3466
C16	Yanac	−7.7704	−77.9799	3471
C17	Mirador I	−9.7224	−77.4601	3477
C18	Conray Chico	−9.6705	−77.4484	3530
C19	Catac	−9.8083	−77.4282	3588

Table 2.3. Mean carbon and nitrogen isotopic compositions for cultigens (± 1σ).

Common Name	**Taxonomic Name**	***n***	**δ^{13}C (‰, VPDB)**	**δ^{15}N (‰, AIR)**	**%C**	**%N**
Beans	*Phaseolus* sp.	24	−25.7 ± 1.6	0.7 ± 2.0	39.8 ± 0.7	3.7 ± 0.6
Beans (Lima)	*Phaseolus lunatus*	2	−26.0 ± 1.4	−0.2 ± 0.4	39.0 ± 0.3	2.7 ± 0.5
Chocho (Andean lupin)	*Lupinus mutabilis*	5	−26.0 ± 1.6	0.6 ± 1.2	48.3 ± 2.8	6.8 ± 1.3
Coca	*Erythroxylum coca*	4	−29.8 ± 0.9	−	45.4 ± 1.5	−
Maize (Grain)	*Zea mays*	27	−11.8 ± 0.4	6.4 ± 2.2	40.4 ± 0.5	1.2 ± 0.2
Maize (Leaf)	*Zea mays*	2	−12.9 ± 0.4	4.5 ± 1.6	41.9 ± 4.6	1.3 ± 1.3
Mashua	*Tropaeolum tuberosum*	3	−25.6 ± 1.9	0.5 ± 4.7	41.5 ± 2.8	3.0 ± 0.7
Oca	*Oxalis tuberosa*	6	−26.4 ± 0.7	5.7 ± 1.3	43.1 ± 3.2	1.6 ± 0.6
Pepper	*Capsicum annuum*	1	−29.6	4.2	48.3	2.1
Potato	*Solanum tuberosum*	12	−26.3 ± 1.3	4.0 ± 5.5	40.5 ± 1.5	1.4 ± 0.4
Quinoa	*Chenopodium quinoa*	3	−25.6 ± 0.9	7.9 ± 1.3	39.9 ± 2.1	2.6 ± 0.3
Ulluco	*Ullucus tuberosus*	2	−25.8 ± 0.0	7.5 ± 1.0	40.6 ± 0.4	3.4 ± 1.0

Table 2.4. Isotopic and elemental data for all cultigens analyzed.

Sample ID	Common Name	Taxonomic Name	Altitude (masl)	Site ID	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	%C	%N
AIS 0477	Beans	*Phaseolus* sp.	2468	C2	-24.1	-0.1	40.0	4.1
AIS 0248	Beans	*Phaseolus* sp.	2524	C3	-26.8	-2.3	39.7	3.4
AIS 0246	Beans	*Phaseolus* sp.	2530	C3	-26.9	0.2	39.5	3.6
AIS 0247	Beans	*Phaseolus* sp.	2530	C3	-28.1	0.5	38.7	3.6
AIS 0253	Beans	*Phaseolus* sp.	2573	C4	-27.1	3.4	40.0	2.7
AIS 0254	Beans	*Phaseolus* sp.	2573	C4	-26.7	7.7	39.4	4.1
AIS 0255	Beans	*Phaseolus* sp.	2573	C4	-24.4	2.9	39.7	3.1
AIS 0256	Beans	*Phaseolus* sp.	2573	C4	-26.8	0.4	40.3	4.4
AIS 0437	Beans	*Phaseolus* sp.	2613	C5	-25.4	2.5	39.6	3.8
AIS 0439	Beans	*Phaseolus* sp.	2613	C5	-24.3	0.0	39.8	4.6
AIS 0287	Beans	*Phaseolus* sp.	2629	C6	-27.1	-0.1	39.2	3.1
AIS 0288	Beans	*Phaseolus* sp.	2629	C6	-25.7	0.9	39.6	4.1
AIS 0459	Beans	*Phaseolus* sp.	2685	C7	-25.7	-1.9	38.8	3.0

Sample ID	Common Name	Taxonomic Name	Altitude (masl)	Site ID	δ^{13}C (‰)	δ^{15}N (‰)	%C	%N
AIS 0461	Beans	*Phaseolus* sp.	2685	C7	-22.4	0.3	39.5	3.6
AIS 0184	Beans	*Phaseolus* sp.	3355	C11	-24.7	0.2	40.0	4.1
AIS 0185	Beans	*Phaseolus* sp.	3355	C11	-26.0	-0.2	40.2	4.0
AIS 0493	Beans	*Phaseolus* sp.	3400	C12	-26.5	0.0	39.4	4.0
AIS 0590	Beans	*Phaseolus* sp.	3437	C13	-28.2	0.4	39.2	4.0
AIS 0513	Beans	*Phaseolus* sp.	3466	C15	-27.6	0.5	42.2	1.7
AIS 0502	Beans	*Phaseolus* sp.	3477	C17	-23.7	0.0	40.1	3.9
AIS 0503	Beans	*Phaseolus* sp.	3477	C17	-24.0	0.3	39.5	3.5
AIS 0504	Beans	*Phaseolus* sp.	3477	C17	-24.7	1.2	40.4	4.7
AIS 0505	Beans	*Phaseolus* sp.	3477	C17	-23.5	0.2	39.8	4.3
AIS 0528	Beans	*Phaseolus* sp.	3588	C19	-26.8	-1.2	39.4	3.7
AIS 0440	Beans (pallar)	*Phaseolus lunatus*	2613	C5	-25.0	0.0	39.3	2.3
AIS 0529	Beans (pallar)	*Phaseolus lunatus*	3588	C19	-27.0	-0.5	38.8	3.1
AIS 0436	Andean lupin	*Lupinus mutabilis*	2613	C5	-25.1	0.6	51.0	7.8
AIS 0172	Andean lupin	*Lupinus mutabilis*	3176	C8	-26.1	-0.3	44.6	4.5

Sample ID	Common Name	Taxonomic Name	Altitude (masl)	Site ID	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	%C	%N
AIS 0181	Andean lupin	*Lupinus mutabilis*	3355	C11	-27.5	-0.3	47.6	7.6
AIS 0259	Andean lupin	*Lupinus mutabilis*	3453	C14	-27.5	0.3	51.0	7.0
AIS 0138	Andean lupin	*Lupinus mutabilis*	3471	C16	-23.8	2.6	47.1	7.1
AIS 0420	Maize	*Zea mays*	2233	C1	-12.3	10.3	40.4	1.4
AIS 0421	Maize	*Zea mays*	2233	C1	-12.4	9.3	41.8	1.4
AIS 0473	Maize	*Zea mays*	2468	C2	-11.9	6.8	39.5	1.2
AIS 0474	Maize	*Zea mays*	2468	C2	-12.0	4.8	40.2	1.4
AIS 0475	Maize	*Zea mays*	2468	C2	-12.0	10.3	40.3	0.9
AIS 0476	Maize	*Zea mays*	2468	C2	-12.1	4.4	40.6	1.3
AIS 0245	Maize	*Zea mays*	2530	C3	-11.8	5.0	40.5	1.0
AIS 0250	Maize	*Zea mays*	2573	C4	-11.8	6.1	40.4	1.5
AIS 0251	Maize	*Zea mays*	2573	C4	-12.1	7.0	40.6	1.6
AIS 0252	Maize	*Zea mays*	2573	C4	-11.6	7.6	40.3	1.3
AIS 0434	Maize	*Zea mays*	2613	C5	-11.7	4.0	40.7	1.3
AIS 0435	Maize	*Zea mays*	2613	C5	-11.8	5.0	40.6	1.0

Sample ID	Common Name	Taxonomic Name	Altitude (masl)	Site ID	δ^{13}C (‰)	δ^{15}N (‰)	%C	%N
AIS 0456	Maize	*Zea mays*	2685	C7	-11.5	5.4	39.3	1.1
AIS 0457	Maize	*Zea mays*	2685	C7	-11.6	7.3	40.8	1.4
AIS 0458	Maize	*Zea mays*	2685	C7	-11.6	7.8	40.3	1.0
AIS 0167	Maize	*Zea mays*	3170	C8	-11.3	5.5	40.6	1.4
AIS 0171	Maize	*Zea mays*	3176	C8	-11.3	3.8	40.4	1.2
AIS 0132	Maize	*Zea mays*	3194	C9	-11.7	7.4	40.5	1.5
AIS 0133	Maize	*Zea mays*	3196	C9	-12.1	4.9	40.4	1.1
AIS 0148	Maize	*Zea mays*	3220	C10	-12.0	3.0	39.9	1.1
AIS 0149	Maize	*Zea mays*	3220	C10	-11.6	6.6	40.3	0.8
AIS 0178	Maize	*Zea mays*	3355	C11	-11.0	3.5	40.6	1.1
AIS 0179	Maize	*Zea mays*	3355	C11	-11.9	4.8	39.4	1.2
AIS 0492	Maize	*Zea mays*	3400	C12	-12.1	11.1	40.4	1.4
AIS 0139	Maize	*Zea mays*	3471	C16	-11.1	9.9	40.7	1.2
AIS 0500	Maize	*Zea mays*	3477	C17	-12.0	5.6	40.3	1.2
AIS 0508	Maize	*Zea mays*	3477	C17	-12.1	4.8	39.8	0.8

Sample ID	Common Name	Taxonomic Name	Altitude (masl)	Site ID	δ^{13}C (‰)	δ^{15}N (‰)	%C	%N
AIS 0453	Mashua	*Tropaeolum tuberosum*	2685	C7	-27.5	-4.9	41.6	3.1
AIS 0176	Mashua	*Tropaeolum tuberosum*	3355	C11	-25.7	1.9	44.3	2.3
AIS 0499	Mashua	*Tropaeolum tuberosum*	3477	C17	-23.7	4.3	38.6	3.7
AIS 0446	Oca	*Oxalis tuberosa*	2613	C5	-25.8	4.2	40.5	1.0
AIS 0187	Oca	*Oxalis tuberosa*	3355	C11	-26.7	4.6	47.4	2.2
AIS 0188	Oca	*Oxalis tuberosa*	3355	C11	-26.1	6.2	43.7	2.2
AIS 0490	Oca	*Oxalis tuberosa*	3400	C12	-25.6	5.7	41.0	1.5
AIS 0589	Oca	*Oxalis tuberosa*	3437	C13	-26.6	7.6	39.5	1.0
AIS 0142	Oca	*Oxalis tuberosa*	3471	C16	-27.5		46.2	
AIS 0447	Pepper	*Capsicum annuum*	2613	C5	-29.6	4.2	48.3	2.1
AIS 0419	Potato	*Solanum tuberosum*	2233	C1	-27.0	7.9	42.6	0.7
AIS 0466	Potato	*Solanum tuberosum*	2468	C2	-27.8	0.4	39.7	1.5
AIS 0249	Potato	*Solanum tuberosum*	2573	C4	-24.7	8.7	43.3	1.6
AIS 0451	Potato	*Solanum tuberosum*	2685	C7	-25.1	2.3	40.6	2.2
AIS 0452	Potato	*Solanum tuberosum*	2685	C7	-28.0	-3.2	39.3	1.7

Sample ID	Common Name	Taxonomic Name	Altitude (masl)	Site ID	δ^{13}C (‰)	δ^{15}N (‰)	%C	%N
AIS 0169	Potato	*Solanum tuberosum*	3176	C8	-28.3		42.5	
AIS 0488	Potato	*Solanum tuberosum*	3400	C12	-24.4	12.6	39.8	1.6
AIS 0588	Potato	*Solanum tuberosum*	3437	C13	-26.4	10.3	39.1	1.2
AIS 0498	Potato	*Solanum tuberosum*	3477	C17	-27.1	-5.1	39.4	1.1
AIS 0584	Potato	*Solanum tuberosum*	3528	C18	-25.6	4.1	39.8	1.5
AIS 0583	Potato	*Solanum tuberosum*	3530	C18	-25.9	1.7	39.5	1.0
AIS 0526	Potato	*Solanum tuberosum*	3588	C19	-25.8	4.1	40.1	0.9
AIS 0166	Quinoa	*Chenopodium quinoa*	3170	C8	-24.9	6.4	42.2	2.6
AIS 0175	Quinoa	*Chenopodium quinoa*	3355	C11	-26.5	8.9	38.1	3.0
AIS 0141	Quinoa	*Chenopodium quinoa*	3471	C16	-25.3	8.4	39.5	2.3
AIS 0454	Ulluco	*Ullucus tuberosus*	2685	C7	-25.8	6.8	40.3	2.7
AIS 0527	Ulluco	*Ullucus tuberosus*	3588	C19	-25.8	8.2	40.9	4.1

Table 2.5. Results of ANOVA post-hoc tests (Dunnett's T3) for cultigen δ^{15}N.

Cultigen %N	Bean (*P. lunatus*)	Andean lupin	Maize	Mashua	Oca	Potato	Quinoa	Ulluco
Bean (*Phaseolus* sp.)	0.860	1.000	**<0.001**	1.000	**0.003**	0.798	**0.028**	0.880
Bean (*P. lunatus*)	–	0.971	**<0.001**	1.000	**0.005**	0.479	**0.037**	0.121
Andean lupin	–	–	**<0.001**	1.000	**0.006**	0.802	**0.020**	0.060
Maize	–	–	–	0.696	1.000	0.983	0.855	0.917
Mashua	–	–	–	–	0.788	1.000	0.626	0.723
Oca	–	–	–	–	–	1.000	0.626	0.723
Potato	–	–	–	–	–	–	0.688	0.780
Quinoa	–	–	–	–	–	–	–	1.000

Values in boldface are statistically significant ($p<0.05$)

Table 2.6. Results of ANOVA post-hoc tests (Dunnett's T3) for cultigen N content.

Cultigen %N	Bean (*P. lunatus*)	Andean lupin	Maize	Mashua	Oca	Potato	Quinoa	Ulluco
Bean (*Phaseolus* sp.)	0.637	0.072	**<0.001**	0.869	**0.009**	**<0.001**	0.123	1.000
Bean (P. lunatus)	–	**0.037**	0.462	1.000	0.619	0.505	1.000	0.995
Andean lupin	–	–	**0.009**	**0.034**	**0.005**	**0.008**	**0.021**	0.295
Maize	–	–	–	0.232	0.981	0.992	0.101	0.566
Mashua	–	–	–	–	**0.019**	1.000	0.216	**0.009**
Oca	–	–	–	–	–	1.000	**0.033**	**0.001**
Potato	–	–	–	–	–	–	**0.033**	**0.001**
Quinoa	–	–	–	–	–	–	–	0.885

Values in boldface are statistically significant (*p*<0.05)

Table 2.7. Environmental data for wild plant sampling sites and summary of number of C_3 and C_4 plant species sampled.

Site ID	Site Name	Latitude	Longitude	Altitude (masl)	Estimated MAP (mm)	C_3 Plant Taxa Sampled	C_4 Plant Taxa Sampled
W1	Las Delicias	−8.1956	−78.9996	10	7	7	2
W2	Río Moche	−8.1267	−78.9963	33	5	9	1
W3	Ciudad Universitaria	−8.1137	−79.0373	38	6	2	0
W4	Cerro Campana	−7.9900	−79.0768	164	11	4	1
W5	La Carbonera	−8.0791	−78.8681	192	56	5	3
W6	Poroto	−8.0137	−78.7972	447	113	17	6
W7	Salpo 5	−8.0089	−78.6962	1181	143	0	2
W8	Salpo 4	−8.0047	−78.6726	1557	140	9	0
W9	Salpo 3	−8.0132	−78.6355	2150	141	16	0
W10	Salpo 2	−7.9973	−78.6481	2421	142	8	0
W11	Salpo 1	−8.0132	−78.6355	2947	171	9	1
W12	Stgo de Chuco	−8.1361	−78.1685	3041	702	21	1
W13	Cahuide	−8.2235	−78.3013	4070	591	15	0

Table 2.8. Carbon and nitrogen isotopic compositions for all wild plant taxa sampled.

				Leaf		**Stem**		**Root**		**Flowers**		**Seeds**	
Taxonomic Name	**Site ID**	**Altitude**	**Type**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**
Eriochloa mutica	W1	10	Grass	−11.6	−1.5	−11.7	1.6	–	–	–	–	−12.1	−0.2
Distichia spicata	W1	10	Grass	−14.9	−3.2	–	–	–	–	–	–	–	–
Baccharis glutinosa	W1	10	Shrub	−27.4	3.3	−26.6	5.1	–	–	−27.0	4.1	−26.9	4.2
Rauvolfia sp.	W1	10	Shrub	−28.0	9.8	−27.9	11.0	–	–	–	–	–	–
Plantago major[1]	W1	10	Herb	−28.6	7.5	−27.5	7.9	−26.7	8.6	–	–	–	–
Typla angustifolia	W1	10	Herb	−29.3	1.3	–	–	−28.7	2.6	–	–	–	–
Blumea crispata[1]	W1	10	Herb	−29.8	13.7	−30.4	13.7	−30.5	11.6	–	–	–	–
Rosippa nastrutium aquaticum[1]	W1	10	Herb	−30.1	12.5	–	–	−30.0	11.4	–	–	–	–
Oxalis corniculata	W1	10	Herb	−30.6	7.1	−31.0	6.0	−31.2	4.7	–	–	–	–
Paspalum racemosum	W2	33	Grass	−12.7	0.8	−12.8	11.7	–	–	–	–	–	–
Salix humboldtiana	W2	33	Tree	−26.4	5.2	−26.5	4.4	–	–	–	–	–	–
Phyla nodiflora	W2	33	Herb	−27.7	6.5	−26.8	5.1	−27.1	2.8	−26.7	7.9		
Melochia lupulina	W2	33	Shrub	−28.3	6.9	−27.6	6.4	–	–	−28.6	6.8	–	–
Ipomoea alba	W2	33	Herb	−28.7	9.3	−28.1	8.1	–	–	–	–	−27.3	8.9

Taxonomic Name	Site ID	Altitude	Type	Leaf δ13C	δ15N	Stem δ13C	δ15N	Root δ13C	δ15N	Flowers δ13C	δ15N	Seeds δ13C	δ15N
Persea americana	W2	33	Tree	−28.8	1.9	−26.8	7.0	–	–	–	–	–	–
Ambrosia peruviana	W2	33	Herb	−29.6	2.2	−30.0	1.7	–	–	–	–	–	–
Arundo donax[1]	W2	33	Grass	−30.3	8.5	−30.1	10.2	–	–	–	–	–	–
Acacia huarango[2]	W2	33	Shrub	−31.0	3.5	−30.0	2.3	–	–	−29.8	3.4	–	–
Psittacanthus obovatus	W2	33	Shrub (Parasitic)	−31.9	5.1	−30.6	6.2	–	–	–	–	–	–
Prosopis pallida[2]	W3	38	Tree	−27.9	4.0	−28.9	1.5	–	–	−29.1	5.8	–	–
Acacia macracantha[2]	W3	38	Tree	−30.7	8.3	−30.1	6.8	–	–	−30.5	8.6	−28.9	5.1
Tillandsia usneoides	W4	164	Epiphyte	−13.6	3.7	−14.2	1.9	−13.9	14.5	−13.6	0.0	–	–
Cryptocarpus pyriformis	W4	164	Shrub	−22.5	10.3	−22.2	10.4	–	–	–	–	−22.4	12.1
Trixis cacalioides	W4	164	Shrub	−26.6	9.2	−26.0	7.6	–	–	–	–	−25.7	9.4
Scutia spicata	W4	164	Shrub	−27.1	4.9	−25.7	4.4	–	–	–	–	–	–
Capparis angulata	W4	164	Shrub	−27.3	10.0	−27.7	10.7	–	–	–	–	−26.0	11.6
Paspalidium paladivagum	W5	192	Grass	−12.5	10.5	−12.8	11.0	−12.0	11.7	–	–	−12.3	13.4
Amaranthus celosiodes	W5	192	Herb	−13.1	9.1	−12.5	11.0	–	–	−13.5	10.9	−12.2	8.6
Tribulus terrestris	W5	192	Herb	−15.6	11.8	−16.2	14.4	–	–	–	–	−14.0	13.6

				Leaf		Stem		Root		Flowers		Seeds	
Taxonomic Name	**Site ID**	**Altitude**	**Type**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**
Hydrocotyle bonariensis	W5	192	Herb	−26.5	9.0	–	–	–	–	–	–	–	–
Cestrum auriculatum	W5	192	Shrub	−26.9	10.6	−26.8	8.5	–	–	–	–	−27.0	12.1
Cucumis dipsaceus	W5	192	Herb	−27.4	5.6	−26.8	4.2	–	–	−27.0	5.5	−28.1	6.5
Argemone subfusiformis	W5	192	Herb	−28.8	6.9	−28.1	6.3	−28.8	6.2	−28.9	5.7	–	–
Picrosia longifolia	W5	192	Herb	−30.6	5.3	−30.5	1.1	–	–	−30.0	9.3	–	–
Cyperus corymbosus	W6	447	Sedge	−13.1	8.3	−11.2	8.8	−11.7	7.8	−14.2	9.1	–	–
Echinochloa crusgalli[1]	W6	447	Grass	−13.4	2.8	−13.8	2.8	–	–	–	–	−13.7	3.9
Cynodon dactylon[1]	W6	447	Grass	−13.9	0.8	–	–	–	–	−14.1	1.2	–	–
Sorghum halepense[1]	W6	447	Grass	−14.0	2.5	−15.0	4.7	–	–	–	–	−13.1	3.7
Trianthema portulacastrum	W6	447	Herb	−14.2	17.3	−13.7	12.3	–	–	–	–	–	–
Amaranthus spinosus	W6	447	Herb	−14.4	13.3	−13.8	16.1	–	–	−14.0	15.3	−14.4	15.3
Gynerium sagittatum	W6	447	Grass	−25.8	2.7	−25.1	2.3			−25.6	5.3		
Alternanthera halimifolia	W6	447	Herb	−26.0	8.4	−26.1	9.2	–	–	−26.1	8.2	–	–
Cissus sicyoides	W6	447	Vine	−26.6	10.9	−26.1	12.4	–	–	–	–	−25.1	11.9
Dalea onobrychis[2]	W6	447	Herb	−27.2	8.7	−27.4	7.8	–	–	–	–	−26.8	7.4
Cleome spinosa	W6	447	Herb	−27.3	9.0	−27.1	9.8	–	–	–	–	−26.9	9.8

				Leaf		Stem		Root		Flowers		Seeds	
Taxonomic Name	**Site ID**	**Altitude**	**Type**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**
Crotalaria incae[2]	W6	447	Shrub	−27.3	0.2	−26.6	−2.4	–	–	−25.4	1.0	−26.0	−0.8
Ludwigia octovalvis[2]	W6	447	Herb	−27.5	0.6	−26.9	1.3	–	–	–	–	–	–
Passiflora foetida	W6	447	Vine	−27.5	9.5	−27.2	1.7	–	–	−27.5	7.8	–	–
Wedelia latilofolia	W6	447	Shrub	−28.0	6.4	−27.3	4.8	–	–	−26.4	8.1	–	–
Baccharis salicifolia	W6	447	Shrub	−28.3	6.5	−27.2	8.4	–	–	–	–	−27.1	8.0
Waltheria ovata	W6	447	Shrub	−28.4	6.1	−28.2	5.9	–	–	−27.7	6.0	–	–
Verbena littoralis	W6	447	Herb	−28.8	7.9	−28.4	5.8	–	–	–	–	−27.7	7.3
Cyperus odoratus	W6	447	Sedge	−28.8	9.2	−27.6	10.1	–	–	−28.0	10.2	–	–
Mimosa pigra	W6	447	Shrub	−29.3	1.7	−28.5	0.3	–	–	–	–	−29.1	1.3
Cajanus cajan[1, 2]	W6	447	Tree	−29.6	−1.4	−28.4	–	–	–	−28.3	0.3	−27.6	−0.7
Polygonum hydropiperoides	W6	447	Herb	−30.2	6.8	−30.6	6.7	–	–	–	–	−27.2	8.1
Mimosa albida[2]	W6	447	Shrub	−30.5	−0.8	−30.1	−1.5	–	–	–	–	−28.8	1.2
Melinis repens[1]	W7	1181	Grass	−13.3	5.6	−13.4	7.3	–	–	–	–	−14.5	3.1
Cenchrus myosuroides	W7	1181	Grass	−13.3	5.7	–	–	–	–	–	–	–	–
Dicliptera peruviana	W8	1557	Herb	−24.7	3.9	−26.3	3.2	–	–	–	–	−25.0	3.2
Tournefortia microcalyx	W8	1557	Shrub	−26.0	6.4	−26.2	6.0	–	–	−25.6	7.2	–	–

				Leaf		**Stem**		**Root**		**Flowers**		**Seeds**	
Taxonomic Name	**Site ID**	**Altitude**	**Type**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**
Ophryosporus peruvianus	W8	1557	Shrub	−26.7	2.9	−23.9	1.8	–	–	–	–	−24.0	2.6
Alternanthera porrigens	W8	1557	Herb	−27.8	2.8	−27.2	2.2	–	–	–	–	−25.7	6.7
Asclepias curassavica	W8	1557	Shrub	−28.9	2.6	−28.7	4.2	–	–	−28.8	0.4	−28.0	0.2
Boerhavia erecta	W8	1557	Herb	−29.3	9.1	−28.3	9.2	–	–	–	–	–	–
Centaurea melitensis	W8	1557	Herb	−29.5	0.5	−29.8	0.2	–	–	–	–	−28.9	1.7
Mentzelia aspera	W8	1557	Herb	−30.0	1.0	−27.6	6.8	–	–	−29.5	1.3	–	–
Sida spinosa	W8	1557	Herb	−30.1	3.1	−30.1	4.7	–	–	−31.3	1.7	–	–
Rubus robustus	W9	2150	Shrub	−25.0	3.0	−24.4	2.7	–	–	–	–	–	–
Puya sp.	W9	2150	Succulent	−25.4	−0.7	–	–	–	–	–	–	–	–
Barnadesia dombeyana	W9	2150	Shrub	−26.0	−2.0	−25.4	−0.3	–	–	−25.7	−2.7	–	–
Iochroma edule	W9	2150	Shrub	−26.1	8.5	−25.8	7.6	–	–	–	–	−25.4	7.3
Eupatorium sp.	W9	2150	Herb	−26.8	2.5	–	–	–	–	–	–	–	–
Capparis scabrida	W9	2150	Shrub	−26.8	1.3	−26.3	0.9	–	–	−26.5	2.2	–	–
Vasquezia oppositifolia	W9	2150	Herb	−27.0	−1.6	–	–	–	–	–	–	−26.9	−1.3
Stipa ichu	W9	2150	Grass	−27.0	0.3	–	–	−27.4	0.2	−27.3	0.6	–	–
Lupinus sp.[2]	W9	2150	Herb	−27.1	1.4	−27.1	3.4	–	–	−26.6	3.2	−26.7	0.8

				Leaf		Stem		Root		Flowers		Seeds	
Taxonomic Name	**Site ID**	**Altitude**	**Type**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**
Alonsoa meridionalis	W9	2150	Herb	−27.5	1.3	−26.4	−1.9	–	–	–	–	−25.9	0.1
Bromus catharticus	W9	2150	Grass	−27.8	1.1	−29.3	−1.3	–	–	–	–	−27.5	−0.7
Baccharis sp.	W9	2150	Shrub	−28.9	−1.1	−28.8	0.1	–	–	−29.5	0.5	–	–
Minthostachys mollis	W9	2150	Herb	−29.0	0.5	−28.1	−1.6	–	–	−27.2	0.1	–	–
Satureja sp.	W9	2150	Herb	−30.2	−3.2	–	–	–	–	−29.8	−2.3	–	–
Achyrocline alata	W9	2150	Shrub	−30.3	0.3	−27.8	1.2	–	–	−27.5	2.0	–	–
Polypogon sp.	W9	2150	Grass	−31.1	−5.3	−27.9	−4.4	−31.0	2.4	−27.8	−3.7	–	–
Browallia americana	W10	2421	Herb	−25.4	−1.6	−26.8	−2.5	–	–	−25.7	−0.8	–	–
Coniza sp.	W10	2421	Herb	−26.7	6.1	−26.1	4.0	–	–	–	–	–	–
Heliotropium sp.	W10	2421	Herb	−26.9	3.7	−28.4	2.2	–	–	–	–	−28.2	3.2
Caesalpina spinosa[2]	W10	2421	Tree	−27.4	2.7	−27.7	−0.4	–	–	–	–	−25.1	0.0
Oenothera rosea	W10	2421	Herb	−27.4	4.9	−27.9	4.6	–	–	–	–	−27.4	2.9
Avena sterilis[1]	W10	2421	Grass	−27.5	2.3	−27.2	2.1	−27.0	0.0	–	–	−22.5	2.2
Berberis sp.	W10	2421	Shrub	−27.7	1.1	−24.6	1.9	–	–	–	–	−26.7	1.9
Alternanthera sp.	W10	2421	Herb	−28.3	−2.9	−27.5	−3.0	–	–	–	–	−27.2	−0.8
Pennisetum purpurem[1]	W11	2947	Grass	−12.5	7.2	−12.8	6.6	–	–	–	–	−15.5	7.1

				Leaf		**Stem**		**Root**		**Flowers**		**Seeds**	
Taxonomic Name	**Site ID**	**Altitude**	**Type**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**
Ruellia floribunda	W11	2947	Herb	−23.7	4.5	−24.0	1.9	–	–	−23.5	4.9	–	–
Schinus molle	W11	2947	Tree	−24.6	2.3	−23.4	0.3	–	–	−21.3	0.8	–	–
Spartium junceum[1, 2]	W11	2947	Shrub	−26.5	1.1	−27.1	−1.1	–	–	−23.7	−1.3	−25.4	0.8
Acacia aroma[2]	W11	2947	Tree	−26.8	9.6	−26.6	9.6	–	–	−26.6	10.1	–	–
Croton ovalifolius	W11	2947	Shrub	−27.0	7.4	−27.6	5.8	–	–	–	–	–	–
Leonotis nepetifolia[1]	W11	2947	Shrub	−28.0	2.2	–	–	–	–	−27.2	3.0	−26.1	2.0
Lycianthes lycioides	W11	2947	Shrub	−28.0	−0.3	–	–	–	–	–	–	−24.3	2.0
Phenax hirtus	W11	2947	Shrub	−28.3	2.5	−29.1	7.1	–	–	–	–	−28.5	6.9
Inga feulleu[2]	W11	2947	Tree	−28.9	0.3	−27.6	−0.8	–	–	–	–	−27.1	1.1
Andropogon sp.	W12	3041	Grass	−13.5	−1.6	–	–	−13.2	−1.0	–	–	–	–
Sebastiania obtusifolia	W12	3041	Shrub	−23.7	0.8	−24.7	0.0	–	–	–	–	−24.0	2.5
Lupinus aridulus[2]	W12	3041	Herb	−24.3	2.0	−23.7	2.2	–	–	−22.7	4.0	−22.0	5.4
Silybum marianum[1]	W12	3041	Herb	−25.9	2.2	−25.8	1.6	–	–	–	–	−25.1	2.2
Phrygilanthus sp.	W12	3041	Shrub (Parasitic)	−25.9	−0.5	−24.7	7.3	–	–	–	–	–	–
Solanum amotapense	W12	3041	Shrub	−25.9	7.9	−25.2	5.1	–	–	–	–	−24.7	8.3

				Leaf		Stem		Root		Flowers		Seeds	
Taxonomic Name	**Site ID**	**Altitude**	**Type**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**
Acacia sp.[2]	W12	3041	Tree	−26.2	−1.0	−25.0	−2.5	–	–	–	–	–	–
Baccharis serpifolia	W12	3041	Shrub	−26.4	2.2	−27.1	1.5	–	–	−26.9	1.0	–	–
Aristida adsensionis	W12	3041	Grass	−26.5	−2.6	−26.2	−2.0	–	–	−26.7	−1.0	–	–
Baccharis emarginata	W12	3041	Shrub	−26.5	−0.2	−25.4	0.1	–	–	–	–	–	–
Brassica campestris	W12	3041	Herb	−27.1	2.3	–	–	–	–	–	–	−25.4	4.3
Mauria sp.	W12	3041	Tree	−27.2	6.1	−25.8	3.1	–	–	–	–	–	–
Solanum agrimoniaefolium	W12	3041	Shrub	−28.0	6.0	−28.2	3.8	–	–	–	–	−26.6	4.1
Salvia punctata	W12	3041	Herb	−28.1	−3.5	–	–	–	–	−27.7	−2.1	−27.3	−1.7
Duranta sp.	W12	3041	Shrub	−28.4	1.3	−27.6	0.8	–	–	–	–	–	–
Flourensia cajabambensis	W12	3041	Shrub	−28.6	2.9	−27.5	2.7	–	–	–	–	−29.4	2.5
Marrubium vulgare	W12	3041	Herb	−28.8	3.8	−26.6	1.4	−27.9	1.0	−26.9	4.0	–	–
Scutellaria sp.	W12	3041	Herb	−28.8	2.2	−28.6	0.6	–	–	–	–	–	–
Viguiera peruviana	W12	3041	Shrub	−28.9	5.3	−27.3	4.6	–	–	–	–	−26.6	5.4
Jungia rugosa	W12	3041	Shrub	−28.9	1.4	−26.8	1.1	–	–	−27.1	2.7	–	–
Saccellium sp.	W12	3041	Shrub	−29.0	2.0	−27.3	1.0	–	–	–	–	–	–
Baccharis libertadensis	W12	3041	Shrub	−29.6	3.8	−28.4	1.9	–	–	–	–	–	–

				Leaf		**Stem**		**Root**		**Flowers**		**Seeds**	
Taxonomic Name	**Site ID**	**Altitude**	**Type**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**
Usnea andina	W13	4070	Lichen	−20.5	−6.5	–	–	–	–	–	–	–	–
Astragalus garbancillo[2]	W13	4070	Shrub	−24.6	4.2	−25.3	3.0	−25.1	3.8	−23.8	3.9	−22.5	5.4
Luzula sp.	W13	4070	Sedge	−25.1	0.9	–	–	−25.0	3.9	−25.1	3.2	–	–
Distichia muscoides	W13	4070	Grass	−25.3	4.4	–	–	−25.2	2.9	–	–	–	–
Muehlenbeckia sp.	W13	4070	Herb	−25.3	6.3	–	–	−25.7	4.9	–	–	–	–
Urtica sp.	W13	4070	Shrub	−25.5	11.9	−25.1	9.0	−26.0	9.4	–	–	−26.6	11.9
Agrostis breviculmis	W13	4070	Grass	−25.9	2.1	–	–	−26.0	4.1	−25.5	2.4	–	–
Chuquiraga spinosa	W13	4070	Shrub	−26.0	−0.5	−24.9	−1.1	−24.4	−1.4	−24.3	−0.7	−24.4	−0.2
Werneria nubigena	W13	4070	Herb	−26.2	1.3	–	–	−25.8	1.8	–	–	–	–
Festuca dolichopylla	W13	4070	Grass	−26.3	−1.8	–	–	−25.4	−0.3	–	–	−26.5	3.6
Hypochaeris sp.	W13	4070	Herb	−26.6	7.3	–	–	−26.9	8.2	–	–	–	–
Plantago tubulosa	W13	4070	Herb	−26.9	−5.2	–	–	−26.0	−3.0	–	–	–	–
Stipa mucronata	W13	4070	Grass	−27.7	−1.4	–	–	−26.2	1.5	–	–	−26.5	1.5

Taxonomic Name	Site ID	Altitude	Type	Leaf $\delta^{13}C$	 $\delta^{15}N$	Stem $\delta^{13}C$	 $\delta^{15}N$	Root $\delta^{13}C$	 $\delta^{15}N$	Flowers $\delta^{13}C$	 $\delta^{15}N$	Seeds $\delta^{13}C$	 $\delta^{15}N$
Stenandrium dulce	W13	4070	Herb	−28.4	0.6	–	–	–	–	–	–	–	–
Senecio nutans	W13	4070	Shrub	−29.4	6.2	−28.6	5.0	−27.6	5.3	–	–	–	–

1. Species is invasive or introduced

2. Member of the family Fabaceae (legume)

Table 2.9. Results of ANOVA post-hoc tests (Dunnett's T3) for foliar δ^{13}C between plant functional groups.

Foliar δ^{13}C	C_3 Grass/Sedge	C_4 Herb/Shrub	C_3 Herb/Shrub	Tree	Vine
C_4 Grass/Sedge	**<0.001**	0.999	**<0.001**	**<0.001**	**<0.001**
C_3 Grass/Sedge	–	**<0.001**	0.993	1.000	1.000
C_4 Herb/Shrub	–	–	0.999	**<0.001**	**<0.001**
C_3 Herb/Shrub	–	–	–	0.997	0.994
Tree	–	–	–	–	1.000

Values in boldface are statistically significant ($p<0.05$)

Table 2.10. Mean (±1σ) isotopic and elemental compositions for sampling locations with >3 plant species sampled (data for C_3 plants only).

Site ID	Latitude	Longitude	Altitude (masl)	MAP (mm)[1]	*n*[2]	δ^{13}C (‰, VPDB)	δ^{15}N (‰, AIR)
W1	−8.1956	−78.9996	10	7	7	−29.1 ± 1.2	7.9 ± 4.5
W2	−8.1267	−78.9963	33	5	9	−29.2 ± 1.7	5.5 ± 2.6
W5	−8.0791	−78.8681	192	56	5	−28.1 ± 1.7	7.5 ± 2.2
W6	−8.0137	−78.7972	447	113	17	−28.1 ± 1.4	5.4 ± 4.0
W8	−8.0047	−78.6726	1557	140	9	−28.1 ± 1.9	3.6 ± 2.7
W9	−8.0132	−78.6355	2150	141	16	−27.6 ± 1.8	0.4 ± 3.0
W10	−7.9973	−78.6481	2421	142	8	−27.2 ± 0.8	2.0 ± 3.1
W11	−8.0132	−78.6355	2947	171	9	−26.9 ± 1.8	3.3 ± 3.3
W12	−8.1361	−78.1685	3041	702	21	−27.3 ± 1.6	2.1 ± 2.8

1. Mean annual precipitation (MAP) estimated as described in the text.
2. Number of C_3 plants sampled.

Table 2.11. Mean (± 1σ) isotopic and elemental compositions for marine algae.

Taxonomic Name	Type	*n*	δ^{13}C (‰, VPDB)	δ^{15}N (‰, AIR)	%C	%N
Ulva lactuca	Chlorophyta	5	−14.3 ± 0.4	6.4 ± 0.1	29.2 ± 0.4	3.6 ± 0.2
Gymnogongrus furcellatus	Rhodophyta	5	−18.7 ± 0.7	2.5 ± 0.9	23.3 ± 2.4	2.1 ± 0.2
Grateloupia doryphora	Rhodophyta	5	−14.2 ± 1.2	6.8 ± 0.3	29.9 ± 1.0	3.2 ± 0.1
Gigartina chamissoi	Rhodophyta	5	−16.7 ± 1.0	5.4 ± 0.5	25.7 ± 0.4	2.7 ± 0.1
Cryptopleura cryptoneuron	Rhodophyta	5	−18.4 ± 0.4	7.8 ± 0.1	21.2 ± 1.6	2.8 ± 0.4

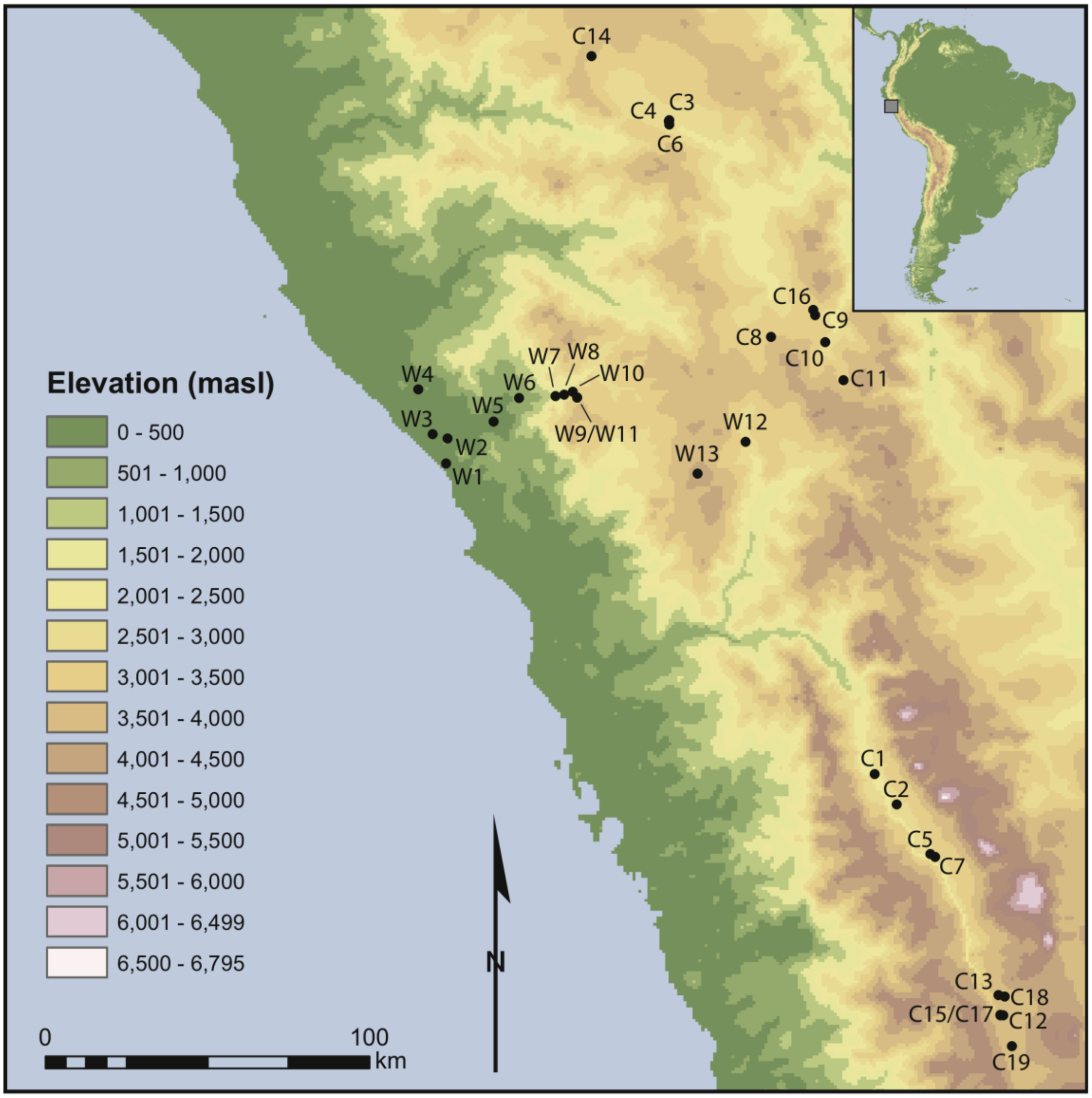

Figure 2.1. Digital elevation model of the study region derived from the Global 30 Arc-Second Elevation (GTOPO30) data set.

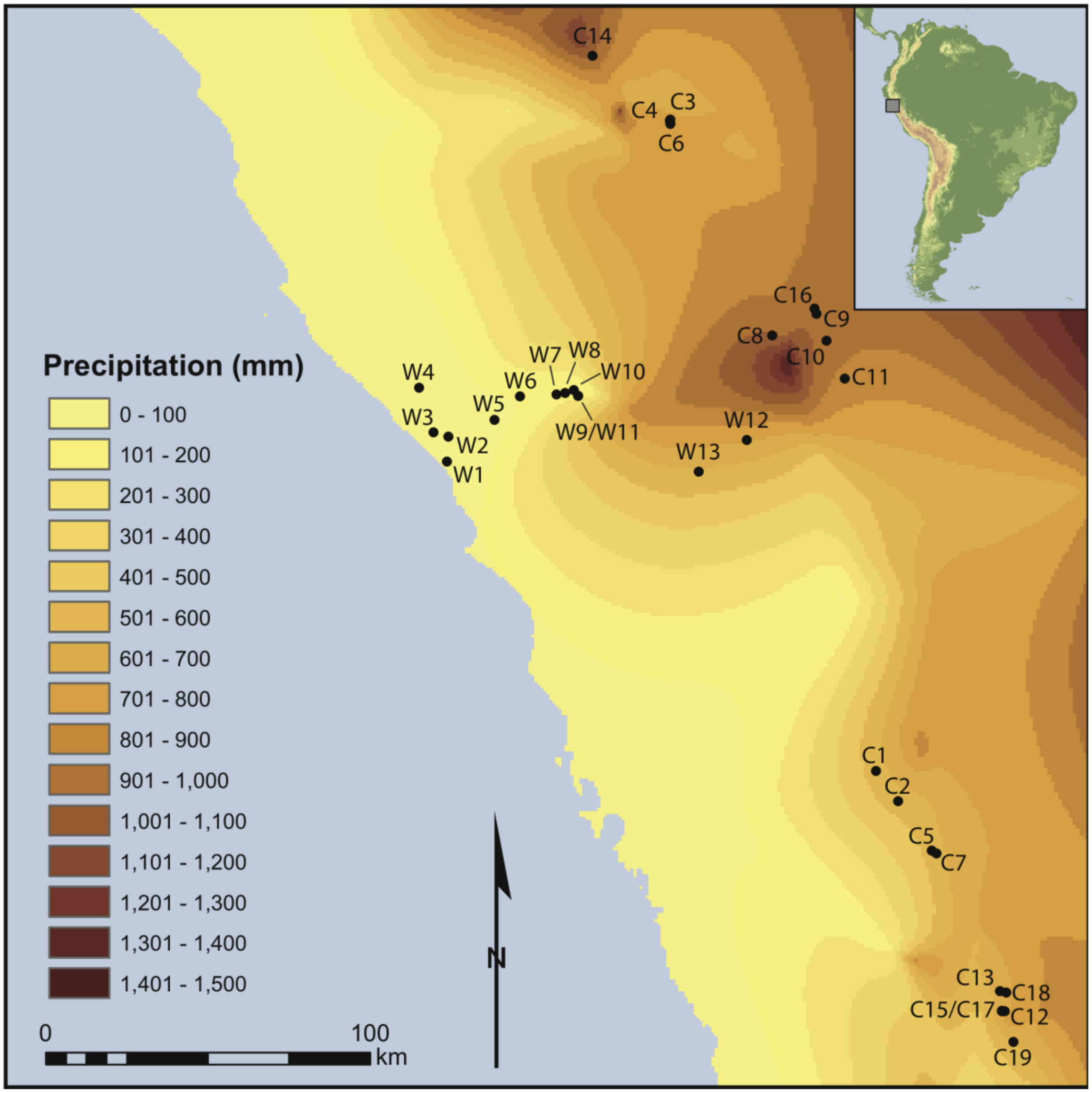

Figure 2.2. Extrapolated mean annual precipitation for study area. Mean annual precipitation data from 493 monitoring stations in Peru (Peterson and Vose, 1997) were extrapolated using the natural neighbor method in ArcMap (ArcGIS 10.0, ESRI).

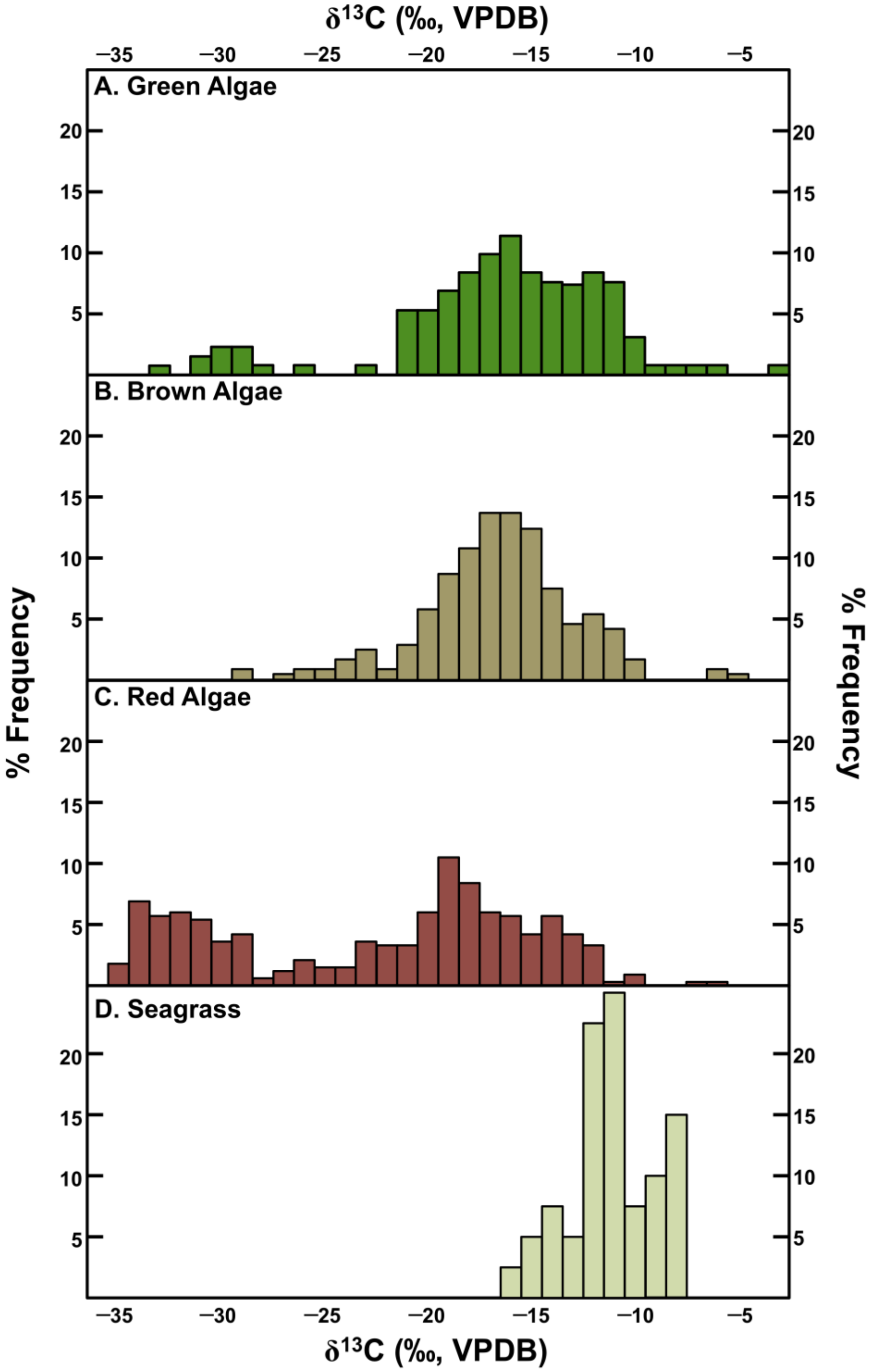

Figure 2.3. Frequency distributions of carbon isotopic compositions of marine macroalgae.

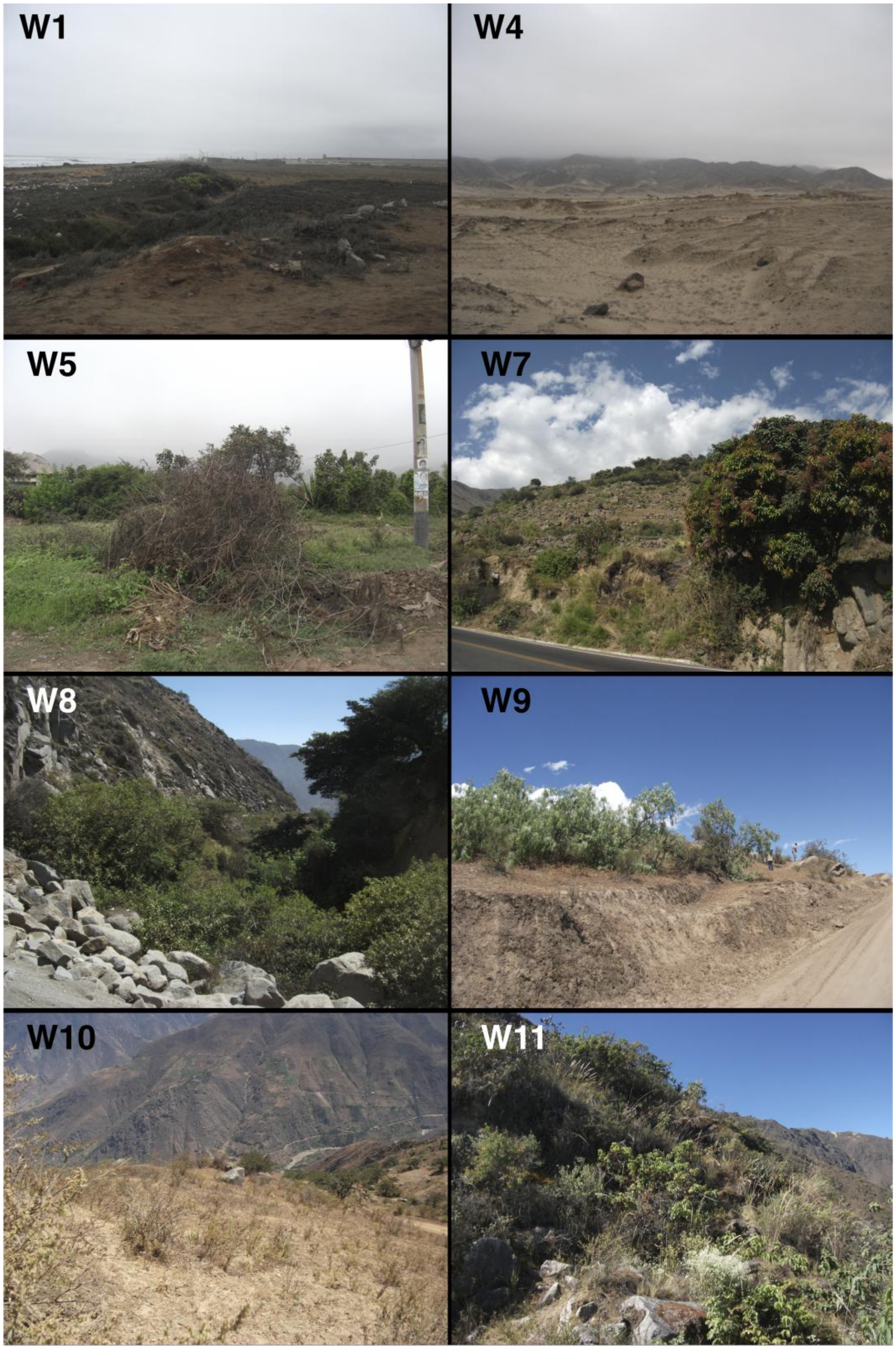

Figure 2.4. Images of eight of the wild plant sampling locations. Corresponding geographical data for these sites can be found in **Table 2.7**.

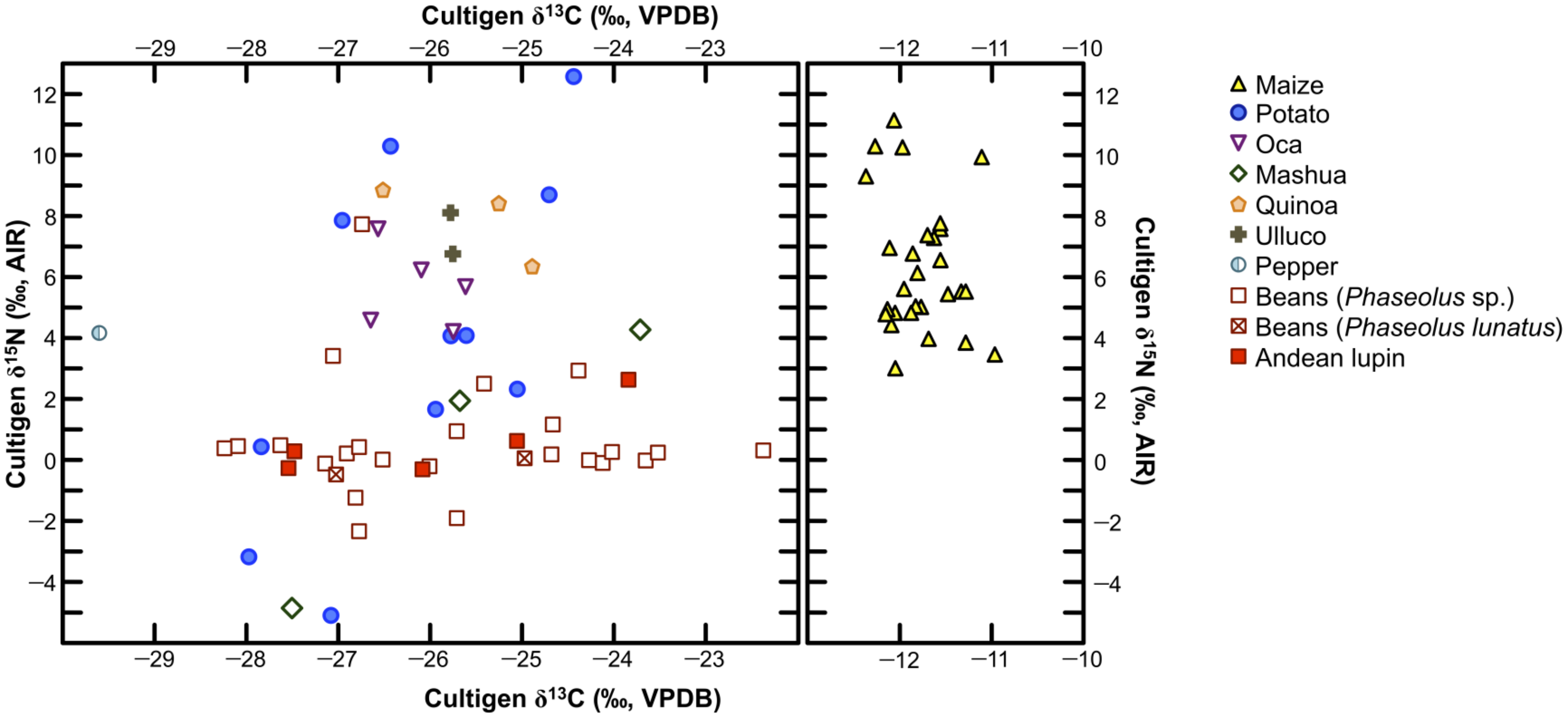

Figure 2.5. Carbon and nitrogen isotopic compositions of cultigens. Note that the x-axis is not continuous.

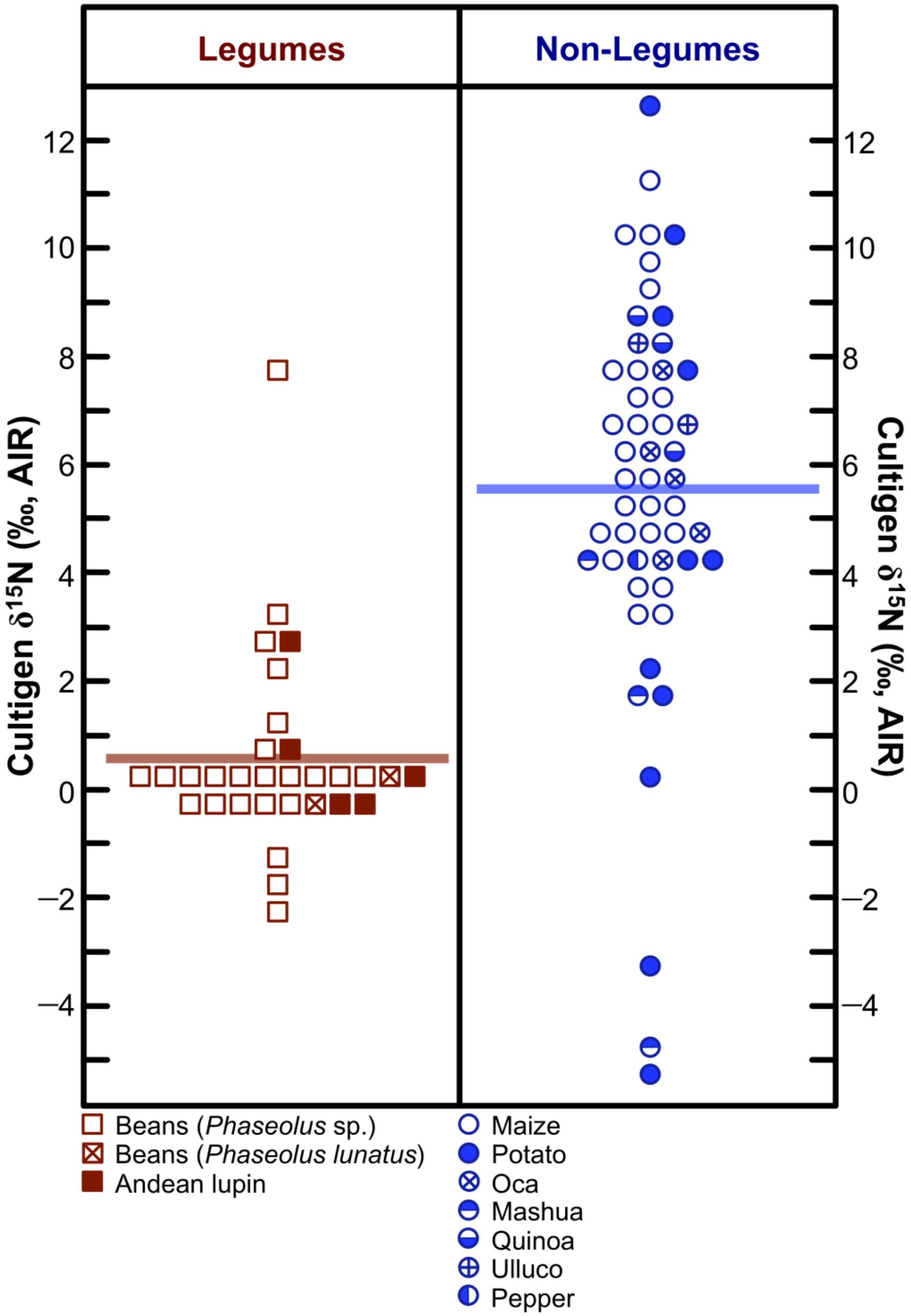

Figure 2.6. Dot-matrix plot of nitrogen isotopic compositions of legumes and non-legumes. Horizontal bars represent means. Increment = 0.5‰.

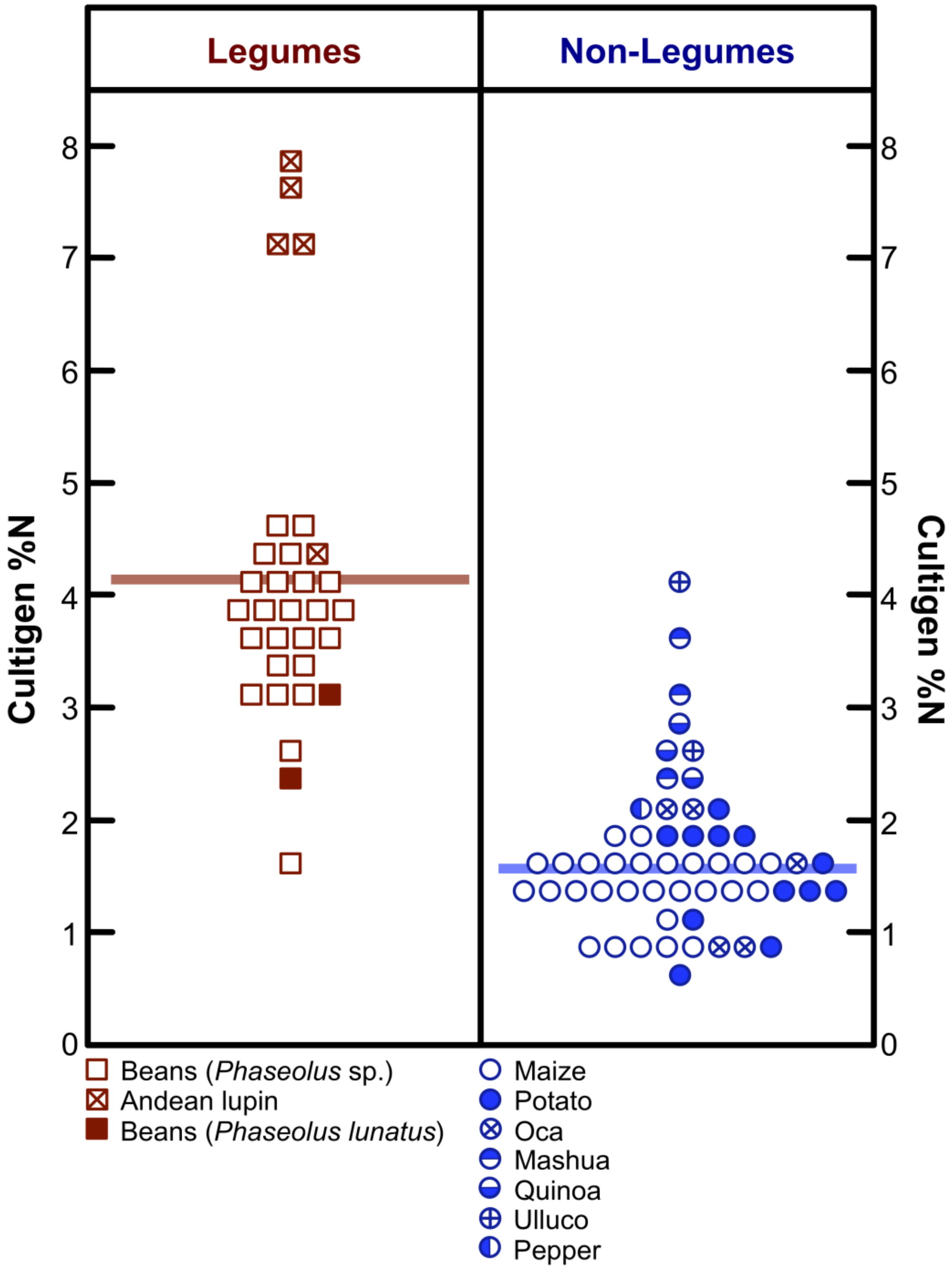

Figure 2.7. Dot-matrix plot of nitrogen content of legumes and non-legumes. Horizontal bars represent means. Increment = 0.25%.

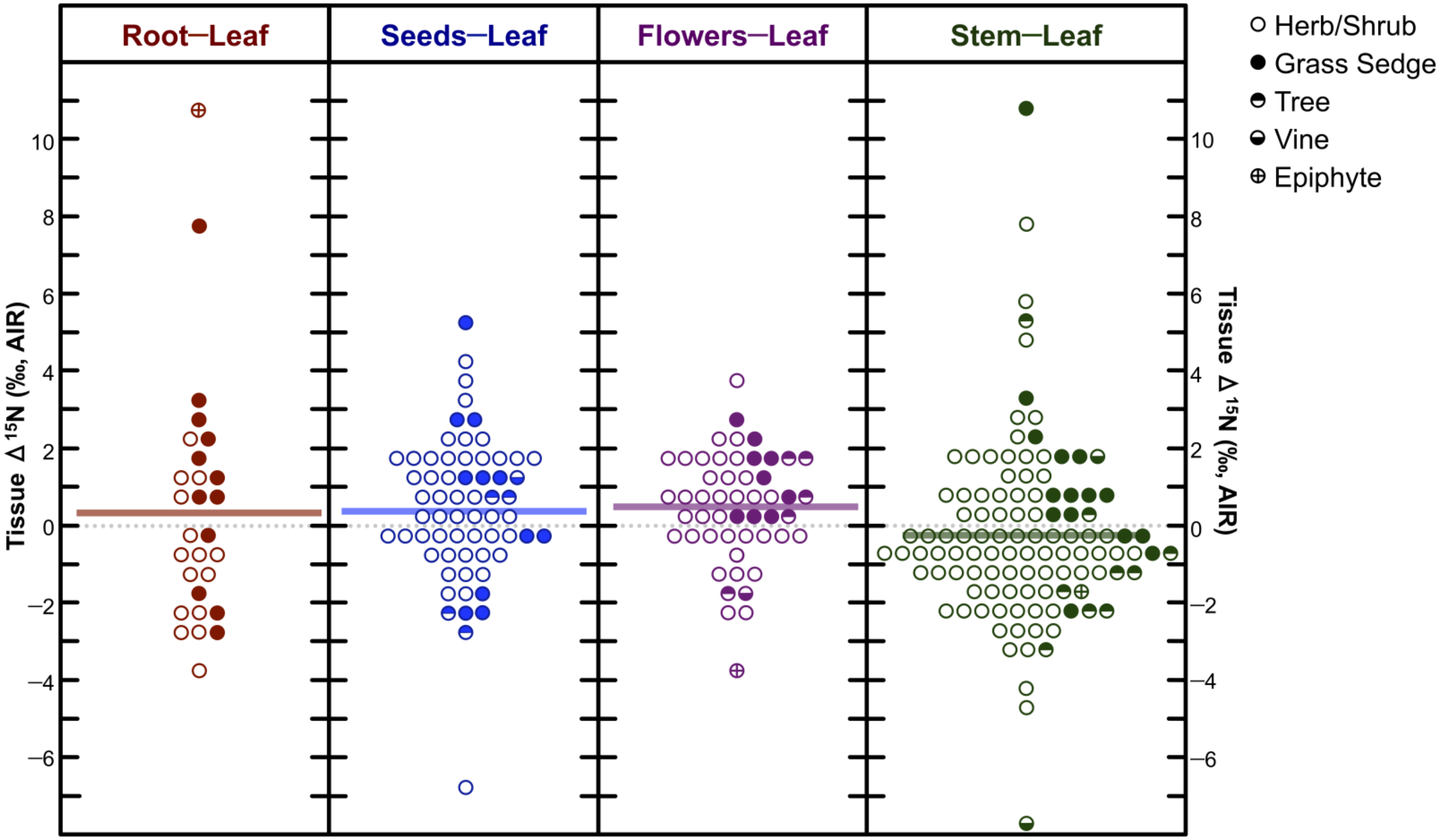

Figure 2.8. Dot-matrix plot of differences in nitrogen isotopic composition between foliar and other tissues ($\Delta^{15}N$). Horizontal bars represent means. Increment = 0.5‰.

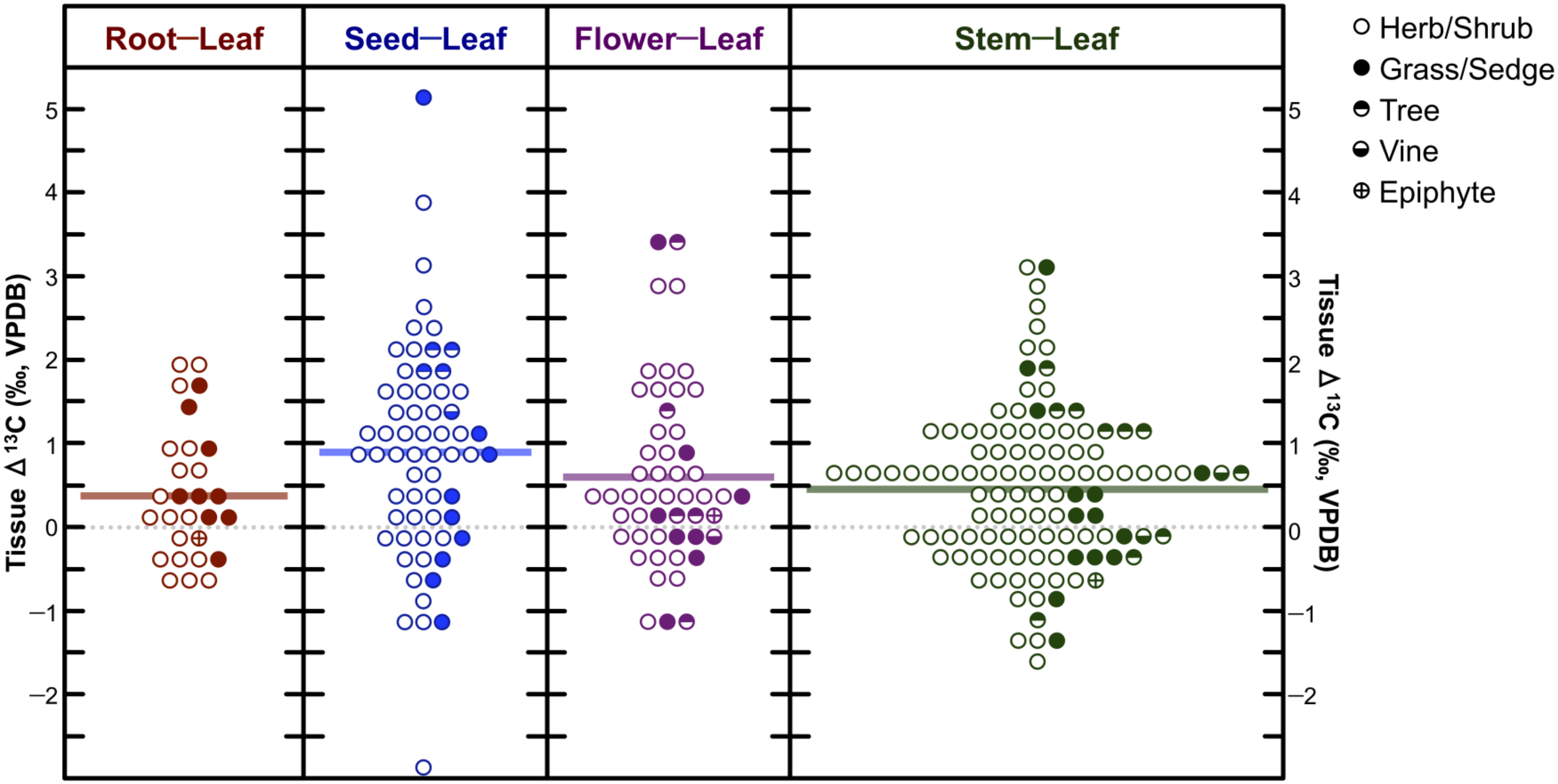

Figure 2.9. Dot-matrix plot of differences in nitrogen isotopic composition between foliar and other tissues ($\Delta^{13}C$). Horizontal bars represent means. Increment = 0.5‰.

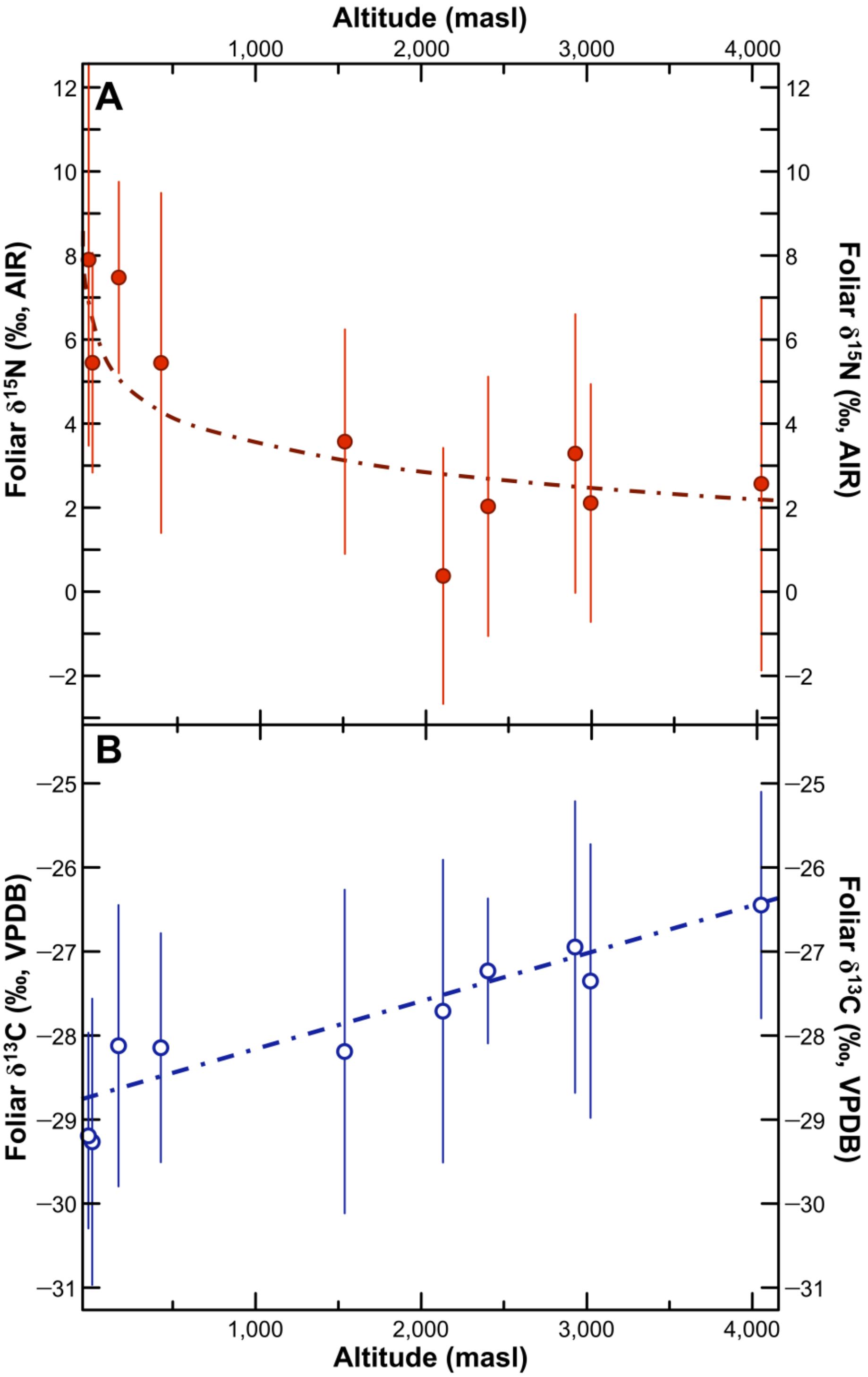

Figure 2.10. Bivariate plots of foliar δ^{15}N and altitude (A) and foliar δ^{13}C (B) for C_3 plants only. Points represent means ± 1σ for sites with ≥5 C_3 plant species sampled. Equation for δ^{15}N and altitude: $y = 10.3 - \log x$, $r^2 = 0.71$; p=0.002. Equation for δ^{13}C and altitude: $y = x/1{,}733 - 28.8$, $r^2 = 0.85$; p<0.001.

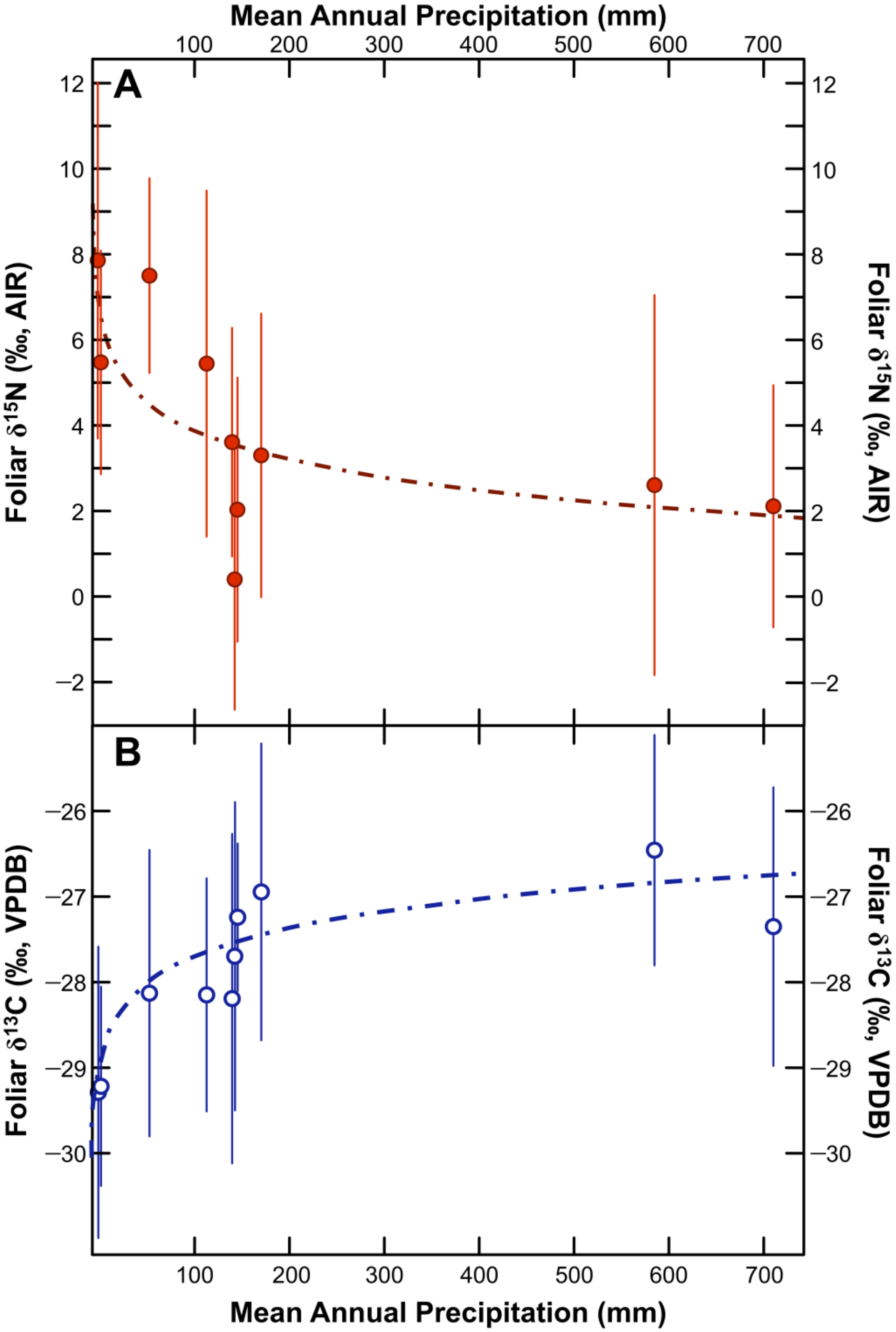

Figure 2.11. Bivariate plots of foliar δ^{15}N and mean annual precipitation (A) and foliar δ^{13}C (B) for C_3 plants only. Points represent means ± 1σ for sites with ≥5 C_3 plant species sampled. Equation for δ^{15}N and MAP: $y = 8.8 - 1.1 \log x$, $r^2 = 0.49$; $p=0.03$. Equation for δ^{13}C and MAP: $y = -30.1 + 0.5 \log x$, $r^2 = 0.81$; $p<0.001$.

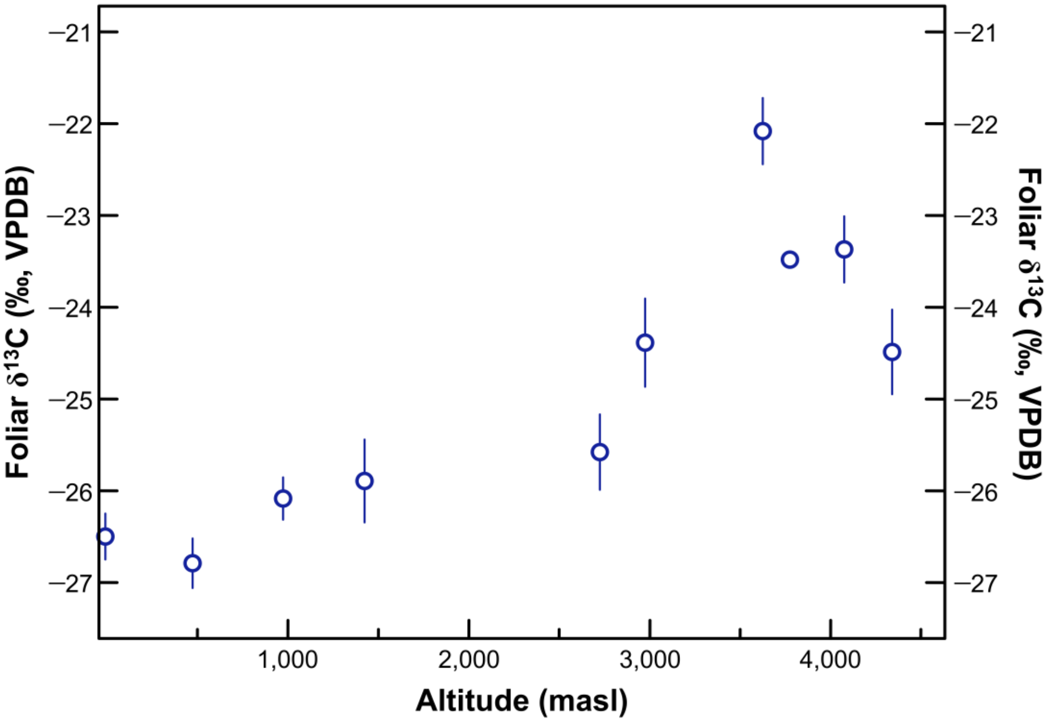

Figure 2.12. Bivariate plot of altitude and foliar δ^{13}C for plants collected in northern Chile (Tieszen and Chapman, 1992).

Chapter 3

3 Stable Isotope Biogeochemistry of Seabird Guano Fertilization: Results from Growth Chamber Studies with Maize (*Zea mays*)

Background: Stable isotope analysis is being utilized with increasing regularity to examine a wide range of issues (diet, habitat use, migration) in ecology, geology, archaeology, and related disciplines. A crucial component to these studies is a thorough understanding of the range and causes of baseline isotopic variation, which is relatively poorly understood for nitrogen ($\delta^{15}N$). Animal excrement is known to impact plant $\delta^{15}N$ values, but the effects of seabird guano have not been systematically studied from an agricultural or horticultural standpoint.

Methodology/Principal Findings: This paper presents isotopic ($\delta^{13}C$ and $\delta^{15}N$) and vital data for maize (*Zea mays)* fertilized with Peruvian seabird guano under controlled conditions. The level of ^{15}N enrichment in fertilized plants is very large, with $\delta^{15}N$ values ranging between 25.5 and 44.7‰ depending on the tissue and amount of fertilizer applied; comparatively, control plant $\delta^{15}N$ values ranged between −0.3 and 5.7‰. Intraplant and temporal variability in $\delta^{15}N$ values were large, particularly for the guano-fertilized plants, which can be attributed to changes in the availability of guano-derived N over time, and the reliance of stored vs. absorbed N. Plant $\delta^{13}C$ values were not significantly impacted by guano fertilization. High concentrations of seabird guano inhibited maize germination and maize growth. Moreover, high levels of seabird guano greatly impacted the N metabolism of the plants, resulting in significantly higher tissue N content, particularly in the stalk.

Conclusions/Significance: The results presented in this study demonstrate the very large impact of seabird guano on maize $\delta^{15}N$ values. The use of seabird guano as a fertilizer can thus be traced using stable isotope analysis in food chemistry applications (certification of organic inputs). Furthermore, the fertilization of maize with seabird guano creates an isotopic signature very similar to a high-trophic level marine resource, which must be considered when interpreting isotopic data from archaeological material.

3.1 Introduction

Seabird excrement (guano) was arguably the most economically significant organic fertilizer in the world prior to the twentieth century. The guano was mined from small, nearshore islands off the arid western coast of South America in the Peru-Humboldt upwelling region. The guano islands of Peru and Chile are typically composed of rocky cliffs essentially devoid of vascular plants, with a relatively small number of fauna (ants, spiders, scorpions, lizards) that are supported by allocthonous inputs from the guano birds (guano, carcasses, feathers, eggshells) (Duffy, 1994). Because the region receives virtually no precipitation, the guano accumulates in sedimentary layers. The once thick deposits of seabird guano (>50 m in some cases) were mined extensively during the guano boom of the 1800s, and today the islands rarely have more than several years worth of droppings accumulated (Duffy, 1994). The trade in guano peaked during the middle of the nineteenth century, with 20 million tons being exported to Europe and North America between 1848 and 1875 (Murphy, 1981). The popularity of guano with European and North American farmers waned in the latter part of the nineteenth century for a number of reasons, including: increasing guano prices, irregular availability, unsuitability for particular crops (especially turnips), a dwindling supply, and the development of the chemical fertilizer industry (Mathew, 1970). In recent years, however, there has been a resurgence in its popularity (particularly in horticulture) as worldwide demand for organically grown produce has increased (Romero, 2008; Zapata and Arrillaga, 2002). The importance of guano as a fertilizer prior to the nineteenth century is less well known, but is mentioned by Spanish chroniclers and in colonial administrative documents (Cieza de León, 1964; Garcilaso de la Vega, 1966). On this basis, some have suggested that it may have been of some importance in prehispanic agriculture (Julien, 1985; Nordt et al., 2004).

From an ecological perspective, the importance of ornithogenic nitrogen to marine and terrestrial ecosystems has long been recognized (Hutchinson, 1950; Ishizuka, 1966; Powell et al., 1991). A number of studies conducted in tropical, temperate, subpolar, and polar regions have shown that seabird guano alters the concentration of soil nutrients (particularly NH_4^+, NO_3^-, PO_4^{3-}, K^+, Mg^{2+}), plant tissue nutrients (N, P, K), and plant productivity (Anderson and Polis, 1999; Burger et al., 1978; Ellis, 2005; Engelskjøn, 1986; Leentvaar, 1967; McColl and Burger, 1976; Ryan and Watkins, 1989; Smith, 1978; Speir and Cowling, 1984). Seabird guano may also affect the diversity of plant species present, though results from such studies are inconsistent (Ellis, 2005). Numerous factors other than the presence of guano may also affect the chemistry, physiology, and ecology of plants growing within or near seabird colonies. In field studies it is often difficult, or impossible, to rule out the effects of these factors, which include: physical disturbance caused by birds such as plant clipping or trampling (Lindeboom, 1984; Vidal et al., 2003), deposition of seabird carcasses, feathers and eggshells (Siegfried et al., 1978; Williams and Berruti, 1978; Williams et al., 1978), and avian-aided seed dispersal (Gillham, 1956).

Particularly large ^{15}N enrichments in soils, plants, and animals (5−40‰) have been recorded in and around seabird nesting sites, allowing for the relative contribution of avian-derived nutrients to be assessed (Table 3.1)(Anderson and Polis, 1999; Barrett et al., 2005; Bokhorst et al., 2007; Cocks et al., 1998; Erskine et al., 1998; García et al., 2002; Harding et al., 2004; Hawke and Holdaway, 2005; Hawke and Newman, 2007; Hobara et al., 2005; Kameda et al., 2006; Kolb et al., 2010; Markwell and Daugherty, 2002; Mizota and Naikatin, 2007; Mizota, 2009a, 2009b; Mizutani et al., 1985b; Mizutani et al., 1986; Mizutani and Wada, 1988; Mizutani et al., 1991a; Schmidt et al., 2004; Stapp et al., 1999; Wainright et al., 1998; Wait et al., 2005; Young et al., 2010; Zhu et al., 2009). Despite this large body of literature, there have been no investigations that examine the biogeochemical effects of seabird guano on the western coast of South America, with the majority of studies focusing on Oceania, Japan, California, and Antarctica (Ellis, 2005). Furthermore, no studies have addressed the isotopic biogeochemistry of seabird guano from an agricultural or horticultural standpoint. The purpose of this study, therefore, is to assess the isotopic and vital effects of Peruvian seabird guano fertilization on maize (*Zea mays*) under controlled conditions. In particular we examine the extent of the enrichment in plant ^{15}N resulting from guano fertilization.

Plants are capable of utilizing several different soil N sources, both organic (amino acids) and inorganic (NH_4^+, NO_3^-, N_2). From a biogeochemical perspective, the uptake, assimilation, and allocation/reallocation of N compounds are all significant. Uptake of NO_3^- in plant root cells occurs through at least three different NO_3^- transport systems (Crawford and Glass, 1998). Once inside the root, NO_3^- can be assimilated into organic N, or translocated to the shoot for assimilation by nitrate reductase (NR), nitrite reductase (NiR), and glutamine synthetase (GS) (Andrews, 1986). Little or no fractionation of ^{15}N is reported to be associated with the uptake of NO_3^- (Mariotti et al., 1980; Yoneyama and Kaneko, 1989; Yoneyama et al., 2003); fractionation of ^{15}N does not appear to vary with respect to source $[NO_3^-]$ (Ariz et al., 2011; Flores-Delgadillo et al., 2011; Yoneyama et al., 2001). Some variability in fractionation is associated with NR activity, and it has been difficult in some cases to differentiate between isotopic fractionation associated with N uptake and assimilation, respectively (Pritchard and Guy, 2005). Ledgard et al. (1985) report the fractionation for the entire process to be −15‰, while a range of 0 to −19‰ is reported by Robinson (2001).

NH_4^+ is taken up by plants via high or low affinity transporters depending on extracellular $[NH_4^+]$ (Glass et al., 2001). NH_4^+ is assimilated into organic N only in the roots via GS and most estimated $\Delta^{15}N$ values for NH_4^+ uptake and assimilation fall between −5 and −20‰ (Robinson, 2001; Yoneyama et al., 1993a). Unlike NO_3^-, however, there are substantial differences in $\Delta^{15}N$ with source $[NH_4^+]$. For example, in two different rice cultivars, Yoneyama et al. (2001) found $\Delta^{15}N$ for NH_4^+ uptake to be −6.1 to −12‰ at low source $[NH_4^+]$, and −13.4 to −28.9‰ at high source $[NH_4^+]$.

3.2 Materials and Methods

3.2.1 *Materials*

All plants were grown in a walk-in growth chamber at the Biotron Centre for Experimental Climate Change Research at the University of Western Ontario. The substrate utilized for all treatments was Pro-mix® for containers (75-85% sphagnum moss, 15-25% perlite and limestone). Peruvian seabird guano (Guano Company International, Cleveland, Ohio, United States) was obtained from an organic gardening outlet. The nitrogen content of the guano was reported to be 10% and determined to be 11.2 ± 0.2% based on five analyses of dried, powdered guano as described for plant samples below. The ‘Early Sunglow’ maize cultivar was used (*Zea mays* cv. Early Sunglow, Lot E1, 2010, Ferry Morse, Fulton, Kentucky, United States) for all experiments because it is a relatively small variety of maize that accommodated physical restrictions on plant height imposed by the growth chamber.

3.2.2 *Growth Chamber Conditions*

Growth chamber temperature was 25/18 ºC (day/night), with a photoperiod of 13 h provided by 185 W fluorescent bulbs. Relative humidity was set at 80% for the first four daylight hours, and 60% for the remainder of the day. These conditions were monitored electronically, and did not deviate from these parameters for the duration of the experiment.

3.2.3 *Maize Germination Experiment*

Guano (well-mixed with soil) was applied to 1.2 L plastic containers (1.0 L of soil) in the following amounts: 0 g, 1.0 g, 2.5 g, 5.0 g, 7.5 g, 10.0 g and 15.0 g. Six replicates of each treatment were prepared. One hour after addition of the guano, maize seeds were planted ~2.5 cm below the surface in the containers. Emergence and growth of the plants were recorded every 2-3 days for 35 days.

3.2.4 *Maize Fertilization Experiment*

Fifteen maize seeds were planted ~2.5 cm below the surface in 1.2 L plastic containers (1.0 L of soil). At this time, guano was mixed with soil in free-draining (perforated at the base) 18.9 L plastic buckets containing 16 L of soil in the following amounts: 0 (C0), 80 g (G1, 5g guano/L), 160 g (G2, 10 g guano/L). Five replicates of each treatment were prepared. Maize is typically fertilized prior to planting, and sometimes again approximately three weeks after emergence, although this second application is uncommon (Subedi and Ma, 2005). To avoid complications associated with additional fertilizer applications, only one fertilizer application was employed. After germination (7 days after sowing) maize plants were moved into the 18.9 L plastic buckets. Plants were watered every 2-3 days and the height and general growth of the plants was monitored. Distal leaf samples (~3cm × 6cm) were taken at 30 and 75 days after planting (d). Plants at 30 d were characterized by only vegetative growth, while plants sampled at 75 d had begun reproductive growth (tassels fully emerged, silks beginning to appear). Anthers were sampled at 75 d. At completion of the experiment (115 d), the following tissues were sampled: leaves, grains, roots, and stalks. All buckets were relocated randomly within the growth chamber five times (30, 45, 60, 75, 100 d) during the course of the experiments to account for any micro-variations in light, temperature or humidity, although such changes were not expected.

3.2.5 *Stable Isotope Analysis*

All plant materials were stored at −25ºC following sampling until needed for analysis. Samples were then dried at 90ºC under normal atmosphere for 72 hours, ground using a Wig-L-Bug (Crescent, Lyons, Illinois, United States) and the resulting powders stored at room temperature in sealed glass vials. Isotopic compositions (δ^{13}C and δ^{15}N values determined separately) and relative percentages of carbon and nitrogen were determined using a Delta V isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany) coupled to an elemental analyzer (Costech Analytical Technologies, Valencia, California, United States). For the analysis of δ^{15}N, excess CO_2 was removed using a Carbo-Sorb trap (Elemental Microanalysis, Okehampton, Devon, United Kingdom). Sample reproducibility was ±0.09‰ for δ^{13}C and ±0.90% for %C (6 replicates), and ±0.12‰ for δ^{15}N and ±0.10% for %N (24 replicates). A δ^{15}N value of 20.31±0.18‰ was obtained for 37 analyses of IAEA-N2, which compared well with its accepted value of 20.30‰. A δ^{13}C value of −29.87±0.29‰ was obtained for 11 analyses of NBS-22, which compared well with its accepted value of −30.00‰.

3.2.6 *Statistical Analyses*

Comparisons between treatments and between organs were completed using one-way analysis of variance (ANOVA). Levene’s test was used to assess homogeneity of variance; if variance was homoscedastic, a *post hoc* Tukey’s honestly significant difference (HSD) test was applied and if variance was not homoscedastic, a *post hoc* Dunnett’s T3 test was applied. All statistical analyses were conducted at a significance level of 5% ($p<0.05$). All statistical analyses were performed in SPSS 16 for Windows.

3.3 Results and Discussion

3.3.1 *Maize Germination and Seedling Establishment*

All unfertilized plants germinated and commenced normal growth (Figure 3.1). There was a clear trend towards the inhibition of germination and seedling emergence with increasing rate of guano applied (Figure 3.1). It is apparent that the presence of seabird guano in the soil has the potential to inhibit germination and that this effect is concentration dependent. Ishida (1997) found lower germination rates in oak and pine trees within, compared to outside of, cormorant colonies but did not offer a detailed explanation for this pattern. Mulder and Keall (2001) also found that seabird guano negatively affected seed germination and seedling survival. Germination inhibition with increasing concentrations of guano probably results from a number of factors, including reduced soil pH and the presence of a high concentration of soluble salts, both of which are characteristic of ornithogenic soils (Speir and Cowling, 1984). Very high concentrations of NO_3^- and especially NH_4^+ are also characteristic of ornithogenic soils and these characteristics can inhibit maize germination (Bremner and Krogmeier, 1989), with the early stages of growth being the most detrimental for plants under NH_4^+ stress (Roosta and Schjoerring, 2007; Schortemeyer et al., 1997).

3.3.2 *Vital Effects of Guano Fertilization*

Plant growth was strongly inhibited in the heavy guano treatment (G2). Maximum plant heights were significantly lower in G2 compared to C0 (p=0.02) and G1 (p=0.008) (Figure 3.2). While the G1 plants did not attain greater maximum heights than the C0 plants (p=0.83), they yielded significantly more grain (p=0.004). The G2 plants yielded less grain than the G1 plants (p=0.03) and more grain than the C0 plants, although this difference was not statistically significant (p=0.42) (Figure 3.2).

In this study, we observed a positive influence of guano on maize growth at moderate concentrations (G1), but a negative influence at high concentrations (G2). A number of studies have found that plant abundance and/or species richness tends to be lower within seabird colonies, but is often higher in areas in relatively close proximity to the colonies (Ryan and Watkins, 1989; Vidal et al., 2003; Weseloh and Brown, 1971; Wootton, 1991).

Very high levels of soil P can have deleterious effects on plant growth (Clarkson and Scattergood, 1982). Ornithogenic soils may contain fifty times more available phosphorous than normal, but the P salts in bird excrement tend to be immobile in soil because of their limited solubility, making them generally unavailable for uptake by plants (García et al., 2002; Ligeza and Smal, 2003; Zapata and Arrillaga, 2002). It is thus unlikely that the reduced growth observed in the G2 plants is the result of P toxicity. The most likely cause for the reduced growth of the G2 plants is NH_4^+ toxicity.

Very high [NH_4^+] is a ubiquitous trait of ornithogenic soils (Mizota, 2009b; Mizutani et al., 1986; Schmidt et al., 2004; Wait et al., 2005; Young et al., 2011). High soil NH_4^+ can negatively impact plants in several ways: (1) soil acidification, particularly of the rhizosphere (Raven and Smith, 1976), 'scorching' of root hairs (Schortemeyer et al., 1997); (2) accumulation of free NH_4^+ in plant tissues, which has the capacity to uncouple plastid energy gradients (Schortemeyer et al., 1997); (3) assimilation of NH_4^+ in the roots and associated translocation of carbon skeletons from the shoot, which is metabolically expensive and places 'carbon stress' on roots (Deignan and Lewis, 1988); (4) suppression of the expression of certain proteins (aquaporins), which can have detrimental effects on the uptake of water (Guo et al., 2007); and (5) the influx and efflux of NH_4^+ through root cells, which is associated with a very high metabolic cost when source [NH_4^+] is high (Britto et al., 2001).

Both the G1 and G2 plants exhibited significantly reduced growth compared to the control plants for the first 45 days of the experiment (Figure 3.2; p=0.01), but this trend did not continue as the G1 plants produced the greatest yields, and had similar maximum heights to the control plants. This is likely the result of initially very high soil [NH_4^+], which negatively impacted the growth of the fertilized plants, followed by increased soil NO_3^- resulting from nitrification of guano-derived NH_4^+. When plants largely supplied with NH_4^+ as an N source are supplemented with NO_3^-, NH_4^+ uptake is suppressed and plants are able to resume normal growth (Deignan and Lewis, 1988). The fact that the G2 plants still produced grain even though they were characterized by reduced heights and less above−ground biomass than either the control or G1 plants suggests that there was some acclimatization of these plants to the high [NH_4^+], and/or nitrification was substantially delayed and [NH_4^+] remained high in the soil for a much longer period of time. Schortemeyer et al. (1997) observed a similar result in maize plants grown with NH_4^+ as the sole N source.

The effects of guano on plants are difficult to generalize. There is considerable variability at the community level and also within a community in accordance with plant physiology (nutrient demands, salt tolerance) at the species level (Wootton, 1991; Young et al., 2011). Even within maize there are differences in NH_4^+ tolerance, with some varieties being able to survive higher concentrations than others (Schortemeyer et al., 1997). Therefore, it cannot be assumed that the results of this study are directly applicable to all maize varieties.

3.3.3 *Nitrogen Isotopic Composition of Seabird Guano*

Most inorganic N fertilizers have $\delta^{15}N$ values close to 0‰, with organic fertilizers generally having highly variable but positive $\delta^{15}N$ values (Table 3.2) (Bateman et al., 2005; Bateman and Kelly, 2007; Choi et al., 2002; Choi and Ro, 2003; Choi et al., 2003; Dijkstra et al., 2006; Kerley and Jarvis, 1996; Lim et al., 2007; Rapisarda et al., 2010; Rogers, 2008; Steele and Daniel, 1978; Yun et al., 2006). The $\delta^{15}N$ value of the seabird guano used in this experiment was 26.7±0.6‰ (5 analyses), which is much higher than any other organic fertilizer analyzed to date. This is the product of avian nitrogen metabolism and excretion, which is quite different than in mammals, combined with the high trophic position of the guano-producing birds. Guano contains 9−21% nitrogen, which is composed primarily of uric acid (~80%), with smaller amounts of protein (~10%), ammonia (~7%), and nitrate (~0.5%) (Gaskell and Smith, 2007; Gillham, 1960; Hartz and Johnstone, 2006; Lindeboom, 1984; McNabb et al., 1980; Mizutani and Wada, 1985; Mizutani et al., 1991b; Staunton Smith and Johnson, 1995). In addition, guano contains ~4% phosphorous (~50% of which is PO_4^{3-}) and 2% potassium (Hadas and Rosenberg, 1992; Hartz and Johnstone, 2006; Staunton Smith and Johnson, 1995).

A simplified pathway for guano nitrogen, with associated nitrogen-isotope fractionation factors, is shown in Figure 3.3 (2008; Evans et al., 1996; Feigin et al., 1974; Hobson and Clark, 1992; Hobson, 1995; Hoch et al., 1992; Kirshenbaum et al., 1947; Ledgard et al., 1985; Mariotti et al., 1982; Miller and Cramer, 2005; 1985a; 1985b; Mizutani et al., 1986; Robinson, 2001; Shearer and Kohl, 1986; Tcherkez and Farquhar, 2006; 1998; Yoneyama et al., 1991; Yoneyama et al., 1993a; Yoneyama et al., 1998; Yoneyama et al., 2001). The principal producers of guano on the western coast of South America are the Peruvian booby (*Sula variegata*), brown pelican (*Pelecanus occidentalis thagus*), and guanay cormorant (*Phalacrocorax bougainvilli*) (Duffy, 1994; Hutchinson, 1950). These birds, and similar species, feed at high trophic levels, and typically have tissue δ^{15}N values in the range of 17 to 20‰ (Forero et al., 2004; Schoeninger and DeNiro, 1984; Szpak et al., 2009), suggesting a $\delta^{15}N_{diet}$ of 14 to 18‰ assuming a diet−tissue fractionation of 3−4‰ for δ^{15}N (Szpak et al., 2012c). Thus, the high trophic level of the birds only partially explains the very high $\delta^{15}N_{bulk\ guano}$ of 26.7‰.

After deposition in the soil, the uric acid in guano is rapidly mineralized to NH_4^+, and this process occurs much more rapidly in the presence of water (Hadas and Rosenberg, 1992; Kirchmann, 1991; Loder et al., 1996). Based on results presented by Mizutani and Wada (1985), uric acid quickly decomposed (75% in ten days) in soil, but the δ^{15}N value of the remaining uric acid was unchanged. A very large isotopic fractionation (−40 to −60‰) occurs during NH_3 volatilization, leaving the remaining soil NH_4^+ highly enriched in ^{15}N (Mizutani et al., 1985b; Robinson, 2001). Ammonia volatilization is largely responsible for the high δ^{15}N values in ornithogenic soils and in some cases, seabird guano (Table 3.1). The relatively high δ^{15}N value of the guano utilized in this study suggests that some of the NH_4^+ in the guano had been subject to volatilization prior to deposition in the soil during the experiment; similar observations have been made concerning other avian manures (Burger and Venterea, 2008).

3.3.4 ^{15}N Enrichment in Guano Fertilized Plants

Plant isotopic compositions are summarized in Table 3.3; raw data are presented in Table 3.4. Plant organs of fertilized plants (G1, G2) sampled at 115 d were significantly enriched in ^{15}N compared to control plants in every case (Table 3.3, Table 3.5, Figure 3.4).

Also, the δ^{15}N values of plant tissues were significantly higher for heavily fertilized (G2) versus more lightly fertilized (G1) plants (Table 3.5). The difference in mean δ^{15}N values between the G1 and G2 plant organs was fairly consistent: 6.2‰ for stalks and roots, 6.4‰ for leaves (at 115 d), 7.6‰ for grain, and 7.8‰ for anthers.

A growing body of literature has emerged in recent years demonstrating that organic fertilizers, specifically those derived from animal waste, can cause large ^{15}N enrichments of plant tissues (Table 3.6) (Choi et al., 2002; Choi et al., 2003; del Amor et al., 2008; Lim et al., 2007; Nakano and Uehara, 2007; Rapisarda et al., 2010; Yun et al., 2006). The δ^{15}N values reported here for plants grown in guano-fertilized soils are significantly higher than any published δ^{15}N values for plants grown on other organic fertilizers to date (Table 3.6), but comparable to δ^{15}N values for plants growing in ornithogenic soils (Table 3.1). The higher δ^{15}N values in the G1 and G2 compared to the C0 plants is the result of the uptake of ^{15}N-enriched guano-derived nitrogen. Moreover, the significantly higher tissue δ^{15}N values in the G2 compared to G1 plants reflects, at least in part, the greater availability of guano-derived nitrogen throughout the course of the experiment. This does not imply that guano-derived N was absent in the G1 treatment towards the end of the experiment, but it is possible that N immobilization had overtaken N mineralization, reducing the amount of guano-derived N available to the plants.

3.3.5 Elemental Concentration in Plant Parts

There were significant differences in N content between fertilized and control plants, with fertilized plants tending to have significantly higher N (Table 3.5). There were no significant differences in C content between control and fertilized plants for all organs, with the exception of the stalks, which had significantly lower %C in the fertilized plants compared to the control, and in G2 compared to G1 plants.

In general, the differences in C and N content between fertilized and unfertilized plants can be attributed to the accumulation of proteins, particularly those related to the GS-GOGAT pathway, that assimilate NH_4^+ and amino acids. Free amino acids tend to accumulate unabated in plant tissues with increasing supply of N irrespective of source, although different amino acids may accumulate at different rates depending on plant species and N source (Näsholm and Ericsson, 1990; Okano et al., 1997; Roosta and Schjoerring, 2007; Ruan et al., 2007; Warren and Adams, 2000). Moreover, many studies have noted an increase in proteins, such as GS, in plant tissue in accordance with increasing NH_4^+ supply (Garnica et al., 2010; Ruan et al., 2007). Thus, the relatively high N content of the organs of fertilized plants likely reflects the accumulation of these N compounds.

The two amino acids that dominate the free amino acid pool when plants are supplied with excess N are glutamine and arginine (Okano et al., 1997; Ruan et al., 2010). Arginine, which has a very low C:N ratio (6:4), has been implicated as an important product for the accumulation of excess N, possibly as a buffering mechanism against NH_4^+ toxicity (Potel et al., 2009; Roosta and Schjoerring, 2007; Smolders et al., 1996). Again, the accumulation of high levels of arginine in NH_4^+-fed plants fits with the pattern observed in the G1, and particularly the G2 plants. The very high levels of N and low levels of C in the stalks of the fertilized plants (compared to the control) suggests that the stalk was the most important accumulator for metabolites produced from excess N.

A notable exception to the pattern of increased N with fertilization is the grain, for which there was no significant difference in N content between treatments (Table 3.5). Our results suggest that at different levels of N supply and plant N content, there was no preferential allocation of accumulated N to the grain, and N that was absorbed post-silking was probably not allocated to the grain. A similar pattern was observed by Ma and Dwyer (1998), although it is important to bear in mind the variability among maize hybrids in N metabolism during grain filling (Rajcan and Tollenaar, 1999).

As plants progress through various stages of growth, their uptake, metabolism and partitioning of N may change dramatically. In maize, a significant portion (45−65%) of the grain N is obtained from endogenous N reallocated primarily from the stalk and leaves, while the remaining grain N is obtained from uptake of exogenous soil N (Below et al., 1981; Gallais and Coque, 2005; Gallais et al., 2006; Tsai et al., 1980). Leaf N content at 75 d and 115 d varied as a function of the amount of guano applied (ie. C < G1 ≤ G2), although this was not the case for leaves sampled at 30 d, where there was no clear relationship between quantity of fertilizer applied and leaf N content (Figure 3.5a). This likely reflects both a reliance on stored seed N early in growth, and the short period of growth prior to transplanting (7 d) during which no fertilizer N was available.

We observed decreases in leaf N content over time, with leaf N content decreasing by 77.9% (C0), 46.9% (G1) and 47.1% (G2) between 30 and 115 d (Figure 3.5a). The maintenance of very high levels of N in G1 and G2 relative to C0 plants suggests the accumulation of plant N as a result of excess source N (Binford et al., 1990).

Based on the results of this study, seabird guano fertilization has the potential to significantly alter the C and N economy of maize plants. Specifically, fertilization results in increased N and decreased C:N ratio in plant tissues, which likely arises because of increased accumulation of N-rich metabolites such as arginine, glutamine, and proteins related to NH_4^+ metabolism.

3.3.6 *Intraplant Variation in $\delta^{15}N$*

Intraplant variability in nitrogen isotopic composition for all treatments was large, with maximum differences between mean organ $\delta^{15}N$ being 3.0‰ for C0, 12.9‰ for G1 and 11.4‰ for G2 (Figure 3.4). We found significant differences in the $\delta^{15}N$ values between maize plant organs for both control ($F_{[4,20]}=7.41$, $p<0.001$) and fertilized ($F_{[4,20]}=18.60$, $p<0.001$ for G1; $F_{[4,20]}=28.73$, $p<0.001$ for G2) treatments (Figure 3.4). In all treatments, the grain possessed the lowest $\delta^{15}N$ value, while anthers had the highest $\delta^{15}N$ values in the control treatment and the second-highest $\delta^{15}N$ values in the fertilized treatments, following stalks (Figure 3.4).

Significant variability in $\delta^{15}N$ within plants has been recorded in several studies (Dijkstra et al., 2003; Evans et al., 1996; Hobbie et al., 2000; Högberg et al., 1996; Högberg et al., 1999; Kolb and Evans, 2002; Yoneyama and Kaneko, 1989; Yoneyama et al., 1991). Evans (2001) suggests that, in general, plants with NO_3^- as the primary N source are characterized by significant intraplant variability, while this is not true for plants with NH_4^+ as their primary N source. This general pattern results largely from the fact that NH_4^+ is assimilated into organic N only in the root, while NO_3^- assimilation occurs both in roots and shoots (Figure 3.3B) (Lewis et al., 1989; Murphy and Lewis, 1987; Raven and Smith, 1976). Therefore, organics derived from NH_4^+ are assimilated from the same N pool in the roots, while NO_3^- that has been translocated to the shoot prior to assimilation has already undergone some fractionation (in the roots) and is thus enriched in ^{15}N (Evans et al., 1996; Evans, 2001; Yoneyama and Kaneko, 1989).

The $\delta^{15}N$ values of the roots were intermediate compared to other above-ground tissues, which does not fit with the scenario described above for NO_3^- fed plants in which shoot tissues have higher $\delta^{15}N$ values than roots. In the C0 and G1 plants, the roots did not differ significantly from stalks, grains, or leaves in terms of $\delta^{15}N$ (Table 3.7). In the G2 plants, root $\delta^{15}N$ was significantly lower relative to the stalk, but significantly higher than the leaf or grain (Table 3.7). The lack of a consistent pattern of root vs. shoot $\delta^{15}N$ observed in this study likely reflects complex N metabolism, with relative reliance on NH_4^+ and NO_3^-, as well as guano-derived N changing over time.

The relatively low grain $\delta^{15}N$ values observed in this study are indicative of the reallocation of stored N. Choi et al. (2002) also observed that grain tended to be depleted of ^{15}N compared to stalks and leaves. This can be attributed to a kinetic isotope effect associated with catabolism and remobilization of stored plant N, which discriminates against ^{15}N (Tcherkez, 2011). The high $\delta^{15}N$ values of stalks suggest that this organ is an important source of accumulated N that is remobilized during grain filling. This supports the findings of Ta (1991), who found that maize stalks functioned as a significant temporary storage reservoir for N-compounds. It is surprising that the leaves at 115 d are not characterized by higher $\delta^{15}N$ values in comparison to the grain, as they are thought to be a significant contributor to grain N (Beauchamp et al., 1976; Donnison et al., 2007); this is discussed in more detail below. The importance of stalk, compared to leaf, N during grain filling may be specific to this variety of maize. Further study of the nitrogen metabolism of different maize hybrids is needed to clarify this issue.

3.3.7 *Temporal Variation in Plant δ^{15}N Values*

There was significant variability in maize leaves over the course of the experiment (Figure 3.5B). Maize leaves sampled at 115 d had lower δ15N values than those sampled at 75 d for all treatments; these differences were statistically significant for the fertilized groups, but not for the control group (Table 3.5). For all treatments, leaf δ^{15}N values were significantly lower at 30 d compared to 75 d (Table 3.5).

Several studies have attempted to document changes in plant δ^{15}N values over time and/or arising from natural leaf senescence. Kolb and Evans (2002) and Garten (1993) found no significant differences in the δ^{15}N values of living and abscised leaves, which suggested a lack of ^{15}N discrimination with N remobilization. Conversely, several other studies have found older or senescent plant leaves to be characterized by higher δ^{15}N values, which has been attributed to a kinetic isotopic fractionation associated with N catabolism and reallocation (Choi et al., 2005a; Gebauer et al., 1994; Näsholm, 1994). We observed no significant difference between leaf δ^{15}N at 75 d and 115 d for the control group, suggesting that under normal circumstances, there is no significant fractionation associated with N remobilization from leaves for this variety of maize. That there was a concurrent decrease in N content and δ^{15}N for leaves between 75 and 115 d in the fertilized plants is counterintuitive, as the reallocation of leaf N to the grain should result in a ^{15}N-enriched leaf. As was previously suggested for the stalk, we suspect that a significant portion of the leaf N pool consisted of accumulated N in the form of free amino acids (especially arginine and glutamine) as a result of high N supply and, in particular, high source [NH_4^+]. The reason that older or senescent plant parts are characterized by higher δ^{15}N values is because the metabolic processes involved (e.g. deamination, transamination) are associated with large kinetic fractionations that concentrate the remaining substrate in ^{15}N (Högberg, 1997). Therefore, if the majority of the decrease in leaf N between 75 and 115 d is the result of the transfer of organic N products (amino acids) to another part in the plant (e.g. the stalk), which is not associated with any known ^{15}N fractionation (Robinson et al., 1998), this would help to explain why the leaves are not relatively enriched in ^{15}N at 115 compared to 75 d.

Leaf δ^{15}N values were more variable at 30 d than at either 75 or 115 d (Figure 3.5c). This is likely a result of variable reliance on stored and absorbed N sources. Kolb and Evans (2002) found that young leaves (*Quercus* and *Encelia*) had an isotopic composition (δ^{15}N) that reflected both stored and absorbed N, while mature leaf δ^{15}N values reflected primarily absorbed N. Very low leaf δ^{15}N values (−12.4, −12.4, −10.2‰) were observed at 30 d for three of the guano-fertilized maize plants. These compositions probably arise from physiological responses to high soil [NH_4^+]. At high extracellular [NH_4^+], influx of NH_4^+ occurs only via a low-affinity transport system, with high-affinity transport system proteins being down-regulated; this process occurs in concert with the active efflux of NH_4^+ from the roots (Ariz et al., 2011). Yoneyama et al. (2001) suggest that when NH_4^+ assimilation is slow (because extracellular [NH_4^+] is high), NH_4^+-N isotopic fractionation is larger, with relatively more ^{15}N-enriched NH_4^+ being effluxed from the cell. Ariz et al. (2011) found plants that were most sensitive to NH_4^+ toxicity also had the lowest tissue δ^{15}N values. The fact that not all plants in the present study were characterized by low leaf δ^{15}N values is difficult to explain, but may be the result of heterogeneous distribution of the guano throughout the soil or genotypic variability in resilience to NH_4^+ toxicity.

Temporal patterns in plant δ^{15}N values are complicated and are determined by a number of factors. We suspect that significant changes in the N source occurred over time as a result of soil nitrification, and there were also significant changes in [source N] over time. This complication, however, is a reality of working with animal fertilizers, rather than hydroponic solutions, and must be taken into account when interpreting data from field settings.

3.3.8 *Guano Fertilization and Plant Carbon Isotopic Composition*

We observed no difference in plant δ^{13}C values resulting from guano fertilization for any of the organs analyzed (Table 3.5). In earlier studies, variable plant N sources have been associated with small, but significant variations in $\delta^{13}C$ values (Yin and Raven, 1998). It is thought that this association arises because different N sources (and different N source concentrations) may alter plant water-use efficiency and thus change the carbon isotope composition of plant tissues (Raven et al., 1992).

Previous studies have found plant $\delta^{13}C$ values to be distinct in organic vs. inorganic fertilization regimens, an outcome ascribed to higher rates of soil microbiological activity (Camin et al., 2011; Georgi et al., 2005). Specifically, Georgi et al. (2005) suggest that CO_2 released during decomposition is depleted of ^{13}C. Because control and fertilized plants were grown in the same growth chamber, there would be no differences in the $\delta^{13}C$ of CO_2 utilized by either group of plants, although this may not be true for an agricultural field fertilized with guano. In general, the influence of nitrogenous fertilizers (both organic and inorganic) on plant $\delta^{13}C$ is unclear. Experimental results have been conflicting, with studies finding $\delta^{13}C$ values to increase (Cabrera-Bosquet et al., 2007; Iqbal et al., 2005; Jenkinson et al., 1995; Kondo et al., 2004; Serret et al., 2008; Zhao et al., 2007), decrease (Shangguan et al., 2000), or be unaffected (Clay et al., 2001; Jenkinson et al., 1995) in response to N fertilization. The relationship between N fertilizer application and plant $\delta^{13}C$ is likely mediated by several factors and warrants further study. We likely did not detect any difference in plant $\delta^{13}C$ values resulting from fertilization because the magnitude of difference would be quite small (Yin and Raven, 1998) and our sample size was also quite small (n=5 per treatment).

3.3.9 *Implications for Food Chemistry*

Seabird guano is becoming increasingly popular as an organic alternative among farmers in the United States and Europe (Romero, 2008). Moreover, as the demand for organically grown produce soars worldwide (Winter and Davis, 2006), there is an increased incentive for farmers in areas in close proximity to guano deposits (e.g. Peru, Ecuador, Chile, and Namibia) to use this fertilizer and market their produce as organic (Romero, 2008). In recent years, there has been a surge in isotopic research directed at demonstrating isotopic distinctions between conventional and organically grown produce (Bateman et al., 2005; Bateman et al., 2007; Camin et al., 2007; Flores et al., 2007; Flores et al., 2011; Rapisarda et al., 2005; Rapisarda et al., 2010; Rogers, 2008; Schmidt et al., 2005a; Šturm et al., 2011; Šturm and Lojen, 2011). The reason that this technique may sometimes be effective is primarily that inorganic fertilizers tend to have $\delta^{15}N$ values close to 0‰, while organic fertilizers tend to have higher $\delta^{15}N$ values, although there is great variability (Table 3.2). Based on the results of this study, the application of seabird guano in an organic fertilization regime would result in a very large ^{15}N enrichment of all plant tissues in comparison to unfertilized plants, or to plants treated with chemical fertilizers. The magnitude of this difference is much greater than what has been observed for other organic fertilizers (Table 3.6), and thus isotopic data would be useful in verifying use of seabird guano. Moreover, the very high $\delta^{15}N$ value of the guano itself suggests that its presence in mixed organic fertilizers should also be detectable via isotope ratio mass spectrometry.

3.3.10 *Implications for Archaeology*

Stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$ in particular) plays an increasingly important role in the reconstruction of prehistoric diet. Dietary reconstruction requires a thorough understanding of the sources of isotopic variation in the foods that were consumed (Schwarcz, 1991). Recently, the notion that animal manure may have influenced the $\delta^{15}N$ values of plants grown in prehistoric Europe has been proposed (Bogaard et al., 2007; Commisso and Nelson, 2007; Fraser et al., 2011) and integrated into regional paleodietary studies. In the Andean region, several fertilizers are thought to have been of some importance in prehispanic agriculture including llama dung (Chepstow-Lusty, 2011) and seabird guano (Julien, 1985; Kubler, 1948; Netherly, 1977). Based on the large settlements that developed on the coast of Peru (e.g. Moche, Chimú) and the relative infertility of local soils, Nordt et al. (2004) have suggested that the application of some kind of nitrogenous fertilizer, possibly seabird guano, would have been necessary to maintain agricultural productivity in at least some parts of the region. Direct evidence for fertilization, however, is very difficult to come by. One of the primary goals of this study was to determine whether or not the enrichment in ^{15}N resulting from guano fertilization would be sufficient to detect this agricultural practice in the isotopic composition of a human or animal consuming the fertilized plant. Based on the results of this study and others that have examined the biogeochemistry of seabird-associated sites (summarized in Table 3.1), the application of seabird guano to agricultural fields would have caused a significant increase in the δ^{15}N value of plants and of animals consuming these plants. In archaeological bone collagen from western South America, high δ^{15}N values are usually accompanied by high δ^{13}C values. This pattern applies to both humans (Knudson et al., 2007; Slovak and Paytan, 2011; Tomczak, 2003) and domestic animals (DeNiro, 1988), and has generally been attributed to the consumption of high trophic-level marine resources (e.g. predatory fish, marine mammals). Conversely, this pattern may also be caused by the consumption of maize (a C_4 plant) fertilized with seabird guano, which appears (isotopically) very much like a high-trophic level marine organism. As such, it is important to be mindful of the possibility of guano-fertilization when interpreting diet, not just on the coast, but in the interior highland region as well. According to ethnohistoric documents, guano was moved great distances and prized by groups living in the highlands as an essential component in maize agriculture (Julien, 1985).

The Andes were certainly not the only region in which seabird guano was used extensively as a fertilizer. Millions of tonnes of guano were exported to Europe and North America during the nineteenth century and Peruvian seabird guano was the most highly prized fertilizer at that time (Cordle, 2007; Cushman, 2003; Simmons, 2006). Isotopic analysis is being employed with increased frequency within the context of historical archaeology (Cox and Sealy, 1997; Cox et al., 2001; Katzenberg et al., 2000; Katzenberg, 1995; Klippel, 2001; Roy et al., 2005; Schroeder et al., 2009; Sealy et al., 1995; Valentin et al., 2006), a period during which the possible influence of seabird guano must also be considered.

Table 3.1. Summary of studies examining the effects of seabird guano on the isotopic composition ($\delta^{15}N$) of plants and soils.

Location	Bird Species	Guano $\delta^{15}N$ (‰, AIR)	Plant $\delta^{15}N$ (‰, AIR)		Soil $\delta^{15}N$ (‰, AIR)		Reference
			Bird	**Non-bird**	**Bird**	**Non-bird**	
California	Mixed	−	36.4±2.7	5.3±0.9	33.6±2.0	7.2±1.2	(Anderson and Polis, 1999)
California	Mixed	−	24.3 to 24.5	6.8 to 7.8	−	−	(Barrett et al., 2005)
Falkland Islands and Antarctica	Mixed	10.9±1.9	−1.8 to 15.8	−7.9 to 7.6	14.0±0.3	0.0 to 9.7	(Bokhorst et al., 2007)
Antarctica	Snow petrel	−	−3.1 to 25.8	−17.6 to −0.5	13.1 to 25.9	−13.4 to −1.0	(Cocks et al., 1998)
Australia	Gentoo penguin	14.6	7.2 to 18.8	−9.8 to −0.7	−	−	(Erskine et al., 1998)
North Africa	Various gulls	−	9.8 to 17.4	−	10.5 to 13.4	16.8 to 20.8	(García et al., 2002)
New Zealand	Westland petrel	−	−	−	14.1±0.3	−	(Harding et al., 2004)
New Zealand	Mixed	−	−3.9 to 9.1	−	−	−	(Hawke and Holdaway, 2005)
New Zealand	Sooty shearwater	7.7	14.2±3.1	−6.1±1.7	−	−	(Hawke and Newman, 2007)
Japan	Great cormorant	−	16.4 to 16.9	−2.5±0.6	10.6 to 16.0	0.4±0.3	(Hobara et al., 2005)
Japan	Great cormorant	13.2±1.3	10.0 to 14.7	−2.3 to 6.8	−	−	(Kameda et al., 2006)
Sweden	Great cormorant	−	13.6±1.7	1.7	−	−	(Kolb et al., 2010)
New Zealand	Mixed	−	4.6 to 6.7	14.4 to 15.9	10.2±1.0	16.2±0.3	(Markwell and Daugherty, 2003)
Fiji	Mixed	39.1 to 50.1^{a}	13.6 to 36.7	−1.3 to 0.8	15.1 to 31.6^{a}	−4.1 to −1.3^{b}	(Mizota and Naikatin, 2007)
Fiji	Mixed	14.9 to 23.3^{b}	−	−	13.5 to 33.0^{b}	−	(Mizota and Naikatin, 2007)
Japan	Black-tailed gull	10.2 to 10.5	3.9 to 14.6	−4.1 to −2.1	10.1 to 43.3^{a}	−4.3 to −2.9^{b}	(Mizota, 2009a)
Japan	Black-tailed gull	−	−	−	−0.2 to 33.7^{b}	−	(Mizota, 2009a)

Location	**Bird Species**	**Guano δ^{15}N (‰, AIR)**	**Plant δ^{15}N (‰, AIR)**		**Plant δ^{15}N (‰, AIR)**		**Reference**
			Bird	**Non-bird**	**Bird**	**Non-bird**	
Japan	Black-tailed gull	9.1 to 12.8	–	–	18.5 to 44.1[a]	–	(Mizota, 2009b)
Japan	Black-tailed gull	–	–	–	−4.1 to 42.2[b]	–	(Mizota, 2009b)
Japan and Antarctica	Penguin and gull	8.0 to 9.4	13.6 to 38.1	–	–	–	(Mizutani and Wada, 1988)
Antarctica	Penguin	7.4	–	–	32.1	–	(Mizutani et al., 1985b)
Japan	Mixed	–	–	–	9.1 to 37.9	−4.6 to 8.6	(Mizutani et al., 1986)
New Zealand	Rockhopper penguin	7.0±0.4	–	–	23.8±3.3	−0.5±0.2	(Mizutani et al., 1991a)
Australia	Mixed	9.9	9.5±2.2	7.0±2.6	–	–	(Schmidt et al., 2004)
California	Mixed	–	27.2 to 27.3	8.3 to 9.5	28.3±5.4	–	(Stapp et al., 1999)
Pribilof Islands	Mixed	12.5	22.0	11.3	–	–	(Wainright et al., 1998)
California	Mixed	–	–	–	35.6±2.6	7.5±0.3	(Wait et al., 2005)
Pacific (Palmyra Atoll)	Mixed	13.9	14.0±1.4	9.3±0.9	16.2±0.3	11.0±0.7	(Young et al., 2010)
Antarctica	Penguin	20.9±4.2	–	–	10.4±3.1	–	(Zhu et al., 2009)

a. NH_4^+
b. NO_3^-

Table 3.2. δ^{15}N values of organic and inorganic fertilizers.

Type	**Fertilizer**	**Fertilizer δ^{15}N (‰, AIR)**	**Reference**
Organic	Alpaca manure	13.9±0.6	(Szpak et al., 2012b)
	Blood	6.0±1.3	(Bateman and Kelly, 2007)
	Bonemeal	4.9±0.3	(Bateman and Kelly, 2007)
	Cattle manure	5.0±0.8	(Dijkstra et al., 2006)
	Cattle manure	2.9±0.5	(Kerley and Jarvis, 1996)
	Cattle manure	4.5	(Rogers, 2008)
	Cattle manure	3.1±0.2	(Ma and Dwyer, 1998)
	Chicken manure	6.2±1.9	(Bateman and Kelly, 2007)
	Fishmeal	7.1±3.6	(Bateman and Kelly, 2007)
	Hoof and horn	6.4±0.2	(Bateman and Kelly, 2007)
	Livestock manure	8.8±4.4	(Bateman and Kelly, 2007)
	Livestock manure	8.7±0.2	(Bateman and Kelly, 2007)
	Pig manure	13.9	(Choi et al., 2002)
	Pig manure	16.9	(Lim et al., 2007)
	Pig manure	11.3	(Rogers, 2008)
	Pig manure	6.5	(Rogers, 2008)
	Pig manure	16.4	(Yun et al., 2006)
	Poultry manure	8.6±0.3	(Rapisarda et al., 2010)
	Poultry manure	2.7	(Rogers, 2008)
	Seabird guano	26.7±0.6	(Szpak et al., 2012a)
	Seabird guano	38.1±0.6	(Szpak et al., 2012b)
	Seabird guano	28.7±2.4	Szpak unpublished
	Seabird guano	23.4±1.3	Szpak unpublished
	Seaweed	2.5±1.5	(Bateman and Kelly, 2007)
	Various composts	17.4±1.2	(Choi et al., 2003)
Inorganic	$(NH_4)_2H_2PO_4$	−0.6±0.4	(Bateman and Kelly, 2007)
	$(NH_4)_2SO_4$	1.7±3.4	(Bateman and Kelly, 2007)
	$(NH_4)_2SO_4$	−1.6	(Rogers, 2008)
	$(NH_4)_2SO_4$	−2.6	(Choi and Ro, 2003)
	$(NH_4)_2SO_4$	−0.7±0.1	(Szpak et al., 2012b)
	KNO_3	−1.2±0.3	(Bateman and Kelly, 2007)
	NH_4NO_3	−1.3	(Bateman et al., 2005)
	NH_4NO_3	−0.6±1.7	(Bateman and Kelly, 2007)
	NH_4NO_3	−1.7	(Rogers, 2008)
	Urea	−2.4±2.1	(Bateman and Kelly, 2007)
	Urea	−1.7	(Rogers, 2008)
	Urea	−0.7	(Yun et al., 2006)

Table 3.3. Isotopic and elemental compositions of plant samples (mean±1σ for *n*=5 samples)

Treatment	Tissue	Sampling Date	δ^{15}N (‰, AIR)	δ^{13}C (‰, VPDB)	%N	%C
C0	Leaf	30 d	−0.3±3.6	−	5.1±0.7	−
	Leaf	75 d	5.5±1.4	−	2.7±0.6	−
	Leaf	115 d	3.9±1.0	−15.7±0.8	1.1±0.3	39.5±2.3
	Grain	115 d	2.7±0.7	−12.9±0.1	2.4±0.3	42.5±1.4
	Anther	75 d	5.7±0.4	−14.0±0.4	2.4±0.4	47.0±2.3
	Root	115 d	3.6±0.9	−15.0±0.5	0.8±0.2	44.7±1.1
	Stalk	115 d	3.2±1.4	−15.2±0.2	1.0±0.5	47.0±1.8
G1	Leaf	30 d	−5.0±10.0	−	4.9±0.9	−
	Leaf	75 d	32.4±2.2	−	4.1±0.3	−
	Leaf	115 d	26.8±2.0	−15.1±0.5	2.6±0.7	40.6±4.7
	Grain	115 d	25.5±1.6	−14.1±0.8	2.5±0.2	45.8±2.8
	Anther	75 d	34.2±3.4	−13.5±0.4	3.2±0.1	48.4±2.1
	Root	115 d	33.1±4.1	−15.2±0.3	1.4±0.7	44.2±4.2
	Stalk	115 d	38.4±1.9	−15.4±0.5	2.9±0.8	36.4±2.6
G2	Leaf	30 d	6.0±4.3	−	5.7±0.4	−
	Leaf	75 d	38.2±0.9	−	4.8±0.2	−
	Leaf	115 d	33.3±2.7	−15.4±1.0	3.2±0.6	42.6±3.9
	Grain	115 d	33.1±2.8	−13.3±0.3	2.6±0.2	44.6±1.7
	Anther	75 d	41.8±2.6	−13.5±0.4	3.3±0.5	45.2±4.4
	Root	115 d	40.1±2.6	−14.5±0.6	2.1±0.7	41.4±1.8
	Stalk	115 d	44.7±0.8	−14.7±0.6	3.4±0.2	29.7±0.8

Table 3.4. Raw isotopic and elemental compositions for all growth chamber plants.

SAMPLE	Tissue	DAT[1]	Treatment	δ^{13}C (‰, VPDB)	δ^{15}N (AIR)	%C	%N
SZPMZPC01	Anther	75	C0	-14.02	4.95	47.63	2.79
SZPMZPC02	Anther	75	C0	-13.61	5.78	49.57	2.73
SZPMZPC03	Anther	75	C0	-13.80	6.03	46.30	2.46
SZPMZPC04	Anther	75	C0	-14.01	5.59	47.87	2.21
SZPMZPC05	Anther	75	C0	-14.56	6.03	43.38	1.70
SZPMZPG06	Anther	75	G1	-13.93	37.36	49.91	3.22
SZPMZPG07	Anther	75	G1	-13.87	30.25	50.49	3.30
SZPMZPG08	Anther	75	G1	-13.36	31.34	49.05	3.17
SZPMZPG09	Anther	75	G1	-13.27	37.67	47.21	3.27
SZPMZPG10	Anther	75	G1	-13.07	34.63	45.33	3.07
SZPMZPG01	Anther	75	G2	-13.89	41.83	47.96	3.81
SZPMZPG02	Anther	75	G2	-13.30	42.41	48.33	3.42
SZPMZPG03	Anther	75	G2	-13.25	41.06	47.50	3.28
SZPMZPG04	Anther	75	G2	-13.93	42.65	44.50	3.34
SZPMZPG05	Anther	75	G2	-13.22	41.06	37.94	2.57
SZPMZFC01	Grain	115	C0	-13.01	2.04	42.23	2.47
SZPMZFC02	Grain	115	C0	-12.66	3.11	44.24	2.30
SZPMZFC03	Grain	115	C0	-13.03	2.32	42.61	2.19
SZPMZFC04	Grain	115	C0	-12.91	2.37	40.85	2.22
SZPMZFC05	Grain	115	C0	-12.91	3.63	43.76	2.91
SZPMZFG06	Grain	115	G1	-13.77	26.66	41.91	2.31
SZPMZFG07	Grain	115	G1	-13.18	22.83	46.87	2.44
SZPMZFG08	Grain	115	G1	-13.99	26.79	44.42	2.63
SZPMZFG09	Grain	115	G1	-14.21	26.09	49.53	2.50
SZPMZFG10	Grain	115	G1	-15.32	25.27	46.27	2.73
SZPMZFG01	Grain	115	G2	-13.81	36.68	45.88	2.78

SAMPLE	Tissue	DAT[1]	Treatment	$\delta^{13}C$ (‰, VPDB)	$\delta^{15}N$ (AIR)	%C	%N
SZPMZFG02	Grain	115	G2	-12.89	34.22	42.88	2.51
SZPMZFG03	Grain	115	G2	-13.28	33.73	43.33	2.38
SZPMZFG04	Grain	115	G2	-13.11	29.05	43.94	2.86
SZPMZFG05	Grain	115	G2	-13.44	31.88	46.73	2.45
SZPMZLC01	Leaf	30	C0		-1.51		5.35
SZPMZLC02	Leaf	30	C0		-4.96		5.83
SZPMZLC03	Leaf	30	C0		4.61		4.02
SZPMZLC04	Leaf	30	C0		-1.41		5.50
SZPMZLC05	Leaf	30	C0		1.72		4.64
SZPMZLC01	Leaf	75	C0		7.94		3.13
SZPMZLC02	Leaf	75	C0		5.01		3.31
SZPMZLC03	Leaf	75	C0		4.42		1.93
SZPMZLC04	Leaf	75	C0		4.62		2.86
SZPMZLC05	Leaf	75	C0		5.32		2.37
SZPMZLC01	Leaf	115	C0	-15.67	3.31	38.99	0.82
SZPMZLC02	Leaf	115	C0	-14.36	4.18	35.85	1.23
SZPMZLC03	Leaf	115	C0	-16.12	2.46	39.62	1.56
SZPMZLC04	Leaf	115	C0	-16.32	4.46	41.45	0.86
SZPMZLC05	Leaf	115	C0	-15.99	4.86	41.62	0.78
SZPMZLG06	Leaf	30	G1		-0.58		5.31
SZPMZLG07	Leaf	30	G1		-12.39		3.23
SZPMZLG08	Leaf	30	G1		10.58		5.58
SZPMZLG09	Leaf	30	G1		-12.37		5.24
SZPMZLG10	Leaf	30	G1		-10.20		4.92
SZPMZLG06	Leaf	75	G1		34.55		4.12
SZPMZLG07	Leaf	75	G1		31.83		4.45
SZPMZLG08	Leaf	75	G1		29.65		3.86
SZPMZLG09	Leaf	75	G1		34.55		4.26

SAMPLE	Tissue	DAT[1]	Treatment	δ^{13}C (‰, VPDB)	δ^{15}N (AIR)	%C	%N
SZPMZLG10	Leaf	75	G1		31.87		3.99
SZPMZLG06	Leaf	115	G1	-15.18	29.12	33.41	3.21
SZPMZLG07	Leaf	115	G1	-15.02	23.81	42.59	1.38
SZPMZLG08	Leaf	115	G1	-15.37	27.14	41.80	2.92
SZPMZLG09	Leaf	115	G1	-14.32	27.56	39.46	2.82
SZPMZLG10	Leaf	115	G1	-15.66	26.51	45.93	2.87
SZPMZLG01	Leaf	30	G2		5.92		5.73
SZPMZLG02	Leaf	30	G2		-0.24		5.36
SZPMZLG03	Leaf	30	G2		4.55		6.35
SZPMZLG04	Leaf	30	G2		9.38		5.43
SZPMZLG05	Leaf	30	G2		10.48		5.79
SZPMZLG01	Leaf	75	G2		38.07		4.95
SZPMZLG02	Leaf	75	G2		39.55		4.93
SZPMZLG03	Leaf	75	G2		36.91		4.84
SZPMZLG04	Leaf	75	G2		38.38		4.57
SZPMZLG05	Leaf	75	G2		38.15		4.88
SZPMZLG01	Leaf	115	G2	-14.31	28.76	49.13	2.53
SZPMZLG02	Leaf	115	G2	-14.70	32.97	41.35	2.70
SZPMZLG03	Leaf	115	G2	-16.65	34.43	40.69	3.44
SZPMZLG04	Leaf	115	G2	-15.04	35.89	38.90	3.09
SZPMZLG05	Leaf	115	G2	-16.40	34.32	43.15	4.07
SZPMZRC01	Root	115	C0	-14.89	3.75	44.99	0.71
SZPMZRC02	Root	115	C0	-14.69	3.78	45.49	1.07
SZPMZRC03	Root	115	C0	-15.73	2.10	42.82	0.71
SZPMZRC04	Root	115	C0	-14.44	3.52	44.72	0.71
SZPMZRC05	Root	115	C0	-15.07	4.51	45.57	0.75
SZPMZRG06	Root	115	G1	-15.02	32.21	48.14	0.86
SZPMZRG07	Root	115	G1	-14.91	37.59	39.91	1.83

SAMPLE	Tissue	DAT[1]	Treatment	δ^{13}C (‰, VPDB)	δ^{15}N (AIR)	%C	%N
SZPMZRG08	Root	115	G1	-15.04	37.22	39.49	2.39
SZPMZRG09	Root	115	G1	-15.59	29.56	46.74	1.08
SZPMZRG10	Root	115	G1	-15.33	28.83	46.91	0.98
SZPMZRG01	Root	115	G2	-14.28	37.54	41.56	1.84
SZPMZRG02	Root	115	G2	-14.37	42.96	40.55	2.38
SZPMZRG03	Root	115	G2	-13.97	42.02	39.53	2.32
SZPMZRG04	Root	115	G2	-15.44	37.19	44.26	1.07
SZPMZRG05	Root	115	G2	-14.31	40.57	40.88	2.81
SZPMZSC01	Stalk	115	C0	-15.26	5.64	45.81	0.48
SZPMZSC02	Stalk	115	C0	-15.05	2.17	45.70	1.07
SZPMZSC03	Stalk	115	C0	-15.16	3.03	48.43	0.52
SZPMZSC04	Stalk	115	C0	-14.94	2.20	49.41	1.42
SZPMZSC05	Stalk	115	C0	-15.40	2.97	45.39	1.44
SZPMZSG06	Stalk	115	G1	-16.19	37.18	34.53	4.42
SZPMZSG07	Stalk	115	G1	-15.64	39.25	36.78	2.38
SZPMZSG08	Stalk	115	G1	-15.09	35.69	40.76	2.87
SZPMZSG09	Stalk	115	G1	-15.39	40.15	34.58	2.50
SZPMZSG10	Stalk	115	G1	-14.89	39.74	35.26	2.51
SZPMZSG01	Stalk	115	G2	-14.18	45.75	29.30	3.59
SZPMZSG02	Stalk	115	G2	-15.12	45.19	31.15	3.14
SZPMZSG03	Stalk	115	G2	-14.01	44.10	29.47	3.50
SZPMZSG04	Stalk	115	G2	-15.49	43.91	28.97	3.29
SZPMZSG05	Stalk	115	G2	-14.45	44.43	29.55	3.53

[1] Days after transplanting.

Table 3.5. Results of ANOVA for differences in isotopic and elemental tissue compositions between treatments.

Tissue	**Treatment**	**G1**				**G2**			
		δ^{15}N (‰, AIR)	**δ^{13}C (‰, VPDB)**	**%N**	**%C**	**δ^{15}N (‰, AIR)**	**δ^{13}C (‰, VPDB)**	**%N**	**%C**
Leaf 30 d	C0	0.707	–	0.889	–	0.096	–	0.347	–
	G1	–	–	–	–	0.171	–	0.176	–
Leaf 75 d	C0	**<0.001**	–	**0.008**	–	**<0.001**	–	**0.002**	–
	G1	–	–	–	–	**<0.001**	–	**0.002**	–
Leaf 115 d	C0	**<0.001**	0.509	**0.003**	0.884	**<0.001**	0.857	**<0.001**	0.414
	G1	–	–	–	–	**0.001**	0.819	0.357	0.686
Stalk	C0	**<0.001**	0.640	**<0.001**	**<0.001**	**<0.001**	0.249	**<0.001**	**<0.001**
	G1	–	–	–	–	**<0.001**	0.056	0.415	**<0.001**
Grain	C0	**<0.001**	0.066	0.760	0.092	**<0.001**	0.150	0.463	0.348
	G1	–	–	–	–	**<0.001**	0.221	0.869	0.632
Anther	C0	**<0.001**	0.118	**0.010**	0.746	**<0.001**	0.135	**0.006**	0.669
	G1	–	–	–	–	**0.017**	0.997	0.940	0.280
Root	C0	**<0.001**	0.746	0.227	0.958	**<0.001**	0.249	**<0.001**	0.163
	G1	–	–	–	–	**<0.001**	0.076	0.415	0.250

Values in boldface are statistically significant (p<0.05)

Table 3.6. Summary of studies examining the influence of organic fertilization on plant δ^{15}N values

Fertilizer	**Fertilizer δ^{15}N (‰, AIR)**	**Plant**	**Plant δ^{15}N (‰, AIR)**	**$\Delta^{15}N_{fertilized-control}$**	**Reference**
Pig manure	13.9	Maize	7.7	+1.1	(Choi et al., 2002)
Various composts	17.4±1.2	Maize	17.7	+13.5	(Choi et al., 2003)
Various composts	17.4±1.2	Nightshade	13.4	+10.7	(Choi et al., 2003)
Various composts	17.4±1.2	Pepper	14.5	+9.8	(Choi et al., 2003)
Various composts	17.4±1.2	Mustard	16.3	+12.7	(Choi et al., 2003)
Various composts	17.4±1.2	Melon	13.3	+10.1	(Choi et al., 2003)
Various composts	17.4±1.2	Lettuce	13.5	+9.4	(Choi et al., 2003)
Various composts	17.4±1.2	Spinach	9.5	+3.9	(Choi et al., 2003)
Various composts	17.4±1.2	Beefsteak plant	19.9	+15.4	(Choi et al., 2003)
Various composts	17.4±1.2	Sesame	17.8	+12.1	(Choi et al., 2003)
Pig manure	16.9	Chrysanthemum	10.3	+3.5	(Lim et al., 2007)
Pig manure	16.9	Cabbage	13.3	+5.6	(Lim et al., 2007)
Sheep manure	−	Sweet pepper	10.0	−	(del Amor et al., 2008)
Chicken manure	−	Sweet pepper	10.2	−	(del Amor et al., 2008)
Horse manure	−	Sweet pepper	9.8	−	(del Amor et al., 2008)
Livestock manure	8.7±0.2	Orange (pulp)	9.0	−	(Rapisarda et al., 2010)
Poultry manure	8.6±0.3	Orange (pulp)	8.5	−	(Rapisarda et al., 2010)
Livestock manure	8.7±0.2	Orange (juice)	8.5	−	(Rapisarda et al., 2010)
Poultry manure	8.6±0.3	Orange (juice)	7.9	−	(Rapisarda et al., 2010)
Pig manure	16.4	Chinese cabbage	12.5	+11.0	(Yun et al., 2006)
Cattle + poultry manure	16.7	Tomato	13.5	+10.2	(Nakano and Uehara, 2007)
Cattle + poultry manure	9.9	Tomato	7.9	+4.6	(Nakano and Uehara, 2007)

Table 3.7. Results of ANOVA for differences in nitrogen isotopic composition between plant parts.

Treatment	Tissue	Leaf	Anther	Root	Stalk
C0	Grain	0.319	**<0.001**	0.626	0.908
	Leaf	–	**0.041**	0.981	0.803
	Anther	–	–	**0.013**	**0.004**
	Root	–	–	–	0.980
G1	Grain	0.915	**0.017**	0.077	**<0.001**
	Leaf	–	**0.035**	0.152	**<0.001**
	Anther	–	–	0.999	0.309
	Root	–	–	–	0.252
G2	Grain	0.999	**<0.001**	**<0.001**	**<0.001**
	Leaf	–	**<0.001**	**<0.001**	**<0.001**
	Anther	–	–	0.709	0.259
	Root	–	–	–	**0.022**

Values in boldface are statistically significant (p<0.05)

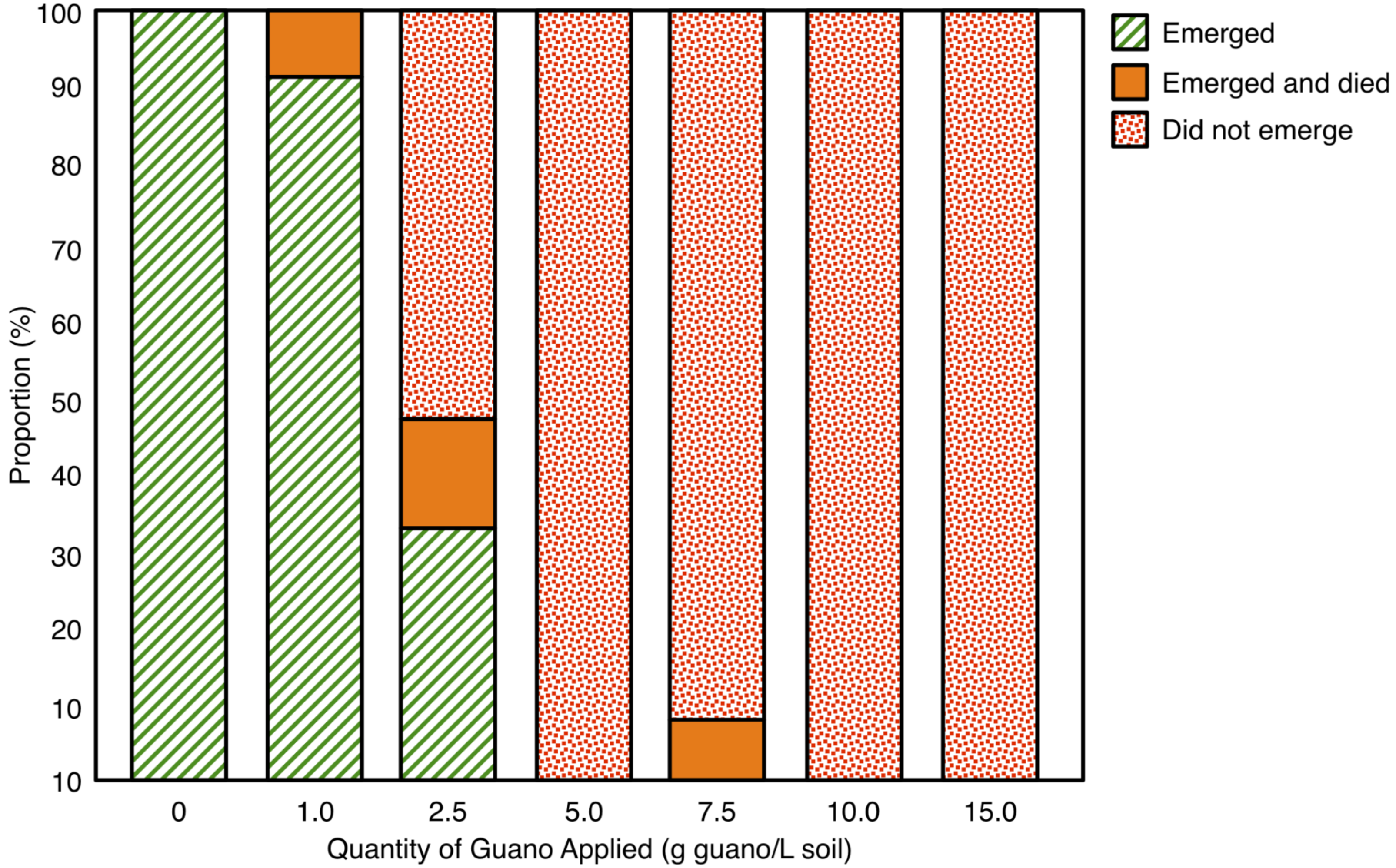

Figure 3.1. Relative percentages of seedlings that germinated and emerged with differing amounts of seabird guano applied.

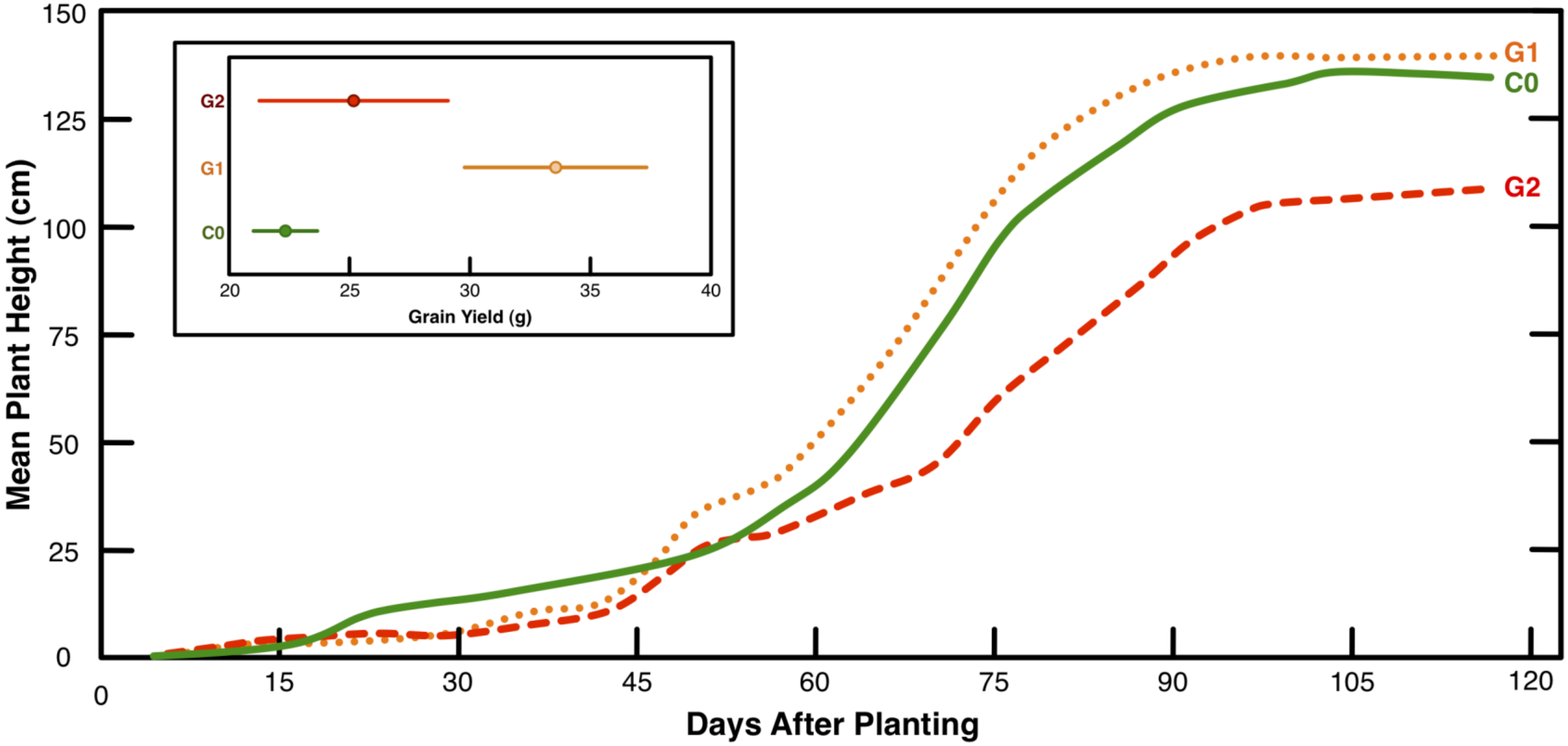

Figure 3.2. Maximum heights of maize plants throughout experiment. Harvest occurred at 115 d. Inset: grain yield for each experiment.

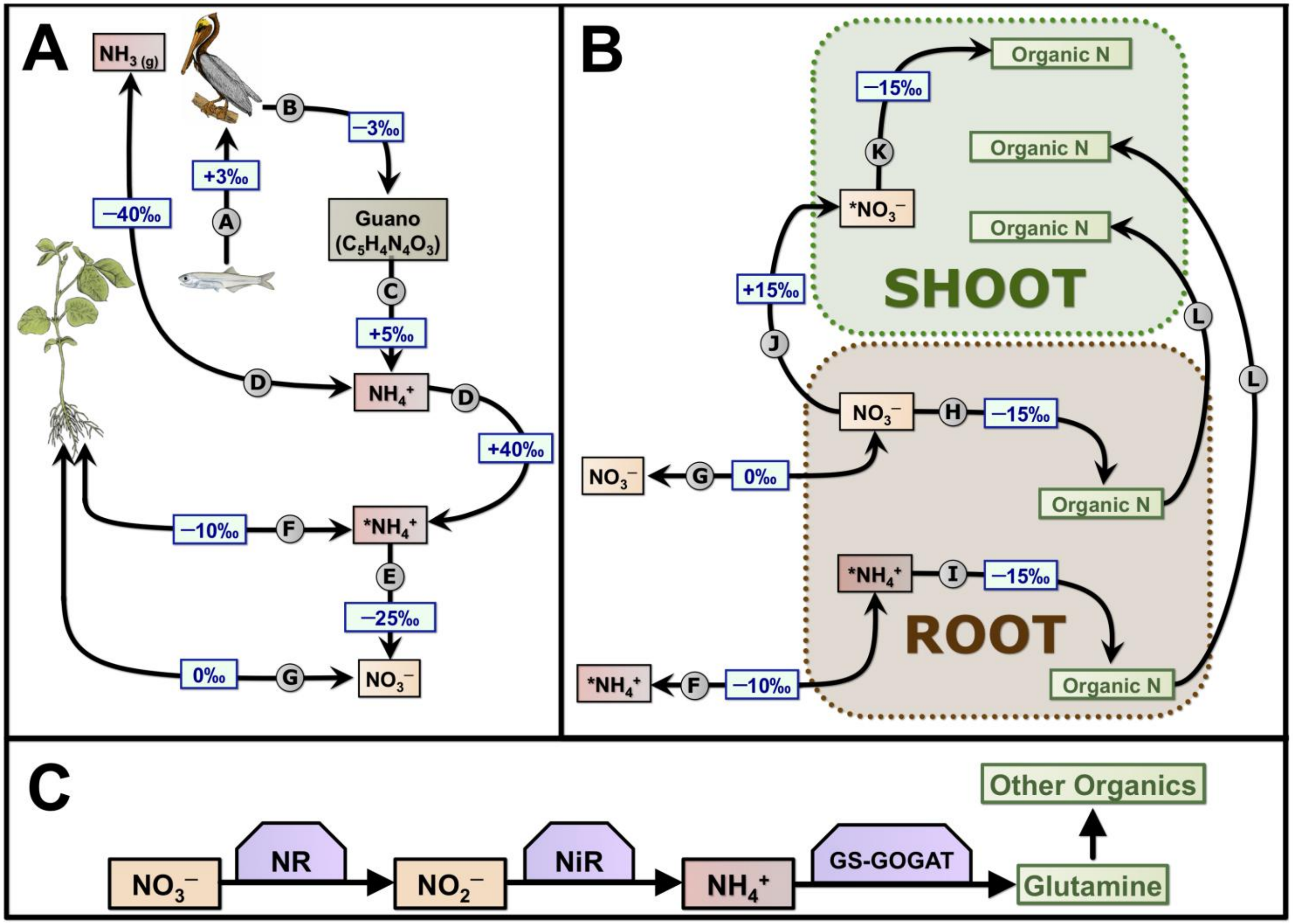

Figure 3.3. Simplified schematic of fractionation factors associated with decomposition and uptake of seabird guano N.

A) Simplified pathway for guano-derived nitrogen. **(a)** Incorporation of dietary N into consumer tissue N. Tissue−diet fractionation for birds has been calculated to be ~3‰ for most tissues (Hobson and Clark, 1992; Hobson, 1995). **(b)** Excretion of dietary N as uric acid. Wainright et al. (1998) found bulk guano to be depleted of ^{15}N by 2.5‰ relative to seabird blood. Moreover, Mizutani et al. (1985a; 1985b) and Bird et al. (2008) found $\delta^{15}N$ of uric acid to be very similar to bulk guano $\delta^{15}N$. **(c)** Conversion of uric acid to NH_4^+, according to the experiment performed by Mizutani et al. (1985a). **(d)** Ammonia volatilization. Many studies have found this process to be associated with a large equilibrium fractionation that concentrates ^{15}N in the remaining substrate ($*NH_4^+$ in the diagram) (Kirshenbaum et al., 1947; Mizutani et al., 1985b; Mizutani et al., 1986). **(e)** Nitrification. The fractionation factor for the entire process of nitrification in the soil ($NH_4^+ \rightarrow NO_2^- \rightarrow NO_3^-$) is estimated to be between −12 and −35‰ (Feigin et al., 1974; Robinson, 2001; Shearer and Kohl, 1986). **(f)** Uptake of NH_4^+ is associated with a nitrogen isotope fractionation ranging from −6 to −30‰ and appears to depend on the concentration of the source NH_4^+ (Hoch et al., 1992; Yoneyama et al., 2001). **(g)** Uptake of NO_3^- by the plant does not appear to be associated with any fractionation (Mariotti et al., 1982; Yoneyama et al., 1998; Yoneyama et al., 2001). Both NO_3^- and NH_4^+ may be effluxed from the plant, passively and in some cases actively (Miller and Cramer, 2005).

B) **(h)** NO_3^- assimilation into organic N occurs in the root by the NR-NiR (nitrate reductase-nitrite reductase) and GS-GOGAT (glutamine synthetase−glutamine:oxoglutarate aminotransferase) pathways. The reduction of NO_3^- to NH_4^+ is associated with a fractionation factor of −15‰ (Ledgard et al., 1985; Tcherkez and Farquhar, 2006). **(i)** NH_4^+ assimilation occurs in the root via the GS-GOGAT pathway and is associated with a fractionation factor of −10 to −15‰ (Yoneyama et al., 1991; Yoneyama et al., 1993a). **(j, k)** NO_3^- may also be mobilized to the shoot for assimilation. In this case, this NO_3^- pool has already been exposed to NO_3^- assimilation in the root and is enriched in ^{15}N (Evans et al., 1996). Therefore, organic N formed from NO_3^- in the shoot ($*NO_3^-$) will have a higher $\delta^{15}N$ value than organic N formed from NO_3^- in the root. **(l)** Organics may be moved between the root and shoot.

C) Simplified schematic for the assimilation of N by plants. For a more detailed description see Miller and Cramer (2005). All fractionation factors are approximate values representing medians of ranges, which may be large (see text for discussion).

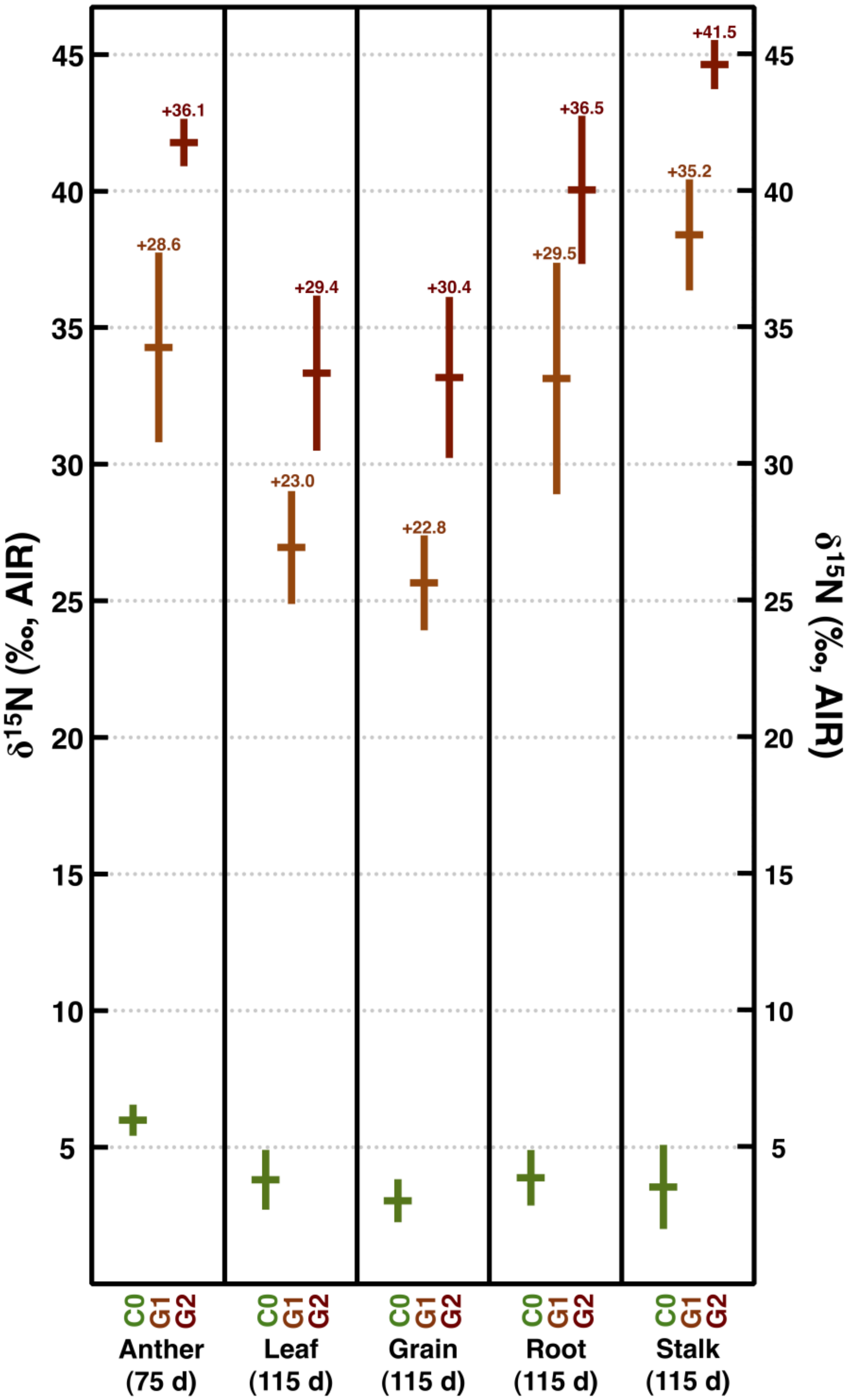

Figure 3.4. Mean nitrogen isotope composition of maize organs; horizontal bars represent means, vertical bars represent standard deviations. Values above G1 and G2 maize represent differences in nitrogen isotopic composition relative to C0 maize.

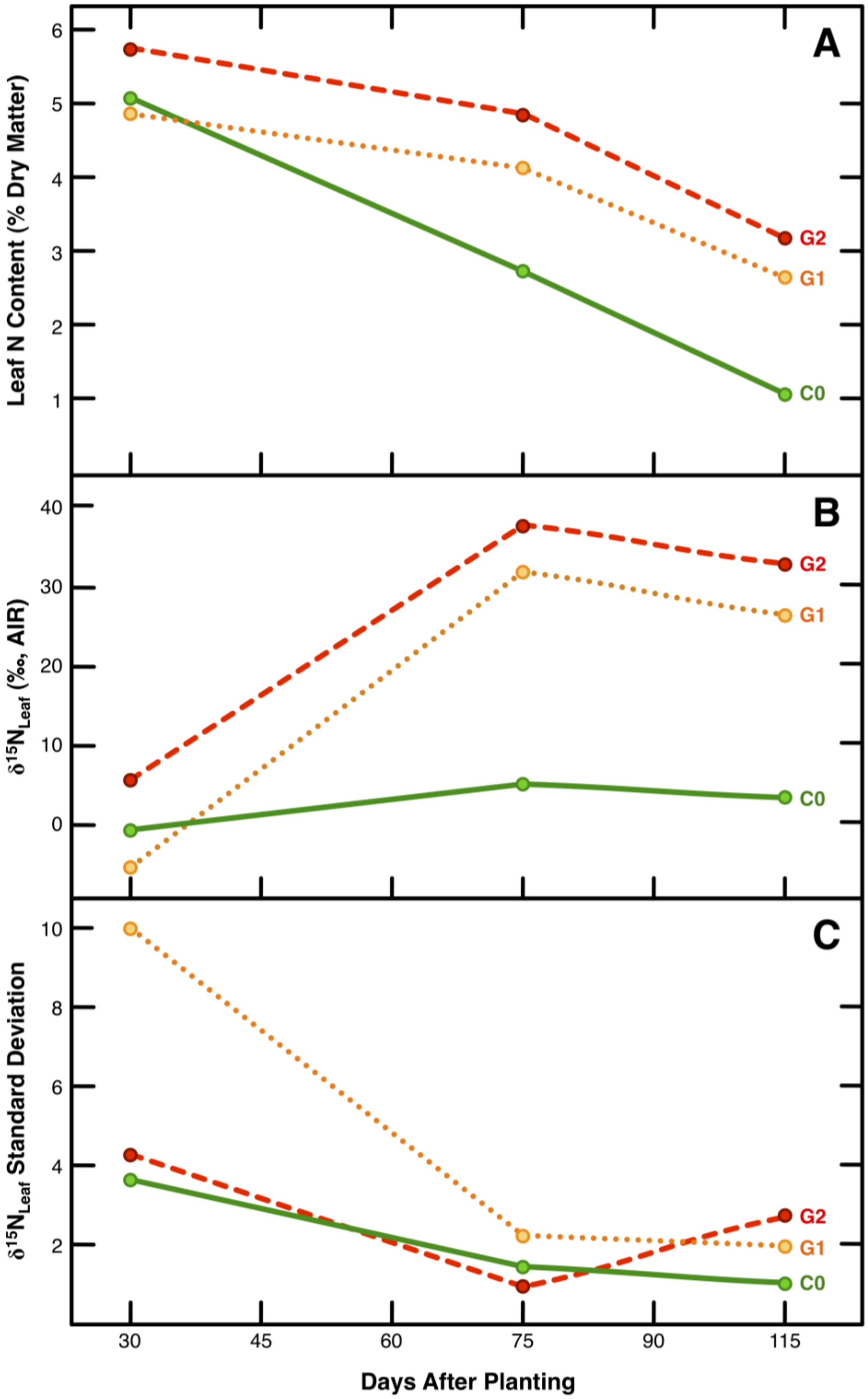

Figure 3.5. Temporal patterns in isotopic and element composition. (A) Leaf N content, (B) Leaf δ^{15}N, and (C) standard deviation for Leaf δ^{15}N.

Chapter 4

4 Influence of Seabird Guano and Camelid Dung Fertilization on the Nitrogen Isotopic Composition of Field-Grown Maize (*Zea mays*)

Organic fertilizers have the capacity to alter the nitrogen isotopic composition of plants. Camelid dung and seabird guano are two potentially important fertilizers in the agricultural systems of western South America, particularly Peru and Chile. This paper presents isotopic data ($\delta^{13}C$ and $\delta^{15}N$) from field grown plants (maize, *Zea mays*) fertilized with the following four treatments: CO (control, no fertilizer applied), AS (ammonium sulfate, a chemical fertilizer), DU (camelid dung), and SG (seabird guano). Plants were grown in experimental plots in the Virú Valley, northern Peru. Plants fertilized with the chemical fertilizer presented very similar isotopic compositions compared to the control. Conversely, the camelid dung fertilized plants were characterized by higher $\delta^{15}N$ values compared to the control plants (by 1.8 to 4.2‰ depending on the plant part). The seabird guano fertilized plants were greatly enriched in ^{15}N in comparison to the control plants (by 11.3 to 20.0‰). The results of this study have important implications for the reconstruction of human diet using isotopic data derived from bone collagen and related tissues, particularly in the prehispanic Andes, but also in Europe and North America during the 19th century, when Peruvian seabird guano was used extensively. Specifically, the interpretation of the relative contributions of plant and animal protein to the diet on the basis of bulk isotopic compositions of bone collagen (or similar tissues) may be confounded by camelid dung fertilization if the carbon isotopic compositions of the two sources are similar. Likewise, the interpretation of the relative contributions of maize and marine protein may be confounded by seabird guano fertilization.

4.1 Introduction

The reconstruction of diet in archaeological contexts has increasingly relied on stable isotope analysis of human remains. Crucial to this process is a thorough understanding of the range and variation in the isotopic compositions of the foods that may have been consumed (Schwarcz, 1991). The processes influencing the stable nitrogen isotopic compositions ($\delta^{15}N$) in biological systems are complex and are only beginning to be understood. Traditionally, in archaeology and related disciplines, variation in $\delta^{15}N$ values of bone collagen and other tissues has been interpreted within the contexts of marine vs. terrestrial resource consumption (e.g. Ambrose et al., 1997; Coltrain, 2009; Richards and Hedges, 1999), animal vs. plant protein consumption (e.g. Katzenberg et al., 1995; Richards et al., 2000), the relative timing of nursing and weaning (e.g. Prowse et al., 2008; Schurr, 1997), and climatic conditions (e.g. Richards and Hedges, 2003; Schwarcz et al., 1999; Szpak et al., 2010).

A growing body of literature has emerged in recent years demonstrating that organic fertilizers, specifically those derived from animal waste, can cause large enrichments in ^{15}N of plant tissues (e.g. Bogaard et al., 2007; Choi et al., 2006; Choi et al., 2002; Choi et al., 2003; del Amor et al., 2008; Flores et al., 2007; Fraser et al., 2011; Lim et al., 2007; Nakano et al., 2003; Nakano and Uehara, 2007; Rapisarda et al., 2005; Rapisarda et al., 2010; Senbayram et al., 2008; Szpak et al., 2012a; Yun et al., 2006; Yun and Ro, 2009; Yun et al., 2011). Following this, the possibility of manuring as a significant source of plant and consumer $\delta^{15}N$ values in prehistoric agropastoral systems has been given some consideration by archaeologists in recent years. Here, we have sought to determine the influence of short-term fertilization of maize with seabird guano, or camelid dung, on maize nitrogen isotopic composition.

4.2 Andean Fertilizers

4.2.1 *Camelid Dung*

South American camelids (llama and alpaca) were the only species of large mammal to have been domesticated in the Americas. They were extremely important in every sphere of prehispanic Andean life, serving as an important source of meat, wool, transportation, and dung (reviewed by Bonavia, 2008; Mengoni Goñalons, 2008). Camelid dung is a relatively poorly known fertilizer because it has never been commercially significant, and has been utilized primarily by subsistence farmers in the Andes.

Camelids are considered to be pseudoruminants because they have a three (rather than four) compartmented stomach, and are distinct from pecoran or 'true' ruminants in a number of other ways (see Fowler, 2008). Most significantly, camelids lose proportionately less nitrogen in their urine than other ruminants (Dulphy et al., 1997; Hinderer and Engelhardt, 1975; Warmington et al., 1989). The total nitrogen content of camelid dung has been reported to be between 1.4 and 1.9% (Alvarez et al., 2006; Alvarez and Lidén, 2008a, 2008b, 2009; Davis et al., 2002), which is similar to other mammalian herbivores (Edwards, 1991; Williams and Haynes, 1995).

Both wild and domestic South American camelids are noted for their habit of communal urination and defecation (Franklin, 1982), which facilitates the collection of manure at a centralized location. This behaviour is thought to serve some function related to orienting herd members to their home territory, and also facilitates the development of preferential graze resulting from the localized addition of nutrients to the soil (Franklin, 1982). In some areas, it appears that camelid herds are allowed to graze seasonally in agricultural fields after the harvest, depositing their dung on the fields as they clear the stubble (Mitchell, 1991). As Bruno (2008) points out, however, the application of dung to fields may be dependent on the purposeful collection because camelids habitually defecate in one particular location.

Based on studies of modern and historic human groups, camelid dung has been used in tuber cultivation in the high altitude *altiplano*, which is characterized by soils with low N content and low organic matter (Camino and Johns, 1988; Flannery et al., 1989; Garcilaso de la Vega, 1966:246; Yamamoto, 1985). Camelid dung may have been used more extensively in the Andes prior to the introduction of European domesticates. The prevalence of camelids in the Andes has markedly declined in the last five hundred years (Mengoni Goñalons, 2008), and the introduction of European livestock (particularly cattle and sheep) has introduced new sources of manure that would not have been available prior to the sixteenth century. For example, in the southern Peruvian *altiplano*, Winterhalder et al. (1974) found that despite being locally abundant, camelid dung is not often used as a fertilizer, and is instead used primarily for fuel; sheep or cattle manure are the preferred animal fertilizers. There are many more ethnographic and ethnohistoric accounts of the use of camelid dung for a fuel in ceramic production and cooking (Arnold, 1993; Arnold, 1988; Bruno, 2008; Chávez, 1984-1985; Deere, 1990; Franke, 1992; Hastorf and Wright, 1998; Johannessen and Hastorf, 1990; Sillar, 2000a, 2000b), but comparatively fewer accounts of the use of camelid dung as a fertilizer.

4.2.2 *Seabird Guano*

For the purpose of this paper, ‘guano’ refers specifically to seabird excrement, and not the excrement of bats or pinnipeds, which is commonly also referred to as guano. In very general terms, seabird guano has been the subject of a fairly large body of scientific research because soils that are significantly impacted by seabird guano (ornithogenic soils) are rather unusual in that the concentration of some nutrients (NO_3^- and NH_4^+ in particular) may be extremely high and the biota that live in and around these soils are subsidized largely or wholly by seabird excrement (Ellis, 2005; Sánchez-Piñero and Polis, 2000). Seabird guano typically contains 8−21% nitrogen by mass, which is in turn composed primarily of uric acid (~80%), protein (~10%), ammonia (~7%), and nitrate (~0.5%) (Gaskell and Smith, 2007; Gillham, 1960; Hartz and Johnstone, 2006; Lindeboom, 1984; McNabb et al., 1980; Mizutani and Wada, 1985; Mizutani et al., 1991b; Staunton Smith and Johnson, 1995; Szpak et al., 2012a).

Mined primarily from small, nearshore islands off the arid western coast of South America in the Peru-Humboldt upwelling region (Figure 4.1), seabird guano was the most economically significant fertilizer prior to the twentieth century. Although seabird colonies are present in many other regions in South America, and in some cases provide guano that may be utilized as a fertilizer (e.g. Frere et al., 2005), the Peruvian deposits are by far the best known and were historically considered to be of the highest quality (Cushman, 2003; Hollett, 2008). The Peruvian guano islands are composed of rocky andesite cliffs, which are devoid of vascular plants (Duffy, 1994). The primary guano-producing seabirds of the Peruvian coast (hereafter simply ‘guano birds’) are the Guanay cormorant (*Phalacrocorax bougainvillii*) and Peruvian booby (*Sula variegata*), and to a lesser extent the Peruvian brown pelican (*Pelecanus occidentalis thagus*) (Duffy, 1983a, 1983b, 1994). The guano birds are supported primarily by the Peruvian anchovy or anchoveta (*Engraulis ringens*), as well as a number of other small mesopelagic fish

(Duffy, 1983c; Ludynia et al., 2010; Pauly and Tsukayama, 1987). The Peru-Humboldt upwelling region is the largest producer of fish biomass in the world (Bakun and Broad, 2003; Chavez et al., 2008), which supports the very large populations of nesting seabirds. Since the catastrophic 1965 El Niño and the 1972 collapse of the anchoveta fishery (Muck and Pauly, 1987), which resulted in massive guano bird mortality, Peruvian guano bird populations have remained at less than five million (Tovar et al., 1987). In the 1950s and early 1960s, populations were at their highest recorded levels, fluctuating between ten and thirty million (Duffy, 1983a; Tovar et al., 1987), largely as a consequence of variations in upwelling conditions and primary productivity (Jahncke et al., 2004). No data or estimates are available for seabird populations in Peru prior to the twentieth century, but it is widely held that the extraction of guano during the nineteenth century (often performed with dynamite) was extremely disruptive to the birds (Tovar et al., 1987). It is likely, therefore, that guano bird populations were even higher prior to the nineteenth century than they were in the twentieth century.

Because the coast of Peru only receives precipitation in exceptional circumstances (during El Niño events), guano accumulates at seabird nesting sites in sedimentary layers. The once thick deposits of seabird guano were removed during the guano boom of the nineteenth century, and today most islands have only several years worth of guano (Duffy, 1994). The guano boom peaked during the middle of the nineteenth century, with millions of tons being exported to North America and Europe (principally the United States and Britain) between the 1850s and the beginning of War in the Pacific (1879) (Murphy, 1981).

The extent to which guano was utilized as a fertilizer prior to the nineteenth century is difficult to assess, but is discussed in various ethnohistoric documents (e.g. Arriaga, 1968; Cieza de León, 1964; Diez de San Miguel, 1964; Garcilaso de la Vega, 1966; Ruiz, 1998; Tschudi, 1854), some of which are described at length by Julien (1985). According to Pedro de Cieza de León (1964:265-266), writing in the middle of the sixteenth century, the guano was obtained using balsa rafts and applied to the fields, and was crucial to the harvest of a fruitful crop of maize in northern Chile. In the early part of the seventeenth century, Garcilaso de la Vega (1966::246) wrote, “on the seacoast, from below Arequipa to Tarapacá, a distance of over 200 leagues along the coast, they use no other manure but the dung of sea birds…In the times of the Inca kings these birds were so carefully watched that no one was allowed to land on the [guano] islands during the breeding season under pain of death." With respect to islands on the south coast of Peru, Netherly (1977) suggests that during the Inca period, highland groups were heavily involved in exploiting guano as fertilizer.

Less is known about the use of seabird guano on the central and north coast of Peru historically, although a number of artifacts and offerings (Figure 4.2) were recovered from stratified guano deposits on the northern islands (Macabi, Guañape) during the guano rush of the nineteenth century (Ashmead, 1903; Kubler, 1948). Most of these artifacts display characteristic Moche elements (ca. 100 to 800 AD) and were recovered at significant depths in the guano deposits (for an extensive discussion on Moche material culture, see Bourget and Jones, 2008; Chapdelaine, 2011; Quilter and Castillo, 2010). Therefore, these islands were likely utilized much earlier than the 1500s, although it is unclear to what end: mining guano, fishing camps, hunting guano birds, ritual activity, or a combination of some or all of these. Many authors have speculated on the potential importance of the guano islands (e.g. Benson, 1972, 1995; Covey, 2000; Fonseca and Richardson, 1978; Hocquenghem, 1977; Netherly, 1977; Shimada, 1987, 1994), but the use of guano has been difficult to demonstrate. If the effects of seabird guano fertilization on the isotopic composition of plants can be understood, it may be possible to assess the potential importance of guano as a fertilizer through the isotopic analysis of human or animal remains, and potentially archaeobotanical remains (Aguilera et al., 2008; DeNiro and Hastorf, 1985; Fiorentino et al., 2012; Lightfoot and Stevens, 2012) or sediment profiles (Griffiths et al., 2010; Liu et al., 2006; Yuan et al., 2010).

4.3 Factors Affecting the Nitrogen Isotopic Composition of Terrestrial Plants

A number of environmental and physiological factors influence the nitrogen isotopic composition of plant tissues (reviewed by Craine et al., 2009; Högberg, 1997; Kohl and Shearer, 1995; Robinson, 2001; Yoneyama, 1995). Plants utilize several forms of inorganic nitrogen, primarily ammonium (NH_4^+) and/or nitrate (NO_3^-), but also gaseous nitrogen (N_2) in some species (e.g. legumes). The extent to which plants rely on these various N sources is significant because the processes that lead to their production in the soil (ammonification, nitrification) and their assimilation into organic N within plants are associated with different fractionation factors (Högberg, 1997; Robinson, 2001). Moreover, because of the differential capacity for NO_3^- to be assimilated in the root or the shoot (NH_4^+ is assimilated only in the root), the extent to which plants rely on these sources may also play an important role in the extent of intraplant isotopic variability (Evans et al., 1996). When NO_3^- is immediately assimilated into organic N in the root, any remaining NO_3^- routed to the shoot for assimilation has already been exposed to an assimilatory event that is associated with isotopic fractionation. Therefore, NO_3^- that is assimilated in the shoot is relatively enriched in ^{15}N compared to NO_3^- assimilated in the root. Shoot $\delta^{15}N$ values should be higher than root $\delta^{15}N$ values in NO_3^- fed plants.

Aside from the N source, a number of other factors play important roles in determining the nitrogen isotopic composition of plant tissues. Throughout a growing season, or the course of their lives, plants will route and re-route nitrogen contained in their tissues depending on, for example, their growth stage (e.g. vegetative vs. reproductive) or environmental conditions (e.g. onset of winter) (Bausenwein et al., 2001a; 2001b; Evans, 2001; Kolb and Evans, 2002). This is true for maize, with a large portion (60-85%) of nitrogen within the plant being reallocated to the grain during ear production (Ta, 1991; Ta and Weiland, 1992). This partitioning and movement of nitrogenous compounds may cause intraplant variation in isotopic composition because the biochemical processes that are involved (protein hydrolysis, protein synthesis) are associated with isotopic fractionations (Bada et al., 1989; Silfer et al., 1992). Therefore, it cannot be assumed that the isotopic composition of any single tissue in a plant necessarily reflects the isotopic composition of the entire plant or its N source.

Animal manures have the capacity to significantly alter the nitrogen isotopic composition of soils and plants (e.g. Bogaard et al., 2007; Choi et al., 2006; Choi et al., 2002; Choi et al., 2003; del Amor et al., 2008; Flores et al., 2007; Fraser et al., 2011; Lim et al., 2007; Nakano et al., 2003; Nakano and Uehara, 2007; Rapisarda et al., 2005; Rapisarda et al., 2010; Senbayram et al., 2008; Szpak et al., 2012a; Yun et al., 2006; Yun and Ro, 2009;

Yun et al., 2011). Specifically, plants grown in fields with animal manures tend to have higher tissue δ^{15}N values than plants grown in unfertilized fields, or fields amended with chemical fertilizers such as ammonium sulfate, ammonium nitrate, or urea. The extent to which the fertilizer will impact the δ^{15}N value of the plant will depend on a number of factors, including: (1) the diet of the animal, (2) the relative amounts of different N bearing compounds in the manure, (3) whether or not the manure has been composted, (4) the amount of time the manure has been composted, and (5) whether the composting occurred under aerobic or anaerobic conditions.

4.4 Materials and Methods

4.4.1 *Field Conditions*

We formed a farmer-researcher partnership (Karlen et al., 1995; Katsvairo et al., 2003) with a local farmer (Jorge Rodrigués Paredez), in order to construct a field-scale study on a small farm near Huancaco in the Virú Valley, northern Peru (Figure 4.1; 8°27′36″S, 78°48′14″W). The field has been cultivated since 2000, with a variety of crops being grown (asparagus, maize, alfalfa, sugar cane, squash). Prior to 2000 when an irrigation canal was constructed, the area had no access to water and was not cultivated. No evidence of prehistoric irrigation canals exist and it is therefore unlikely that this particular area was cultivated for at least the last several hundred years. Animals are not encouraged to graze these fields, although it is possible that small numbers of goats may have passed through the area prior to it being opened up for cultivation in 2000. We therefore do not expect an appreciable contribution of animal fertilizers not associated with this experiment to the field. The farmer that cultivates the field has used a chemical fertilizer (ammonium sulfate) and not animal manure. It is thus possible that some N derived from previous chemical fertilizer applications may have been present in the soil during the course of this experiment. The majority of residual N from chemical fertilizer applications, however, tends to be quickly immobilized, with only a small amount (~5%) being present in mineralized form and available for plant uptake (Olson, 1980). Additionally, leaching of chemical fertilizer N as NO_3^- is recognized as a major problem (Costa et al., 2003; Rozas et al., 2004).

Maize used in this experiment is a variety commonly grown on the coast of Peru and is known locally as *diente de mula*. Seeds were planted on April 28, 2010 and maize was harvested on October 4, 2010. All numeric dates referred to hereafter (e.g. 35 d) represent days elapsed after planting. Four plots were separated based on the type of fertilizer used: AS (ammonium sulfate), CO (control, no fertilizer), DU (camelid dung), and SG (seabird guano) (Figure 4.3). Each of the four plots was $36m^2$ (6×6m), and was fed by a separate irrigation channel; irrigation was the only source of water throughout the course of the experiment. Plots were separated by raised furrows to minimize the exchange of materials. The experimental area was previously part of a single zone of cultivation, with the four plots being constructed for the purposes of this experiment. The history of cultivation did not differ in any way between the different plots in which maize was grown in this study. Therefore, we have no reason to believe that there would be any differences in the soil quality, potential residual fertilizer N, or chemical composition of dissolved minerals in irrigation water, between the plots.

Fertilizer was applied to the soil surface on May 17, 2010 (19 d) and June 2, 2010 (35 d), in the following amounts: 12 kg (AS), 11 kg (DU), 8 kg (SG). These amounts are equivalent to the following N application rates: 700 kg $N{\cdot}ha^{-1}$ (AS), 75 kg $N{\cdot}ha^{-1}$ (DU), 200 kg $N{\cdot}ha^{-1}$ (SG). No fertilizer was applied to the control plot (CO). These particular amounts of fertilizer were selected largely following the advice and wishes of the farmer who owned and cultivated this field and the surrounding area. Fertilizers were applied after seedling establishment because seabird guano has the potential to inhibit seedling germination and establishment (Szpak et al., 2012a).

Seabird guano was purchased at a local market in Peru and camelid dung was collected from a pasture north of Sausacocha Lake near Huamachuco (Figure 4.1). Only alpacas were observed depositing dung on this pasture, but because it is possible that a small amount of llama dung may also have been included, we refer to the dung as ‘camelid’.

Temperature and relative humidity were typical for northern Peru during the study period; no rain events were recorded during the study period.

Leaf samples were taken from five plants selected at random twice a month (on the 15th and last day of each month) beginning 21 days after planting. At the conclusion of the experiment, stalks and grains were sampled from eight plants.

4.4.2 *Isotopic Methodology*

All plant materials were air-dried on site at room temperature following sampling. Samples were then air-dried at 90ºC for at least 72 hours in the laboratory. Following this, samples were ground using a Wig-L-Bug (Crescent) and stored at room temperature in sealed glass vials.

Five aliquots of ~25g each of ammonium sulfate, camelid dung and seabird guano were ground to fine powders using a mortar and pestle. The purpose of the analysis of these aliquots was to attempt to account for any variability in the nitrogen isotopic compositions of the fertilizers. This material was air-dried as described above prior to isotopic analysis. Nitrogen isotopic compositions and elemental nitrogen contents were determined using a Thermo Finnigan Delta V isotope ratio mass spectrometer coupled to a Costech elemental analyzer. For the analysis of δ^{15}N, excess CO_2 was removed with a Carbo-Sorb® trap (Elemental Microanalysis). Sample reproducibility was ±0.09‰ for δ^{15}N (21 replicates), and ±0.08 for %N (20 replicates). A δ^{15}N value of 6.31±0.11‰ was obtained for 75 analyses of an internal keratin standard calibrated against international standards USGS-40 (glutamic acid) and USGS-41 (glutamic acid), which compared well with its average value of 6.36‰.

4.4.3 *Statistical Analyses*

Differences in isotopic and elemental compositions between treatments and plant parts were assessed with a one-way analysis of variance (ANOVA). Homogeneity of variance was assessed using Levene’s test, and a *post hoc* Tukey’s honestly significant difference (HSD) statistic was applied if variance was homoscedastic, or Dunnett’s T3 test was applied if variance was not homoscedastic. For all statistical analyses, a significance level of $p<0.05$ was used. Statistical analyses were performed in SPSS 16.

4.5 Results and Discussion

4.5.1 *Nitrogen Isotopic Composition of Fertilizers*

The δ^{15}N values for the three fertilizers used in this study were significantly different from one another ($F_{[2,12]}$=7,977.5, p<0.001): ammonium sulfate −0.7±0.1‰, camelid dung 13.9±0.6‰, seabird guano 38.1±0.6‰. All data for fertilizers are listed in Table 4.1. The low δ^{15}N value of the ammonium sulfate is typical of chemical fertilizers, which tend to have nitrogen isotopic compositions close to 0‰ (Bateman et al., 2005; Bateman and Kelly, 2007; Choi and Ro, 2003; Choi et al., 2007; Rogers, 2008; Yun et al., 2006). The N content of the ammonium sulfate fertilizer was determined to be 21.1±0.1%.

The camelid dung had a much higher δ^{15}N value (13.9±0.6‰) than the chemical fertilizer, and was also considerably higher than δ^{15}N values that have been recorded for cattle manure (2.9 to 5.0‰; Dijkstra et al., 2006; Kerley and Jarvis, 1996; Rogers, 2008; Steele and Daniel, 1978), but comparable to δ^{15}N values for composted pig manure (13.9 to 16.9‰; Choi et al., 2002; Lim et al., 2007; Yun et al., 2006; Yun et al., 2011). The total N content of the camelid dung was determined to be 2.4±0.6%.

The reason for the relatively high camelid dung δ^{15}N values likely relates to isotopic fractionation associated with ammonia volatilization and the communal defecation/urination practices of the South American camelids. A simplified schematic showing the fate of camelid manure N is presented in Figure 4.4. Several studies of different herbivore manures have found that a large portion of manure nitrogen is lost as gaseous ammonia relatively rapidly after excretion (James et al., 1999; Lee et al., 2011; Martins and Dewes, 1992; Thomsen, 2000). This process is much more significant in urinary N than in fecal N for mammals (Lockyer and Whitehead, 1990; Petersen et al., 1998). Because the volatilization of ammonium to gaseous ammonia is associated with a large fractionation (−25 to −60‰), which concentrates the remaining substrate (in the manure) in ^{15}N (Hermes et al., 1985; Kreitler, 1975; Mizutani et al., 1985a; Mizutani et al., 1985b; Robinson, 2001), the δ^{15}N value of manure tends to increase (by 3 to 10‰) within days following excretion (Hristov et al., 2006; Hristov et al., 2009; Kim et al., 2008; Lee et al., 2011). In addition to this, the manner in which camelids habitually defecate and urinate in the same area suggests the contribution of some urinary N to manure collected to be used as fertilizer (somewhat akin to ‘slurry’ fertilizers). If this is the case, this would help to explain the relatively high δ^{15}N values observed for camelid dung in this study. It is likely that the diets of prehistoric camelids (e.g. DeNiro, 1988; Finucane et al., 2006; Thornton et al., 2011; Verano and DeNiro, 1993) and the conditions under which dung may have been collected and stored differed markedly between and potentially within regions. It is therefore probable that the physical and chemical properties of camelid dung (including nitrogen isotopic composition) used for fertilizer were highly variable. Additional studies exploring the biogeochemistry of camelid dung fertilization are necessary to fully understand this and related issues.

The seabird guano had a δ^{15}N value of 38.1±0.6‰, which is the highest recorded for an organic fertilizer to date. The total N content of the seabird guano was determined to be 8.2±0.9%. A simplified schematic showing the fate of seabird guano N is presented in Figure 4.5. The δ^{15}N value determined for the guano is much higher than what would be expected based solely on the trophic level of the birds that produced the excrement (3.5 to 4.5). Tissue δ^{15}N values for Peruvian guano birds and similar species range typically between 16 and 22‰ (Forero et al., 2004; Schoeninger and DeNiro, 1984; Tieszen and Chapman, 1992). Bird et al. (2008) reported the difference between bulk guano and diet to be 1.5 to 2.5‰, and Wainright et al. (1998) reported an average δ^{15}N value of bulk guano to be 2.5‰ lower than seabird blood. As was the case with the camelid dung, ammonia volatilization likely played an important role in the elevated δ^{15}N values of the guano.

Ammonia volatilization has been recognized as an extremely important process in the vicinity of seabird nesting sites (Lindeboom, 1984; Zhu et al., 2011). As discussed above, seabird guano, and the excreta of all birds, is compositionally very different than mammalian excreta. It is a mixture of urine and feces, which tends to contain proportionately more nitrogen on a dry weight basis, with the bulk of this nitrogen as uric acid (Nicholson et al., 1996; Wright, 1995). This is significant because uric acid is very rapidly and completely mineralized in soils to ammonium (Kirchmann, 1991). In seabird rookeries, much of this ammonium (possibly >75%; Lindeboom, 1984) is lost through volatilization to gaseous ammonia. As discussed above, this process is associated with a large fractionation, which leaves the remaining ammonium highly enriched in ^{15}N. Therefore, the guano collected from the islands was likely subjected to ammonia volatilization and subsequent enrichment in ^{15}N prior to collection. That said, ammonia volatilization occurs much more rapidly in moist soil (Ernst and Massey, 1960; Ferguson and Kissel, 1985), and it is thus unlikely to have been as significant as in other wetter environments because of the hyper-arid conditions of the Peruvian guano islands.

The nitrogen isotopic compositions of animal fertilizers are highly variable and are influenced by a number of factors other than the diet or trophic level of the animal. As discussed above, the isotopic composition of manure depends on the relative proportions of N bearing compounds in the manure (organic N, urea, uric acid, nitrate, ammonia), the speed at which they are mineralized (for organic N), and the fractionations associated with their decomposition in the soil.

The detection of fertilization practices using isotopic analysis is complicated by the fact that the isotopic composition of manure can change over time. These changes may occur after the manure is applied to the soil, and/or prior to the application of manure to the soil. Several authors have noted that composting significantly impacts the δ^{15}N values of animal manures (Hristov et al., 2006; Hristov et al., 2009; Lee et al., 2011). The type of bedding material used may also impact composted manure δ^{15}N values (Kim et al., 2008). Further investigation and consideration of the elemental and isotopic compositions of a wider range of fertilizers that may have been important in antiquity is crucial. Equally as important, however, is a thorough understanding of the availability of various N bearing species from manures (cf. Choi et al., 2006).

4.5.2 *Nitrogen Isotopic Composition of Fertilized Plant Organs*

Mean nitrogen isotopic compositions and elemental nitrogen contents for plant organs sampled at harvest, as well as leaves sampled throughout the course of the experiment are presented in Table 4.2. Individual results for all plant tissues are presented in Table 4.3. There were significant differences in δ^{15}N values between the SG and CO treatments for all tissues sampled, and between DU and CO for grain and leaves, but not for stalk (Table

4.2, Figure 4.6). The AS plants had significantly lower grain $\delta^{15}N$ values than the CO plants, but stalk and leaf $\delta^{15}N$ value did not differ significantly. The magnitude of the difference in $\delta^{15}N$ between the SG and CO plants ($\Delta^{15}N_{SG-CO}$=14.9‰ for grain, 11.3‰ for stem, 20.0‰ for leaves at 138 d) was much greater than between DU and CO ($\Delta^{15}N_{DU-CO}$=1.8‰ for grain, 2.3‰ for stem, 4.2‰ for leaves at 138 d) (Figure 4.6).

While the nitrogen isotopic composition of AS grain was significantly lower than the CO grain, the magnitude of this difference was only 0.5‰. A lack of differentiation in $\delta^{15}N$ between control plants and plants fertilized with ammonium sulfate has been observed in other studies examining the effect of chemical fertilizers on plant nitrogen isotopic composition. Kriszan et al. (2009) found no significant differences in $\delta^{15}N$ between plants grown with no fertilizer or with ammonium sulfate in a temperate grassland. Similarly, Yun et al. (2011) found no significant difference in $\delta^{15}N$ between ammonium sulfate fertilized and control plants for rice (*Oryza sativa* L.) roots and grains, but a significant difference for shoots (~3‰).

The camelid dung fertilized maize was characterized by higher $\delta^{15}N$ values relative to the control maize for all tissues analyzed. The magnitude of the difference in $\delta^{15}N$ between the CO and the DU plant tissues (1.8 to 4.2‰) is comparable to other studies that have utilized mammalian manures (Bateman et al., 2005; Fraser et al., 2011; Lim et al., 2007; Nakano and Uehara, 2007; Yun et al., 2011). The pattern observed in this study demonstrates significant uptake of camelid dung-derived N by maize after a single season of fertilization at a relatively low application rate (75 kg $N \cdot ha^{-1}$).

It is possible that long-term application of this manure to agricultural fields and/or application at a higher rate would result in a greater increase in plant $\delta^{15}N$. Fraser et al. (2011) observed that the distinction in plant $\delta^{15}N$ values between fertilized (cattle manure) and unfertilized plots was much greater in long-term (manure applied for several years or decades) than in short-term (single application of manure) studies. Specifically, they suggested a ‘pronounced manuring effect’ becomes apparent a decade after plot establishment. Other studies have demonstrated greater increases in plant $\delta^{15}N$ values with higher application rates of organic fertilizers (Yun and Ro, 2009) because the availability of N derived from organic fertilizers tends to increase with the rate of application (Burger and Venterea, 2008; Habteselassie et al., 2006). This is true both in the short term because of the rapid release and mineralization of labile N, and in the long term because of the slow release of manure N, which was initially immobilized, over a period of many years (Burger and Venterea, 2008; Sørensen and Amato, 2002). Additionally, the influence of urinary N that has mixed with fecal N at camelid defecation sites may play an important role in the immediate 'manuring effect' that was observed in the nitrogen isotopic composition of maize in this study. This N, which is rapidly mineralized, may provide an initial pulse of inorganic N for plants shortly after fertilizer application.

As was the case with the DU plants, there was a significant difference in plant tissue δ^{15}N values between the SG and CO maize, although the magnitude of this difference was much greater. This is partially explained by the very high δ^{15}N values of the seabird guano (38.1±0.6‰), but equally important is the availability of nitrogen from the seabird guano. The rate of application of the two fertilizers (camelid dung and seabird guano) was similar, but because the seabird guano contained approximately three times as much nitrogen as the camelid dung, the rate of application, in terms of total N, was much higher in the seabird guano plot. Moreover, the guano N was more readily available for plant uptake than the camelid dung N. The primary N-bearing compound in bird excrement (uric acid) is rapidly and completely converted to NH_4^+, and in turn to NO_3^-, such that a very large portion of the guano N is mineralized and available for plant uptake within a few days or weeks of application (Hadas and Rosenberg, 1992; Kirchmann, 1991; Sims and Wolf, 1994). For these reasons, a much greater amount of guano-derived, compared to dung-derived, nitrogen would likely be available to plants, particularly in the short term.

4.5.3 *Intraplant δ^{15}N Variability*

The biochemical processes associated with the catabolism and synthesis (e.g. deamination, transamination) of N-bearing species within a plant may be associated with significant fractionations (Macko et al., 1986; Macko et al., 1987; Tcherkez, 2011;

Werner and Schmidt, 2002) that should concentrate nitrogen sources (e.g. senescent leaves) in ^{15}N, and produce nitrogen sinks (e.g. grains) that are comparatively depleted of ^{15}N (e.g. Choi et al., 2002; Choi et al., 2005a; Gebauer et al., 1994; Näsholm, 1994), although some studies have not observed this effect (e.g. Fraser et al., 2011; Garten, 1993; Kolb and Evans, 2002).

Intraplant differences in δ^{15}N were significant for CO and AS treatments, but not for SG and DU treatments (Table 4.3). For CO, AS, and DU treatments, the stalk had the highest δ^{15}N values, while the leaves had the lowest δ^{15}N values. No clear pattern of intraplant variability was evident in the SG treatment. The generally high stalk δ^{15}N values relative to the grain suggests that the stalk serves as an important source for absorbed N that is later reallocated to the grain during ear production, enriching the source (stalk) in ^{15}N relative to the sink (grain) as described above. This pattern of ^{15}N enrichment in stalks relative to grains was suggested previously by Szpak et al. (2012a) based on isotopic data from growth chamber grown maize fertilized with seabird guano. More generally, there is a large body of experimental evidence demonstrating the role of the stalk as an important, or dominant, source of absorbed N that is later allocated to the grain during ear development (Rizzi et al., 1991; Subedi and Ma, 2005; Ta, 1991; Ta and Weiland, 1992; Ta et al., 1993).

One of the more important implications of the intraplant variability observed in this study relates to the consumption of different plant parts by humans and animals, respectively. The practice of allowing animals to graze on byproducts in agricultural fields is widely known from modern observations throughout the world (e.g. Goland, 1993; Ibrahim et al., 1988; Miehe, 1986; Salzman, 1971; Wiegers et al., 1999), including for camelids in the Andes (McCorkle, 1987; Mitchell, 1991; Nielsen, 2001). In some cases, this act of animal grazing is seen as particularly beneficial because the animal excrement that is left on the fields acts as a fertilizer for the next growing season (Salzman, 1971). The significant point here is that if animals subsisted to a large extent on agricultural byproducts, it is very possible that this could lead to animals having tissues relatively enriched in ^{15}N compared to humans that consumed grain from the same plants. The consumption of these animals by humans adds another complication to the interpretation of the relative contributions of plant and animal protein. The relationship between the isotopic compositions of grains/fruits and leaves/stems requires further exploration before any generalizations can be made in this respect.

4.5.4 *Implications for Dietary Reconstruction using Stable Isotopes*

On the basis of studies conducted with manures derived from other terrestrial herbivores, differentiating human diets composed primarily of plant or animal protein using stable isotope analysis of bone collagen or similar tissues would be difficult if crops were amended with manure. As discussed by Bogaard et al. (2007), the differentiation of largely plant vs. animal based diets is dependent on the observation that there is a consistent enrichment in ^{15}N at each trophic level (Caut et al., 2009; Minagawa and Wada, 1984). There is considerable variability in ^{15}N trophic enrichment, but based on a survey of published literature, Szpak et al. (2012c) found it to be +3.7±1.6‰ for mammalian bone collagen. Therefore, the difference in δ^{15}N values between the CO and DU maize grain (1.8‰) is roughly equivalent to half a trophic level, with greater differences for the stem (2.3‰) and leaves (4.2‰). As discussed previously, it is possible that higher application rates and long-term fertilization could have an even more pronounced effect on plant δ^{15}N values. This implies that in the Andes, the fertilization of crops with camelid dung has the potential to complicate interpretations of the consumption of plant vs. animal protein using bulk isotopic analysis of tissues such as bone collagen. This is a particularly important consideration as the possibility that fertilization with camelid dung was an integral part of the successful wide-scale adoption of maize agriculture in southern Peru (Cuzco area) has recently been suggested (Chepstow-Lusty, 2011). The use of camelid dung could have been much more widespread, however, including lower altitudes zones and the coast, where there is evidence for the breeding of camelids (Rostworowski, 1981; Shimada and Shimada, 1985; Wilson, 1988).

A limited number of archaeological camelids from coastal and low altitude sites that have been subjected to isotopic analysis are characterized by relatively high δ^{15}N values (>10‰), which are thought to be indicative of the consumption of marine resources, *lomas* plants, or fertilized plants (DeNiro, 1988; Thornton et al., 2011). The consumption of self-fertilized wild vegetation or crops by camelids is certainly possible and may partially explain these relatively high δ^{15}N values. Another very plausible explanation for these unusually high δ^{15}N values is related to the arid nature of much of the Peruvian coastal region. It is established that such conditions may cause markedly high plant nitrogen isotopic compositions (Hartman, 2011; Heaton, 1987; Murphy and Bowman, 2006, 2009; Sealy et al., 1987), which are also reflected in local fauna (Ambrose and DeNiro, 1987; Gröcke et al., 1997; Pate and Anson, 2008; Schwarcz et al., 1999). Intensive regional sampling programs of Peruvian plants for isotopic analysis will aid in clarifying these issues.

In comparison to the relatively modest enrichment in ^{15}N in the DU plants, the SG plants were characterized by much higher δ^{15}N values. Whereas plants fertilized with camelid dung, or the dung of other mammalian herbivores (e.g. cow, sheep, horse), may be isotopically similar (in terms of δ^{15}N) to the tissues of such herbivores, the seabird guano fertilized plants exhibited δ^{15}N values that are comparable to, and often greater than, high-trophic level marine animals, such as pinnipeds, predatory fish, and piscivorous seabirds (Forero et al., 2004; Mayr et al., 2011; Schoeninger and DeNiro, 1984; Tieszen and Chapman, 1992). Even higher δ^{15}N values were observed for guano-fertilized maize grown in containers under controlled conditions (Szpak et al., 2012a).

Maize is a C_4 plant, with δ^{13}C values in the range of −15 to −10‰ (Jahren et al., 2006; Lasa et al., 2011; Piasentier et al., 2003; Szpak et al., 2012a; Tieszen and Fagre, 1993; White et al., 2001), which are comparable to those of many high trophic level marine animals (Richards and Hedges, 1999; Schoeninger and DeNiro, 1984; Szpak et al., 2009). The use of animal manure fertilizers has been suggested by some investigators to cause plants to have ^{13}C-depleted tissues relative to plants grown with chemical fertilizers, although the differences are very small in magnitude (≤1‰; Camin et al., 2011; Georgi et al., 2005; Lim et al., 2007). In many other studies, however, no systematic variation has been observed (Birkhofer et al., 2011; Bol et al., 2005; Camin et al., 2007; Flores et al., 2007; Nakano et al., 2003; Rapisarda et al., 2010; Szpak et al., 2012a). Those studies that have observed differences in plant $\delta^{13}C$ values associated with organic fertilization have contrasted organically and inorganically fertilized plants, rather than organically fertilized and control plants. Previously, we found no relationship between maize $\delta^{13}C$ values and the application of Peruvian seabird guano fertilizer in a growth chamber experiment (Szpak et al., 2012a). There is, therefore, no evidence that suggests plant $\delta^{13}C$ values would change substantially as a result of fertilization with animal manure.

When maize is fertilized with seabird guano, the carbon and nitrogen isotopic compositions of the plant's tissues will be very similar to those of high trophic level marine animals. Therefore, in the same way that the differentiation between plant and animal protein is complicated by the possibility of fertilization with livestock manure, the differentiation between terrestrial and marine protein is complication by fertilization of maize with seabird guano. This is particularly relevant since many of the areas where guano fertilization is suspected are located on, or in close proximity, to the coast (Bawden, 1996; Benson, 1972, 1995; Hocquenghem, 1977; Netherly, 1977; Nordt et al., 2004; Shimada, 1987, 1994), and hence, both guano and marine resources would have been accessible.

As a very simple illustrative example, we have applied the IsoSource mixing model (inputs: tolerance=0.1, increment=1) presented by Phillips and Gregg (2003) to three different scenarios that differ only in the nitrogen isotopic composition of maize caused by fertilization (Table 4.4; Figure 4.8). In each of the three scenarios, the consumer (represented by a black × in Figure 4.8) has an isotopic composition ($\delta^{13}C = -10‰$, $\delta^{15}N = 22‰$) that would traditionally be interpreted as being indicative of a marine-intensive diet. In Scenario A (no fertilization), the reconstructed diet is dominated by sea lion, followed by sardine; the three terrestrial foods (maize, potato, llama) contribute very little (Table 4.4). For a consumer with high carbon and nitrogen isotopic compositions (as presented in Figure 4.8), the small shift in nitrogen isotopic composition resulting from maize fertilization with camelid dung (Scenario B) has little impact on the relative contributions of the different foods (Figure 4.8B). This would not necessarily be true in other contexts where the impact of marine foods is smaller, and the main animal protein source has a similar carbon isotopic composition to the fertilized maize; this might be expected in the high altitude regions of the Andes, where camelid dung fertilization is suspected to have been important (Chepstow-Lusty, 2011).

In Scenario C (guano fertilization), the relative contributions of the terrestrial foods (llama and potato) remains very low, the mean contributions of the marine foods (sardine and sea lion) remain high, and the mean contribution of maize increases significantly. More important than this, however, is the change that occurs in the shape of the mixing polygon formed by the sources (top panels of Figure 4.8). The convergence in δ^{15}N values between the maize and the marine sources (particularly the sea lion) causes a narrowing of the polygon, which leads to more diffuse solutions for the sea lion and guano fertilized maize (Figure 4.8C). This contrasts to Scenarios A and B (Figure 4.8A, B), in which the solutions for maize and sea lion are well constrained. In a practical sense, this simply demonstrates that when maize is fertilized with seabird guano, the quantitative differentiation between maize consumption and marine resource consumption on the basis of bulk tissue isotopic composition becomes more difficult. The application of carbon isotopic analysis of individual amino acids isolated from bone collagen (e.g. Corr et al., 2005) may be necessary to truly differentiate between maize and marine-based diets where the potential use of seabird guano fertilizer exists, but this avenue of research requires much additional exploration.

While a growing number of studies have examined the isotopic composition of archaeological human (e.g. Finucane et al., 2006; Finucane, 2007; Kellner and Schoeninger, 2008; Knudson et al., 2007; Slovak and Paytan, 2011; Tomczak, 2003; Verano and DeNiro, 1993; White et al., 2009; Williams and Katzenberg, 2012) and animal (e.g. DeNiro, 1988; Finucane et al., 2006; Thornton et al., 2011; Verano and DeNiro, 1993) remains from the Andean region, it is relatively difficult to assess any particular cases that provide *direct* evidence for the use of seabird guano and/or camelid dung as a fertilizer. Some of the extremely high (>20‰) δ^{15}N values presented for numerous individuals from several Chiribaya sites in the Osmore drainage of southern Peru (Tomczak, 2003) are certainly suggestive of the potential importance of guano, but as discussed above, the isotopic analysis of bulk tissues such as bone collagen does not provide sufficient resolution to differentiate between the consumption of high trophic level marine resources and guano-fertilized maize. Therefore, both of these alternatives must be considered as potential explanatory factors when interpreting isotopic data from archaeological materials from the Andes.

The uncertainty inherent in the interpretation of isotopic data as discussed above highlights the importance of integrating multiple lines of evidence in the reconstruction of ancient diet, particularly the consideration of relevant zooarchaeological and paleoethnobotanical data. With respect to zooarchaeology in particular, these data can provide basic and very essential information in terms of the presence and abundance of particular taxa in the subsistence economy. In cases where a significant maritime adaptation is evident in the zooarchaeological assemblages (e.g. Marcus et al., 1999; Reitz, 1988a, 2001; Sandweiss et al., 1989; Sandweiss, 1992), a more reasonable case can be made for the consumption of marine resources being responsible for particularly high carbon and nitrogen isotopic compositions. With respect to paleoethnobotany, in addition to documenting the presence of particular crops that may have been cultivated and fertilized, the isotopic analysis of macrobotanical remains (Aguilera et al., 2008; Araus et al., 1997; Araus et al., 1999; Araus et al., 2001; DeNiro and Hastorf, 1985; Fiorentino et al., 2012; Heaton et al., 2009; Lightfoot and Stevens, 2012) hold the greatest potential to provide unequivocal evidence of the fertilization of crops. This is especially true for seabird guano because the enrichment in plant tissue ^{15}N is much larger than what would be expected in unfertilized crops. Conversely, camelid dung fertilization would be more difficult to detect with such analyses due to the much more modest enrichment in plant tissue ^{15}N. This is particularly true in the dry coastal region of Peru and Chile, where higher plant δ^{15}N values may simply be related to water availability; such effects have been observed throughout the world on many scales (Craine et al., 2009; Handley et al., 1999a; Swap et al., 2004), and in several other crop species in particular (Lopes et al., 2004; Lopes and Araus, 2006).

4.5.5 *Implications for Historical Dietary Reconstruction*

The implications of this study are not limited to the Andes. Millions of tonnes of guano were exported to Europe and North America during the nineteenth century (Figure 4.9). Peruvian seabird guano was the most highly prized fertilizer at the time and a focal point of the Peruvian economy (Cushman, 2003; Hollett, 2008; Mathew, 1972). Between 1851 and 1872, ten million tons of guano were exported from the Chincha Islands group (Figure 4.1) alone, the value of which would be equivalent to approximately $13.6 billion 2011 USD (Hollett, 2008). Great Britain and the United States were by far the most significant importers of guano during the nineteenth century, although many other European countries (France, the Netherlands, Italy, Belgium, Norway, Sweden, Russia) were also involved in the trade (Clark and Foster, 2009; Hollett, 2008).

It is very difficult to discern to which crops guano was predominantly applied during the guano boom of the nineteenth century as no records are readily available, but it appears that various grasses, wheat, and potatoes all received significant fertilization with guano in Britain (Mathew, 1970). In the United States, guano was definitely used on corn, wheat, oats, tobacco, and cotton (Jordan, 1950; Taylor, 1947), although it was marketed as a miracle fertilizer that would aid in the growth of any crop (e.g. Tegarden, 1854). It is thus probable that a much wider variety of crops were fertilized with guano.

In recent years, stable isotope analysis of historic human skeletal material has provided considerable insight into the diet and lifeways of these individuals (e.g. Cox and Sealy, 1997; Cox et al., 2001; Katzenberg et al., 2000; Katzenberg, 1995; Klippel, 2001; Roy et al., 2005; Schroeder et al., 2009; Sealy et al., 1995; Valentin et al., 2006). Given the historic importance of guano fertilization, particularly in the United States and Britain, the potential influence of guano on the isotopic composition of foods that humans may have been consuming must be considered.

4.5.6 *Implications for Prehispanic Andean Use of the Guano Islands*

As discussed previously, direct evidence for the use of seabird guano in the Andes prior to the sixteenth century is lacking. Speculation about the potential use of guano and/or the guano islands has therefore largely been informed by prehispanic ceramic art and material culture, which has focused heavily on the Moche for two reasons. First, guano birds, the guano islands, and related imagery play significant roles in Moche material culture (Figure 4.10). Scenes depicting the hunting of seals or sea lions are also common

(Figure 4.11) and often portray what have been interpreted as guano islands (Figure 4.12). Depictions of boats loaded with what have been suggested to be captives destined for the guano islands have also been found (Figure 4.13). Second, the vast majority of the objects recovered from deposits on the guano islands during the nineteenth century display Moche stylistic elements (Kubler, 1948), even those from islands off the south coast of Peru (e.g. Chincha). The relatively small number of isotopic data for human bone collagen analyzed thus far from Moche sites are characterized by relatively low δ^{15}N values when compared with human δ^{15}N values from southern Peru (Figure 4.14). Given the clear evidence from both growth chamber and field studies for the potentially massive increase in plant tissue δ^{15}N values resulting from guano fertilization, the data recorded thus far for archaeological bone collagen suggest that the Moche were not making use of seabird guano as a fertilizer for maize or for other crops. Nevertheless, it is almost certain that the guano islands were significant locales for the Moche even if the extraction of seabird guano for agriculture was unimportant. A more detailed discussion of these issues would be largely speculative and beyond the scope of this paper (but see Fonseca and Richardson, 1978; Lumbreras, 1978; Shimada, 1987, 1994; Topic, 1977; Van Deusen, 2000).

4.6 Summary and Conclusions

The application of camelid dung and seabird guano fertilizers to maize resulted in significantly higher plant δ^{15}N values during the first year of growth after a single application of these fertilizers. The magnitude of the increase in plant δ^{15}N was moderate for camelid dung (1.8 to 4.2‰) and substantial for seabird guano (11.3 to 20.0‰). Additional studies of this nature are required to clarify the potential effects of long term fertilization with both camelid dung and seabird guano on the isotopic composition of plants. Moreover, studies examining the influence of these fertilizers applied in different concentrations, and on different varieties of plants (e.g. leguminous plants), would be useful to better understand how the isotopic composition of plants with variable N-use strategies are affected by these, and other fertilizers. The stable isotope biogeochemistry of additional fertilizers and crops that may have been significant in other parts of the world must also be studied.

The increase in plant $\delta^{15}N$ values resulting from camelid dung fertilization has the potential to complicate dietary interpretations in terms of the relative proportions of plant and animal protein in the diet, provided these sources have similar carbon isotopic compositions. The increase in plant $\delta^{15}N$ values resulting from seabird guano fertilization of maize has the potential to complicate dietary interpretations in terms of the relative proportions of maize and marine protein in the diet. This must be taken into account in areas where the potential for maize fertilization with seabird guano exists, which includes the Andes, as well as the United States and Europe during the guano boom of the middle to late nineteenth century. The results of this study also demonstrate the inherent difficulties associated with quantitative dietary reconstruction using the bulk isotopic composition of bone collagen or similar tissues. The development and refinement of compound-specific isotopic techniques will likely aid in resolving these and similar issues.

Table 4.1. Nitrogen isotopic and elemental compositions of fertilizers used in this study.

Sample ID	**Type**	**δ^{15}N (‰, AIR)**	**%N**
AIS 1234 DU-A	Camelid dung	13.99	2.64
AIS 1234 DU-B	Camelid dung	14.19	1.99
AIS 1234 DU-C	Camelid dung	13.20	2.75
AIS 1234 DU-D	Camelid dung	13.41	1.73
AIS 1234 DU-E	Camelid dung	14.55	3.05
	Mean	**13.9±0.6**	**2.4±0.6**
AIS 1235 AS-A	Ammonium sulfate	−0.02	20.91
AIS 1235 AS-B	Ammonium sulfate	0.09	21.04
AIS 1235 AS-C	Ammonium sulfate	−0.17	21.16
AIS 1235 AS-D	Ammonium sulfate	−0.16	21.18
AIS 1235 AS-E	Ammonium sulfate	−0.07	21.09
	Mean	**−0.7±0.1**	**21.1±0.1**
AIS 1236 SG-A	Seabird guano	39.12	6.71
AIS 1236 SG-B	Seabird guano	37.76	8.65
AIS 1236 SG-C	Seabird guano	38.08	8.56
AIS 1236 SG-D	Seabird guano	37.57	8.78
AIS 1236 SG-E	Seabird guano	37.81	8.50
	Mean	**38.1±0.6**	**8.2±0.9**

Table 4.2. Nitrogen isotopic and elemental compositions of maize tissues (mean±1σ)

Treatment	Tissue	Sampling Date	*n*	$\delta^{15}N$ (‰, AIR)	%N
CO	Leaf	18	3	6.0 ± 1.8	5.6 ± 0.5
	Leaf	31	3	6.4 ± 2.1	2.7 ± 2.4
	Leaf	46	3	4.5 ± 0.9	4.1 ± 0.1
	Leaf	61	3	3.3 ± 0.3	4.3 ± 0.1
	Leaf	76	3	4.5 ± 0.9	3.7 ± 0.4
	Leaf	91	3	4.9 ± 2.3	3.6 ± 0.4
	Leaf	107	3	4.4 ± 1.7	2.8 ± 0.2
	Leaf	122	3	3.5 ± 0.9	2.4 ± 0.9
	Leaf	138	6	3.7 ± 2.0	2.0 ± 0.2
	Grain	157	6	6.3 ± 0.3	1.9 ± 0.1
	Stalk	157	6	9.8 ± 0.6	0.6 ± 0.1
DU	Leaf	18	3	9.7 ± 2.2	4.6 ± 0.3
	Leaf	31	3	7.8 ± 3.6	4.9 ± 0.8
	Leaf	46	3	7.8 ± 1.7	4.0 ± 0.5
	Leaf	61	3	7.2 ± 0.4	4.0 ± 0.4
	Leaf	76	3	7.3 ± 1.5	3.8 ± 0.8
	Leaf	91	3	10.0 ± 5.3	2.6 ± 0.5
	Leaf	107	3	10.1 ± 3.7	2.9 ± 0.7
	Leaf	122	3	5.9 ± 1.2	2.0 ± 0.7
	Leaf	138	6	7.9 ± 2.7	2.1 ± 0.5
	Grain	157	6	8.1 ± 1.6	1.6 ± 0.1
	Stalk	157	7	12.1 ± 4.0	0.9 ± 0.5
SG	Leaf	18	3	12.6 ± 2.1	4.4 ± 0.4
	Leaf	31	3	23.1 ± 0.6	4.6 ± 0.6
	Leaf	46	3	30.9 ± 6.4	2.9 ± 0.6
	Leaf	61	3	30.4 ± 0.2	4.0 ± 0.6
	Leaf	76	3	30.1 ± 3.9	3.6 ± 0.3
	Leaf	91	3	28.0 ± 5.5	3.2 ± 0.1
	Leaf	107	3	30.4 ± 2.4	1.5 ± 0.3
	Leaf	122	3	25.4 ± 3.9	1.9 ± 0.3

Treatment	**Tissue**	**Sampling Date**	***n***	**δ^{15}N (‰, AIR)**	**%N**
	Leaf	138	6	23.7 ± 2.0	2.0 ± 0.5
	Grain	157	6	21.2 ± 0.2	1.5 ± 0.1
	Stalk	157	6	21.2 ± 3.0	0.4 ± 0.1
AS	Leaf	18	3	5.1 ± 0.8	5.4 ± 0.2
	Leaf	31	3	1.4 ± 1.0	4.7 ± 0.2
	Leaf	46	3	4.8 ± 2.3	4.2 ± 0.3
	Leaf	61	3	5.9 ± 1.1	4.1 ± 0.4
	Leaf	76	3	4.2 ± 3.5	4.0 ± 0.0
	Leaf	91	3	4.5 ± 1.4	3.5 ± 0.2
	Leaf	107	3	3.4 ± 2.0	2.9 ± 0.4
	Leaf	122	3	4.9 ± 1.0	2.7 ± 0.2
	Leaf	138	6	5.0 ± 0.8	2.7 ± 0.2
	Grain	157	6	5.8 ± 0.2	1.6 ± 0.0
	Stalk	157	7	13.7 ± 3.2	1.2 ± 0.4

Table 4.3. Nitrogen isotopic and elemental compositions for all plant tissues analyzed.

Sample ID	Treatment	Tissue	Sampling Date	δ^{15}N (‰, AIR)	%N
AIS 1238A	AS	Leaf	2010/05/18	4.91	5.61
AIS 1238B	AS	Leaf	2010/05/18	4.35	5.33
AIS 1238C	AS	Leaf	2010/05/18	6.01	5.24
AIS 1242A	AS	Leaf	2010/05/31	0.33	4.82
AIS 1242B	AS	Leaf	2010/05/31	2.41	4.43
AIS 1242C	AS	Leaf	2010/05/31	1.47	4.82
AIS 1246A	AS	Leaf	2010/06/15	7.36	4.43
AIS 1246B	AS	Leaf	2010/06/15	3.12	4.21
AIS 1246C	AS	Leaf	2010/06/15	3.87	3.84
AIS 1250A	AS	Leaf	2010/06/30	4.64	3.63
AIS 1250B	AS	Leaf	2010/06/30	6.60	4.23
AIS 1250C	AS	Leaf	2010/06/30	6.61	4.31
AIS 1254A	AS	Leaf	2010/07/15	1.68	4.05
AIS 1254B	AS	Leaf	2010/07/15	8.12	4.04
AIS 1254C	AS	Leaf	2010/07/15	2.69	4.05
AIS 1259A	AS	Leaf	2010/07/30	2.80	3.37
AIS 1259B	AS	Leaf	2010/07/30	5.31	3.51
AIS 1259C	AS	Leaf	2010/07/30	5.31	3.70
AIS 1263A	AS	Leaf	2010/08/15	4.30	2.98
AIS 1263B	AS	Leaf	2010/08/15	4.86	2.45
AIS 1263C	AS	Leaf	2010/08/15	1.07	3.22
AIS 1267A	AS	Leaf	2010/08/30	3.85	2.89
AIS 1267B	AS	Leaf	2010/08/30	5.64	2.53
AIS 1267C	AS	Leaf	2010/08/30	5.34	2.80
AIS 1271A	AS	Leaf	2010/09/15	5.86	2.29
AIS 1271B	AS	Leaf	2010/09/15	5.67	2.81
AIS 1271C	AS	Leaf	2010/09/15	3.60	2.66
AIS 1271D	AS	Leaf	2010/09/15	4.92	2.78
AIS 1271E	AS	Leaf	2010/09/15	4.61	2.64
AIS 1271F	AS	Leaf	2010/09/15	5.23	2.77

Sample ID	Treatment	Tissue	Sampling Date	$\delta^{15}N$ (‰, AIR)	%N
AIS 1275A	AS	Grain	2010/10/04	5.53	1.60
AIS 1275B	AS	Grain	2010/10/04	5.74	1.66
AIS 1275C	AS	Grain	2010/10/04	5.58	1.62
AIS 1275D	AS	Grain	2010/10/04	5.86	1.64
AIS 1275E	AS	Grain	2010/10/04	5.93	1.58
AIS 1275F	AS	Grain	2010/10/04	6.07	1.63
AIS 1277A	AS	Stem	2010/10/04	20.25	0.87
AIS 1277B	AS	Stem	2010/10/04	15.50	0.74
AIS 1277C	AS	Stem	2010/10/04	10.99	1.61
AIS 1277D	AS	Stem	2010/10/04	12.89	1.19
AIS 1277E	AS	Stem	2010/10/04	13.00	1.15
AIS 1277F	AS	Stem	2010/10/04	11.41	1.62
AIS 1277G	AS	Stem	2010/10/04	12.06	1.47
AIS 1239A	CO	Leaf	2010/05/18	8.03	5.86
AIS 1239B	CO	Leaf	2010/05/18	5.03	5.85
AIS 1239C	CO	Leaf	2010/05/18	4.80	4.95
AIS 1243A	CO	Leaf	2010/05/31	6.18	0.11
AIS 1243B	CO	Leaf	2010/05/31	8.64	3.26
AIS 1243C	CO	Leaf	2010/05/31	4.42	4.76
AIS 1247A	CO	Leaf	2010/06/15	5.37	4.07
AIS 1247B	CO	Leaf	2010/06/15	3.57	4.18
AIS 1247C	CO	Leaf	2010/06/15	4.53	4.15
AIS 1251A	CO	Leaf	2010/06/30	3.15	4.18
AIS 1251B	CO	Leaf	2010/06/30	3.09	4.31
AIS 1251C	CO	Leaf	2010/06/30	3.66	4.46
AIS 1255A	CO	Leaf	2010/07/15	3.56	4.12
AIS 1255B	CO	Leaf	2010/07/15	5.35	3.56
AIS 1255C	CO	Leaf	2010/07/15	4.70	3.35
AIS 1260A	CO	Leaf	2010/07/30	3.47	3.85
AIS 1260B	CO	Leaf	2010/07/30	3.60	3.75
AIS 1260C	CO	Leaf	2010/07/30	7.56	3.09

Sample ID	Treatment	Tissue	Sampling Date	δ^{15}N (‰, AIR)	%N
AIS 1264A	CO	Leaf	2010/08/15	3.99	2.97
AIS 1264B	CO	Leaf	2010/08/15	6.36	2.61
AIS 1264C	CO	Leaf	2010/08/15	2.96	2.93
AIS 1268A	CO	Leaf	2010/08/30	2.49	2.95
AIS 1268B	CO	Leaf	2010/08/30	3.75	1.39
AIS 1268C	CO	Leaf	2010/08/30	4.22	2.93
AIS 1272A	CO	Leaf	2010/09/15	2.11	2.39
AIS 1272B	CO	Leaf	2010/09/15	4.14	1.88
AIS 1272C	CO	Leaf	2010/09/15	4.42	1.84
AIS 1272D	CO	Leaf	2010/09/15	2.89	2.20
AIS 1272E	CO	Leaf	2010/09/15	4.32	1.87
AIS 1272F	CO	Leaf	2010/09/15	4.33	1.92
AIS 1278A	CO	Grain	2010/10/04	6.08	2.04
AIS 1278B	CO	Grain	2010/10/04	6.13	1.88
AIS 1278C	CO	Grain	2010/10/04	5.96	1.77
AIS 1278D	CO	Grain	2010/10/04	6.53	1.92
AIS 1278E	CO	Grain	2010/10/04	6.61	1.69
AIS 1278F	CO	Grain	2010/10/04	6.54	1.79
AIS 1280A	CO	Stem	2010/10/04	8.84	0.56
AIS 1280B	CO	Stem	2010/10/04	10.66	0.88
AIS 1280C	CO	Stem	2010/10/04	9.87	0.59
AIS 1280D	CO	Stem	2010/10/04	10.18	0.59
AIS 1280E	CO	Stem	2010/10/04	9.55	0.60
AIS 1280F	CO	Stem	2010/10/04	9.92	0.58
AIS 1240A	DU	Leaf	2010/05/18	7.21	4.87
AIS 1240B	DU	Leaf	2010/05/18	10.63	4.24
AIS 1240C	DU	Leaf	2010/05/18	11.31	4.57
AIS 1244A	DU	Leaf	2010/05/31	3.78	5.90
AIS 1244B	DU	Leaf	2010/05/31	10.49	4.43
AIS 1244C	DU	Leaf	2010/05/31	9.28	4.43
AIS 1248A	DU	Leaf	2010/06/15	7.84	4.55

Sample ID	Treatment	Tissue	Sampling Date	δ^{15}N (‰, AIR)	%N
AIS 1248B	DU	Leaf	2010/06/15	9.51	3.51
AIS 1248C	DU	Leaf	2010/06/15	6.14	4.01
AIS 1252A	DU	Leaf	2010/06/30	6.72	4.40
AIS 1252B	DU	Leaf	2010/06/30	7.29	3.78
AIS 1252C	DU	Leaf	2010/06/30	7.47	3.69
AIS 1256A	DU	Leaf	2010/07/15	8.12	4.34
AIS 1256B	DU	Leaf	2010/07/15	8.20	2.91
AIS 1256C	DU	Leaf	2010/07/15	5.49	4.17
AIS 1261A	DU	Leaf	2010/07/30	16.10	2.62
AIS 1261B	DU	Leaf	2010/07/30	7.49	3.10
AIS 1261C	DU	Leaf	2010/07/30	6.51	2.14
AIS 1265A	DU	Leaf	2010/08/15	7.92	3.66
AIS 1265B	DU	Leaf	2010/08/15	14.29	2.70
AIS 1265C	DU	Leaf	2010/08/15	7.98	2.40
AIS 1269A	DU	Leaf	2010/08/30	7.23	1.56
AIS 1269B	DU	Leaf	2010/08/30	5.36	2.84
AIS 1269C	DU	Leaf	2010/08/30	5.11	1.52
AIS 1273A	DU	Leaf	2010/09/15	6.22	1.53
AIS 1273B	DU	Leaf	2010/09/15	6.16	2.60
AIS 1273C	DU	Leaf	2010/09/15	13.31	1.29
AIS 1273D	DU	Leaf	2010/09/15	7.60	2.26
AIS 1273E	DU	Leaf	2010/09/15	7.09	2.36
AIS 1273F	DU	Leaf	2010/09/15	6.72	2.48
AIS 1281A	DU	Grain	2010/10/04	7.77	1.48
AIS 1281B	DU	Grain	2010/10/04	7.71	1.62
AIS 1281C	DU	Grain	2010/10/04	7.64	1.60
AIS 1281D	DU	Grain	2010/10/04	8.32	1.46
AIS 1281E	DU	Grain	2010/10/04	8.41	1.64
AIS 1281F	DU	Grain	2010/10/04	8.55	1.52
AIS 1283A	DU	Stem	2010/10/04	7.17	0.33
AIS 1283B	DU	Stem	2010/10/04	6.28	1.21

Sample ID	Treatment	Tissue	Sampling Date	δ^{15}N (‰, AIR)	%N
AIS 1283C	DU	Stem	2010/10/04	14.35	0.25
AIS 1283D	DU	Stem	2010/10/04	10.79	0.53
AIS 1283E	DU	Stem	2010/10/04	15.27	1.39
AIS 1283F	DU	Stem	2010/10/04	15.50	1.37
AIS 1283G	DU	Stem	2010/10/04	15.26	1.41
AIS 1241A	SG	Leaf	2010/05/18	12.52	4.72
AIS 1241B	SG	Leaf	2010/05/18	10.57	4.46
AIS 1241C	SG	Leaf	2010/05/18	14.74	3.92
AIS 1245A	SG	Leaf	2010/05/31	22.89	4.21
AIS 1245B	SG	Leaf	2010/05/31	23.78	5.22
AIS 1245C	SG	Leaf	2010/05/31	22.76	4.23
AIS 1249A	SG	Leaf	2010/06/15	38.26	3.29
AIS 1249B	SG	Leaf	2010/06/15	26.78	2.19
AIS 1249C	SG	Leaf	2010/06/15	27.67	3.12
AIS 1253A	SG	Leaf	2010/06/30	30.45	4.56
AIS 1253B	SG	Leaf	2010/06/30	30.19	4.10
AIS 1253C	SG	Leaf	2010/06/30	30.54	3.32
AIS 1257A	SG	Leaf	2010/07/15	33.33	3.91
AIS 1257B	SG	Leaf	2010/07/15	31.27	3.53
AIS 1257C	SG	Leaf	2010/07/15	25.77	3.38
AIS 1262A	SG	Leaf	2010/07/30	26.81	3.18
AIS 1262B	SG	Leaf	2010/07/30	23.13	3.25
AIS 1262C	SG	Leaf	2010/07/30	33.98	3.06
AIS 1266A	SG	Leaf	2010/08/15	32.18	1.09
AIS 1266B	SG	Leaf	2010/08/15	27.71	1.57
AIS 1266C	SG	Leaf	2010/08/15	31.27	1.75
AIS 1270A	SG	Leaf	2010/08/30	21.49	2.12
AIS 1270B	SG	Leaf	2010/08/30	29.34	2.07
AIS 1270C	SG	Leaf	2010/08/30	25.40	1.65
AIS 1274A	SG	Leaf	2010/09/15	20.78	1.39
AIS 1274B	SG	Leaf	2010/09/15	23.42	2.57

Sample ID	Treatment	Tissue	Sampling Date	$\delta^{15}N$ (‰, AIR)	%N
AIS 1274C	SG	Leaf	2010/09/15	25.90	1.98
AIS 1274D	SG	Leaf	2010/09/15	22.68	1.41
AIS 1274E	SG	Leaf	2010/09/15	25.99	2.05
AIS 1274F	SG	Leaf	2010/09/15	23.65	2.57
AIS 1284A	SG	Grain	2010/10/04	21.38	1.56
AIS 1284B	SG	Grain	2010/10/04	21.24	1.45
AIS 1284C	SG	Grain	2010/10/04	21.06	1.51
AIS 1284D	SG	Grain	2010/10/04	21.29	1.42
AIS 1284E	SG	Grain	2010/10/04	20.90	1.43
AIS 1284F	SG	Grain	2010/10/04	21.57	1.48
AIS 1286A	SG	Stem	2010/10/04	16.36	0.39
AIS 1286B	SG	Stem	2010/10/04	18.75	0.22
AIS 1286C	SG	Stem	2010/10/04	22.13	0.43
AIS 1286D	SG	Stem	2010/10/04	23.17	0.41
AIS 1286E	SG	Stem	2010/10/04	22.99	0.38
AIS 1286F	SG	Stem	2010/10/04	23.66	0.47

Table 4.4. Results of ANOVA for differences in nitrogen isotopic and elemental compositions between treatments

Tissue	Treatment	DU	SG	AS
Leaf (138 d)	CO	**0.004**	**<0.001**	0.612
	DU	−	**<0.001**	0.055
	SG	−	−	**<0.001**
	AS	−	−	−
Grain (157 d)	CO	**<0.001**	**<0.001**	**0.027**
	DU	−	**<0.001**	**<0.001**
	SG	−	−	**<0.001**
	AS	−	−	−
Stalk (157 d)	CO	0.631	**<0.001**	0.087
	DU	−	**0.004**	0.944
	SG	−	−	**0.007**
	AS	−	−	−

Values in boldface are statistically significant ($p<0.05$)

Table 4.5. Results of ANOVA for differences in nitrogen isotopic and elemental compositions within treatments, between plant parts

Treatment	**Tissue**	**Grain (157 d)**	**Stalk (157 d)**
CO	Leaf (138 d)	**0.002**	**<0.001**
	Grain (157 d)	−	**<0.001**
DU	Leaf (138 d)	0.996	0.126
	Grain (157 d)	−	0.099
SG	Leaf (138 d)	0.070	0.281
	Grain (157 d)	−	0.999
AS	Leaf (138 d)	0.155	**<0.001**
	Grain (157 d)	−	**0.002**

Values in boldface are statistically significant ($p<0.05$)

Table 4.6. Inputs and summarized results for the mixing model presented in Figure 4.8.

Source	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C'$**	**$\delta^{15}N'$**	**% Contribution Mean ± SD (1st-99th percentile)**
Scenario A (no fertilization)					
Maize	-13.0	5.0	-9.3	8.6	2.2 ± 1.5 (0-5)
Potato	-25.0	5.0	-21.3	8.6	2.4 ± 1.7 (0-6)
Llama	-22.0	7.5	-18.3	11.1	3.3 ± 2.3 (0-8)
Sardine	-14.5	13.0	-10.8	16.6	6.8 ± 4.5 (0-16)
Sea lion	-13.0	20.0	-9.3	23.6	85.1 ± 2.4 (80-89)
Scenario B (camelid dung fertilization)					
Maize	-13.0	7.0	-9.3	10.6	2.6 ± 1.7 (0-6)
Potato	-25.0	5.0	-21.3	8.6	2.4 ± 1.7 (0-6)
Llama	-22.0	7.5	-18.3	11.1	3.3 ± 2.3 (0-8)
Sardine	-14.5	13.0	-10.8	16.6	6.7 ± 4.5 (0-16)
Sea lion	-13.0	20.0	-9.3	23.6	84.8 ± 2.2 (80-89)
Scenario C (seabird guano fertilization)					
Maize	-13.0	21.5	-9.3	25.1	29.0 ± 18.9 (0-65)
Potato	-25.0	5.0	-21.3	8.6	1.4 ± 1.2 (0-4)
Llama	-22.0	7.5	-18.3	11.1	2.2 ± 1.7 (0-6)
Sardine	-14.5	13.0	-10.8	16.6	21.8 ± 5.8 (11-34)
Sea lion	-13.0	20.0	-9.3	23.6	45.4 ± 23.6 (1-82)

$\delta^{13}C'$ and $\delta^{15}N'$ have been adjusted for diet-tissue fractionation (+3.7 for $\Delta^{13}C'$ and +3.6 for $\Delta^{15}N'$)

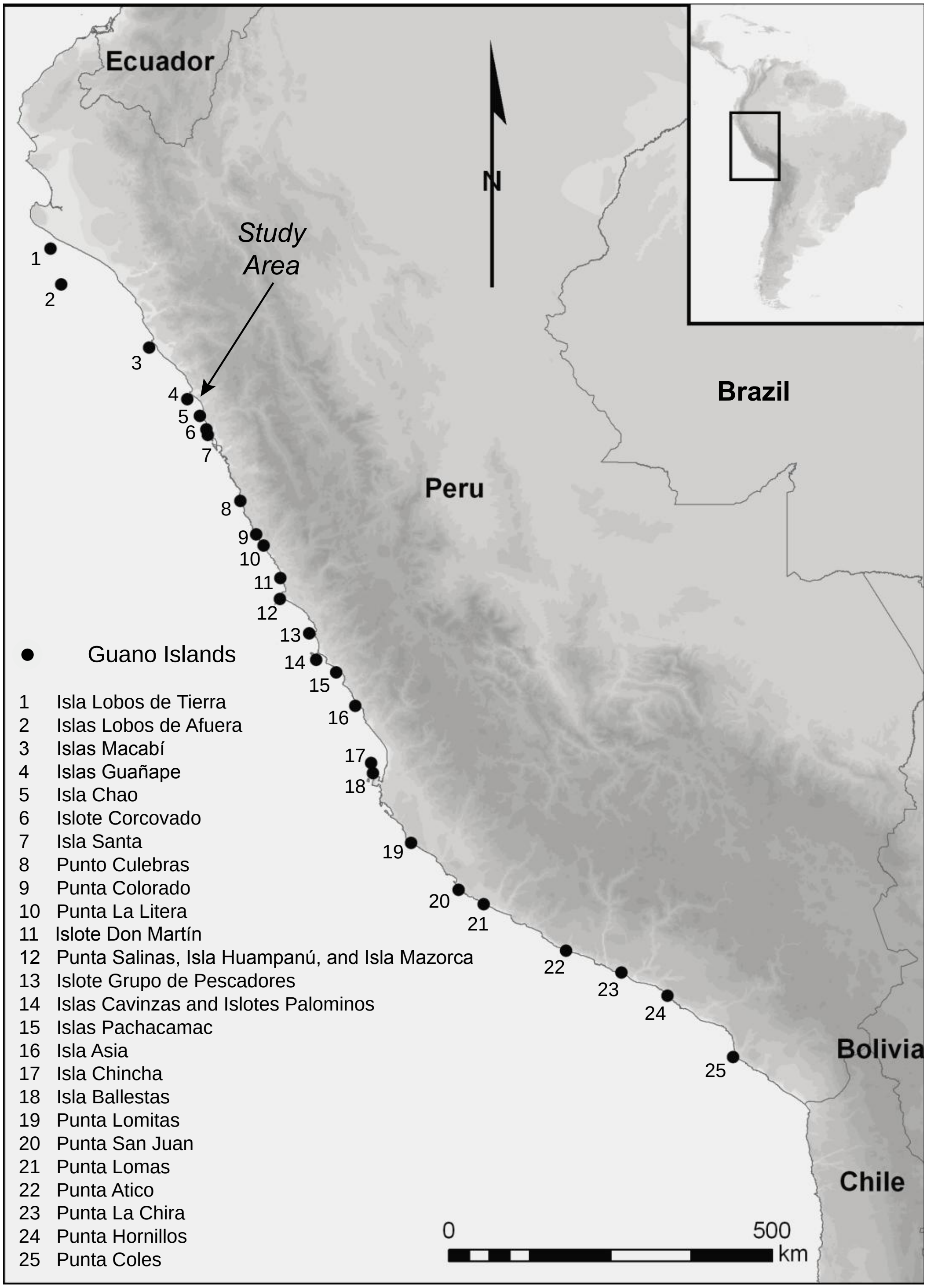

Figure 4.1. Map depicting the Peruvian guano islands. The experimental field used in this study is indicated by an arrow.

Figure 4.2. Example of a Moche artifact recovered from the guano islands depicting a nude captive with a rope around his neck (Catalogue #A151476-0, Department of Anthropology, Smithsonian Institution). As is the case for many of these objects, the exact context is unclear. Additional examples of objects recovered from the guano islands are described in detail in Kubler (1948). Photo courtesy of Christopher B. Donnan.

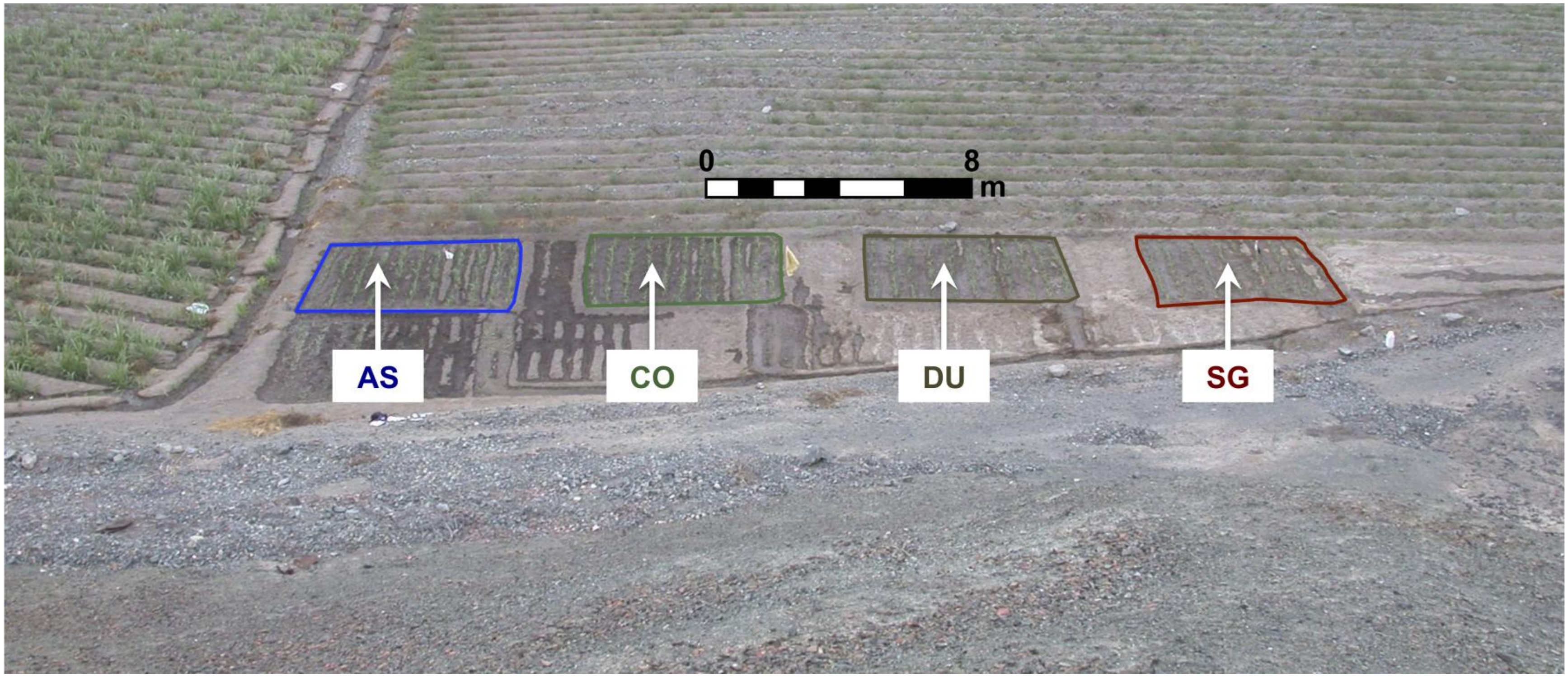

Figure 4.3. Picture of experimental plots. From left to right: AS (ammonium sulfate), CO (control, no fertilizer), DU (camelid dung), SG (seabird guano).

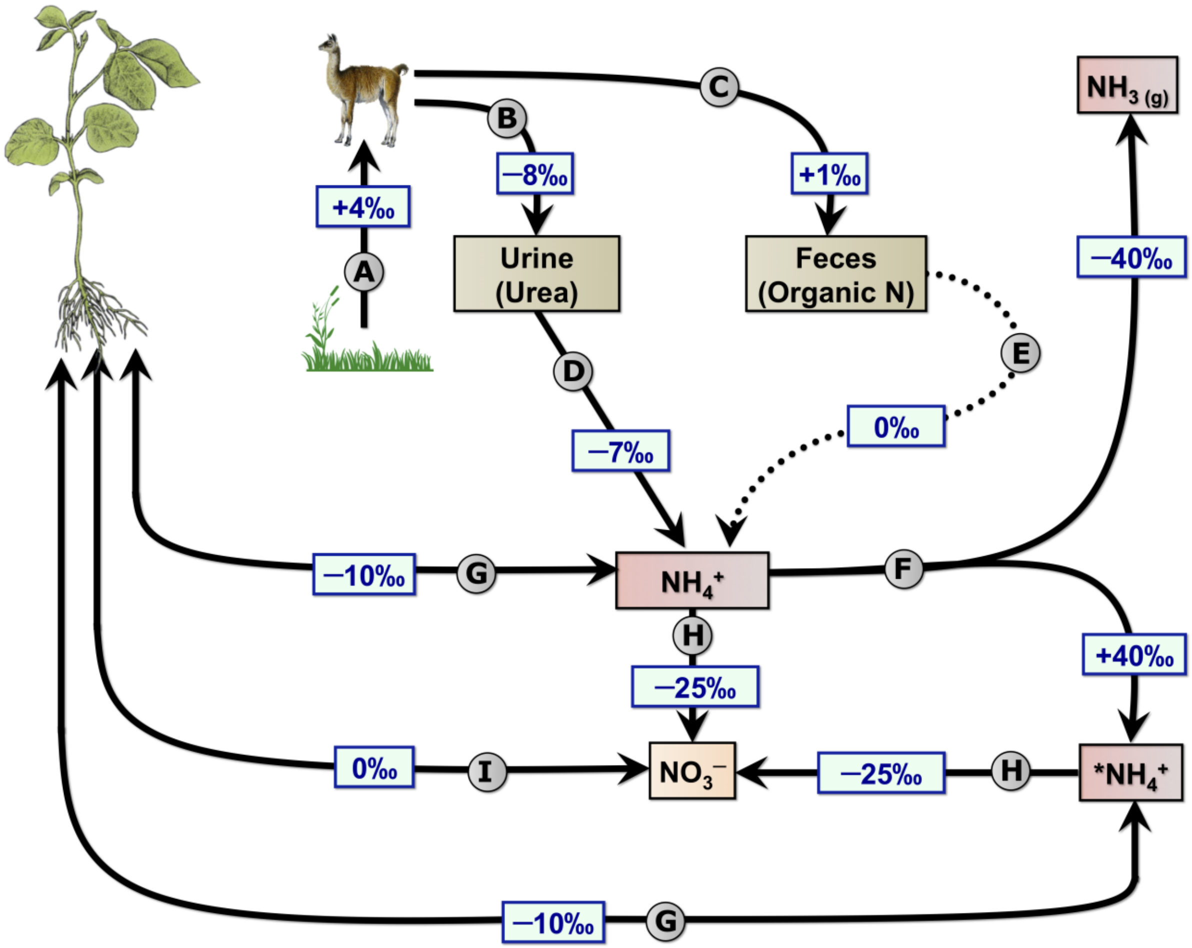

Figure 4.4. Simplified pathway for camelid dung-derived nitrogen.

(A) Trophic level enrichment of ^{15}N for most mammalian tissues is estimated to be ~3 to 4‰ (Bocherens and Drucker, 2003; Caut et al., 2009; Szpak et al., 2012c). (B) Urinary-N δ^{15}N tends to be lower in comparison to tissue-N (Knobbe et al., 2006; Sponheimer et al., 2003b; Steele and Daniel, 1978; Sutoh et al., 1987). (C) Fecal-N δ^{15}N tends to be similar to or slightly higher than body tissue δ^{15}N (Hwang et al., 2007; Sponheimer et al., 2003b; Steele and Daniel, 1978; Sutoh et al., 1987; Sutoh et al., 1993). (D) Because South American camelids habitually defecate and urinate in the same location (Franklin, 1982), dung that may be used for fertilizer likely contains an appreciable amount of urinary N. This urinary N, which consists primarily of urea, is rapidly hydrolyzed to NH_4^+ in the soil (Petersen et al., 1998; Whitehead and Bristow, 1990), which is associated with a nitrogen isotope fractionation of ~−7‰ (Balter et al., 2006; Schmidt and Medina, 1991). This NH_4^+ is initially highly prone to volatilization, but a substantial portion will be immediately available for plant uptake (Frank et al., 2004; Petersen et al., 1998). (E) Most mammalian fecal N is bound as organic matter and requires a significant amount of time to undergo mineralization (ammonification) (Kirchmann, 1991), which is not associated with fractionation of ^{15}N (Robinson, 2001). This process occurs over extremely long periods of time, as evidenced by relatively high modern plant δ^{15}N values growing on areas of ancient human activity (Commisso and Nelson, 2008). (F) Volatilization of ammonium to gaseous ammonia, which is known to be characterized by a large equilibrium fractionation (−25 to −60‰), which results in the remaining substrate ($^*NH_4^+$ in the diagram) being comparatively enriched of ^{15}N (Mizutani et al., 1985b; Mizutani et al., 1986). (G) Dependent on the extracellular concentration of ammonium, its uptake is associated with a nitrogen isotope fractionation ranging from −6 to −30‰ (Hoch et al., 1992; Yoneyama et al., 2001). The nitrogen isotopic composition of the ammonium taken up by the plant will vary over time depending on the speed with which NH_3 volatilization and nitrification take place. (H) The fractionation of ^{15}N associated with nitrification (oxidation of ammonium to nitrate) has been estimated at between −12 and −35‰ (Robinson, 2001; Shearer and Kohl, 1986). (I) There is no fractionation associated with the uptake of nitrate (Mariotti et al., 1982; Yoneyama et al., 1998; Yoneyama et al., 2001). Ammonium and nitrate may be effluxed from the plant, depending on environmental and physiological conditions (see Miller and Cramer, 2005).

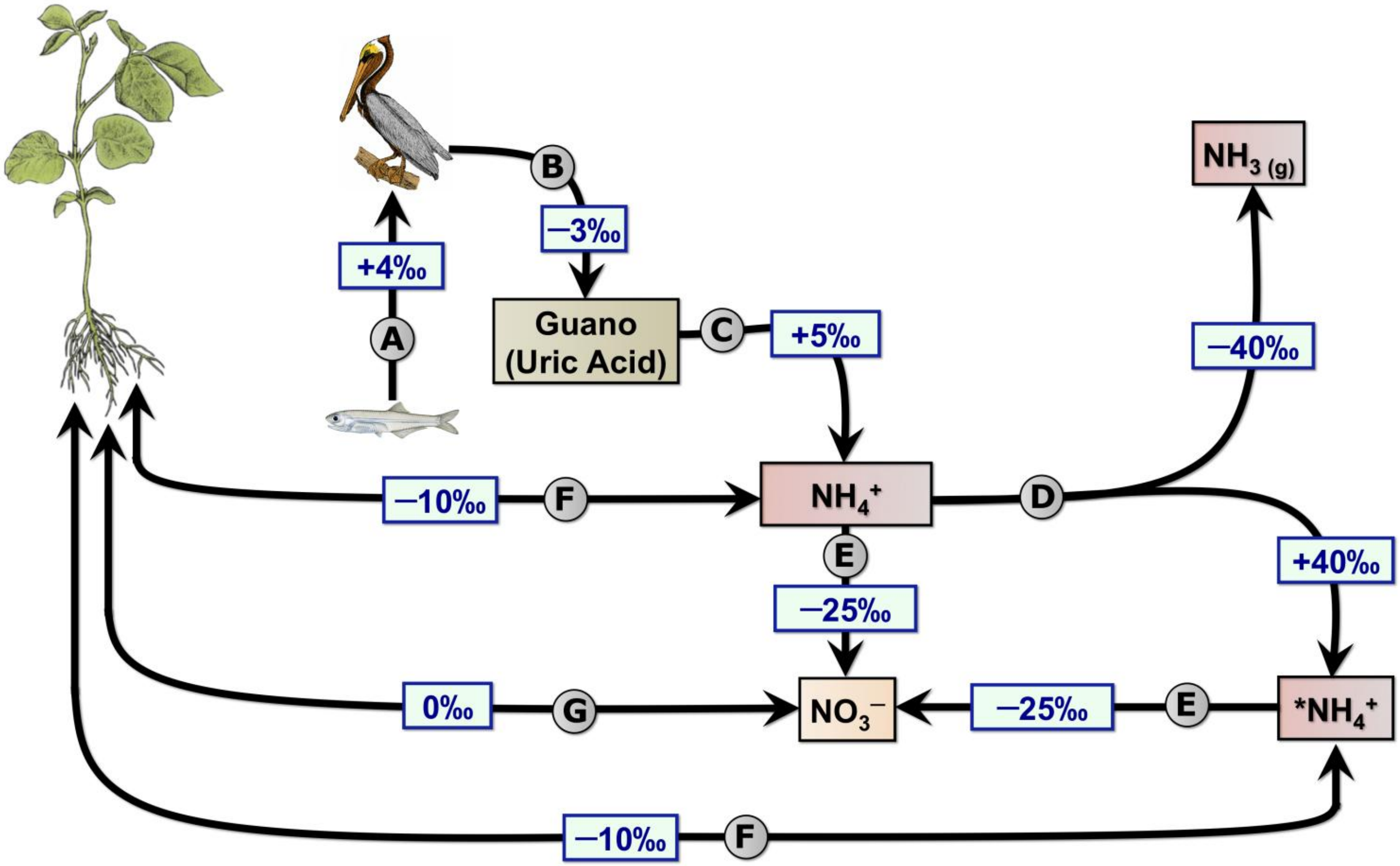

Figure 4.5. Simplified pathway for guano-derived nitrogen (after Szpak et al., 2012a).

(A) The primary diet of the Peruvian guano birds is the anchoveta (*Engraulis ringens*). Trophic level enrichment of ^{15}N for most avian tissues is estimated to be ~3 to 4‰ (Caut et al., 2009; Hobson and Clark, 1992; Hobson, 1995). (B) The primary N-bearing molecule in bird excreta is uric acid ($C_5H_4N_4O_3$) (Wainright et al., 1998). Seabird guano (bulk) is ~2.5‰ depleted of ^{15}N relative to blood (Wainright et al., 1998). Based on the observations of several investigators (Bird et al., 2008; Mizutani et al., 1985a; Mizutani et al., 1985b) uric acid and bulk guano $\delta^{15}N$ are very similar to one another. (C) Uric acid is rapidly mineralized to ammonium in the soil (Kirchmann, 1991); the fractionation of 5‰ is from Mizutani et al. (1985a). (D) Volatilization of ammonium to gaseous ammonia, which is known to be characterized by a large equilibrium fractionation (−25 to −60‰), which results in the remaining substrate ($^*NH_4^+$ in the diagram) being comparatively enriched in ^{15}N by ~40‰ (Mizutani et al., 1985b; Mizutani et al., 1986). (E) The fractionation of ^{15}N associated with nitrification (oxidation of ammonium to nitrate) has been estimated at between −12 and −35‰ (Robinson, 2001; Shearer and Kohl, 1986). (F) Dependent on the extracellular concentration of ammonium, its uptake is associated with a nitrogen isotope fractionation ranging from −6 to −30‰ (Hoch et al., 1992; Yoneyama et al., 2001). The nitrogen isotopic composition of the ammonium taken up by the plant will vary over time depending on the speed with which NH_3 volatilization and nitrification take place. (G) There is no fractionation associated with the uptake of nitrate (Mariotti et al., 1982; Yoneyama et al., 1998; Yoneyama et al., 2001). Ammonium and nitrate may be effluxed from the plant, depending on environmental and physiological conditions (see Miller and Cramer, 2005).

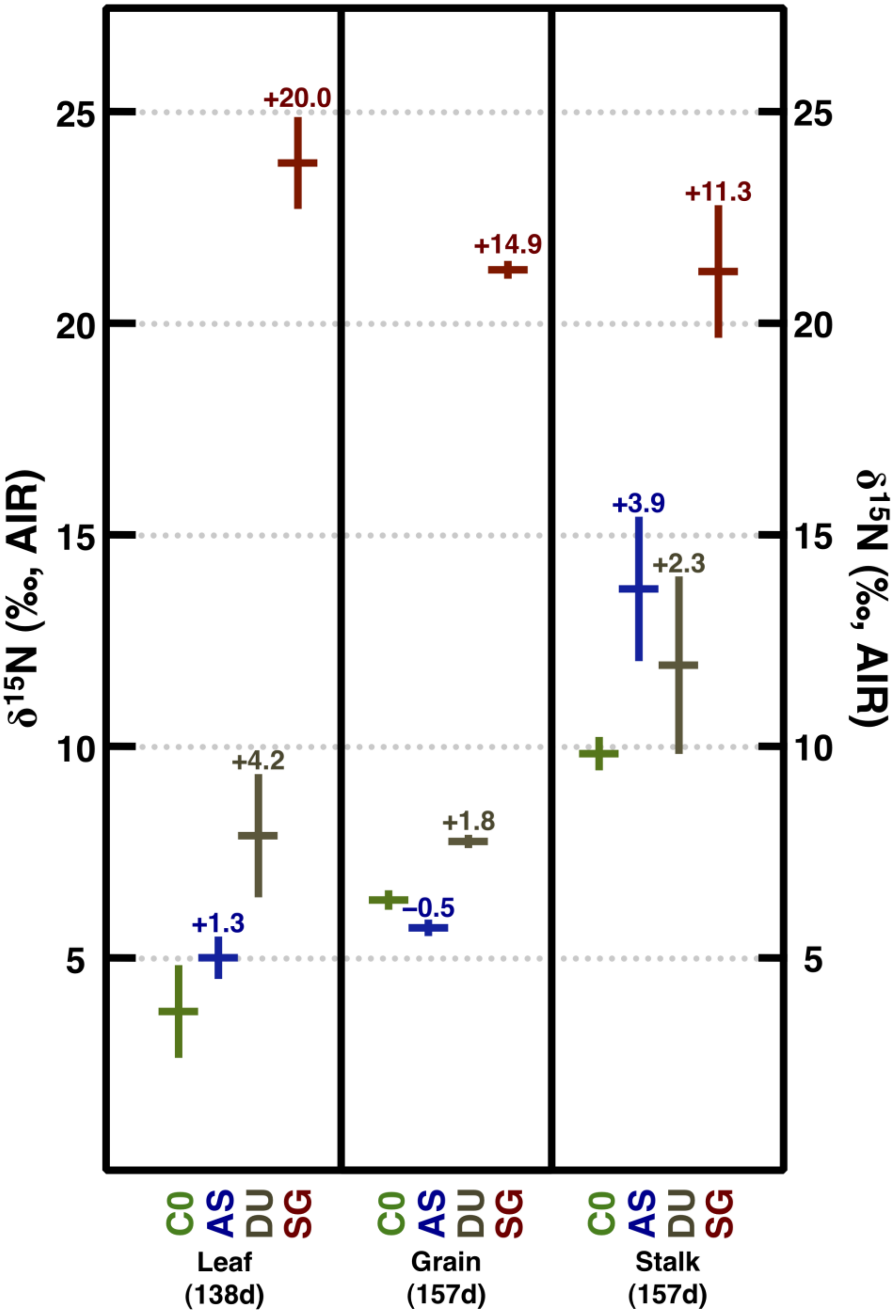

Figure 4.6. Nitrogen isotopic compositions of maize tissues. Horizontal bars represent means and vertical lines represent standard deviations. Numeric values above AS, DU, and SG data represent differences in δ^{15}N relative to CO plants ($\Delta^{15}N_{treatment-control}$).

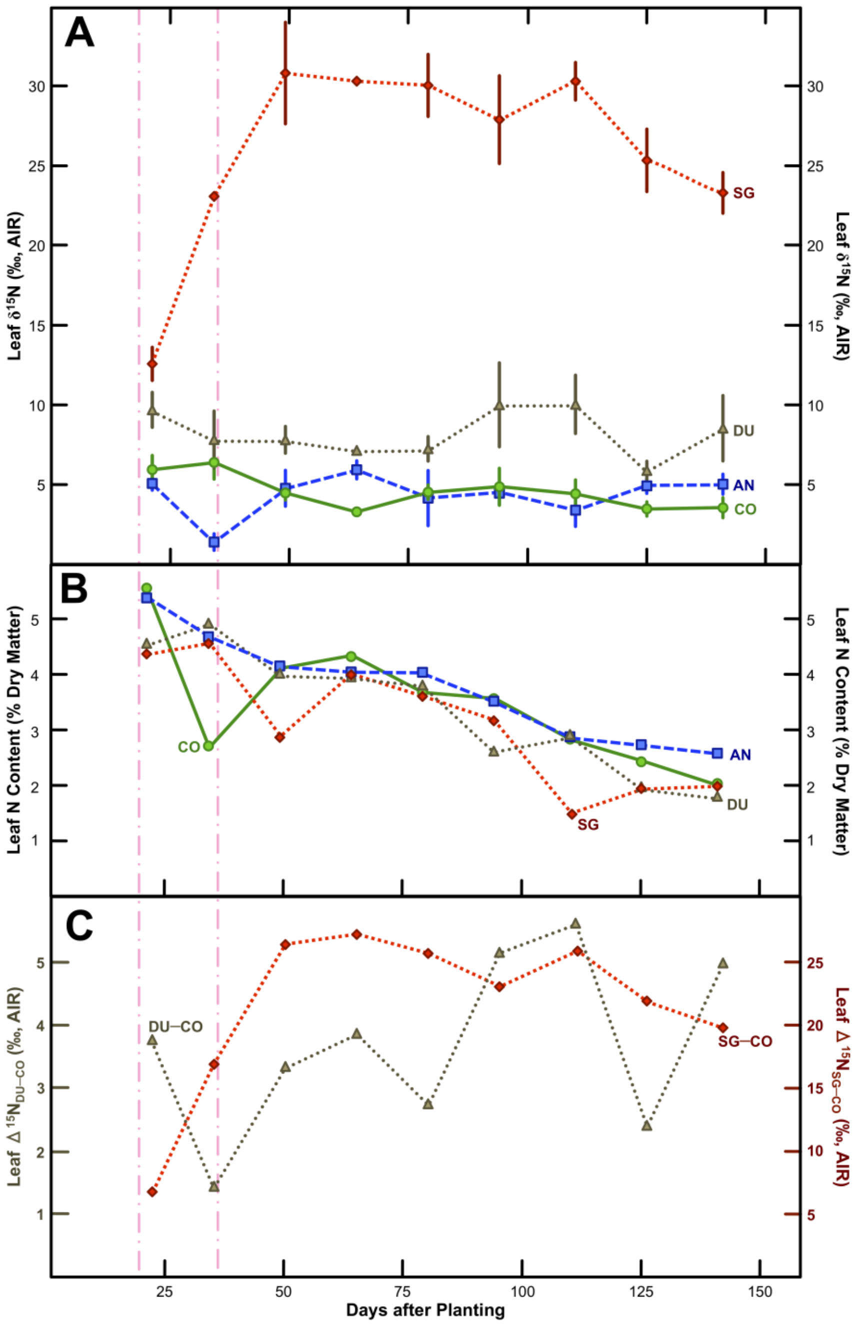

Figure 4.7. Temporal patterns in isotopic and elemental composition. (A) Maize leaf δ^{15}N values; each point represents the mean of three randomly sampled plants, with the exception of the last point, which represents six randomly sampled plants; vertical bars represent standard deviations. (B) Leaf N content. (C) Differences between fertilized and control leaf δ^{15}N values for DU (primary y-axis) and SG (secondary y-axis) plants.

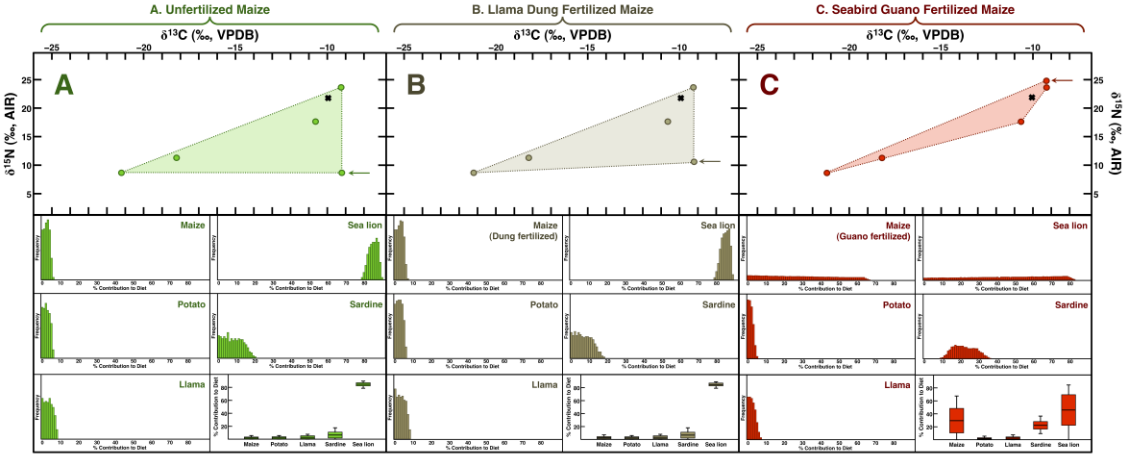

Figure 4.8. Results of IsoSource mixing model for three different scenarios: (A) unfertilized maize, (B) camelid dung fertilized maize, (C) seabird guano fertilized maize. Top panels show mixing polygons (shaded area) for each scenario. Filled circles represent food sources (listed in Table 3), which have been adjusted for trophic level fractionation (following Szpak et al., 2012c); × represents the isotopic composition of the consumer; arrows indicate the position of maize. Lower panels represent frequencies of relative contributions of sources to the consumer (increment of 1) for all feasible solutions produced by the model. Lower right panels are frequencies of relative contributions represented as means ± standard deviation (horizontal bar and shaded box) with ranges (vertical bars).

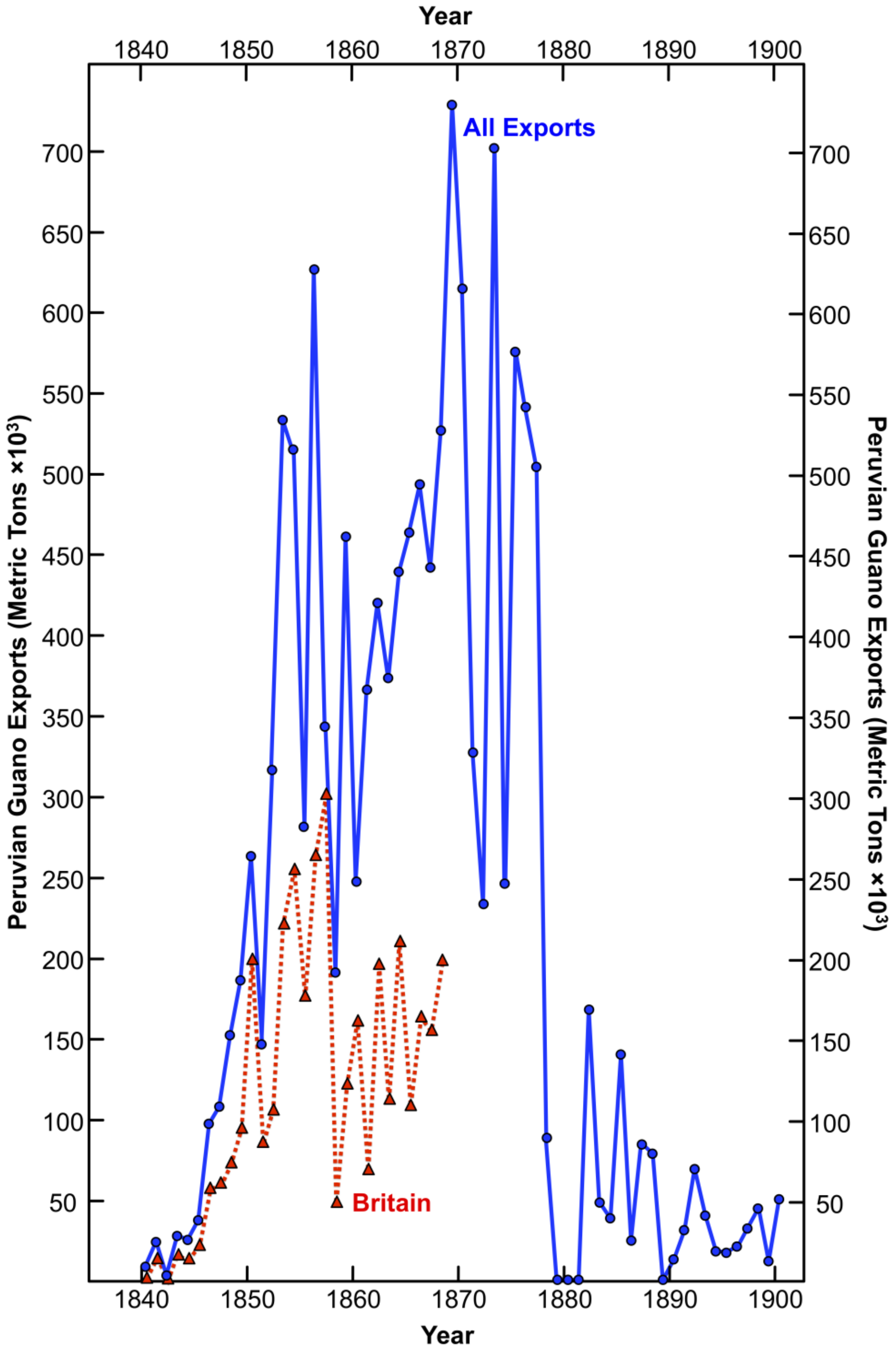

Figure 4.9. Peruvian exports of guano from 1840−1900; guano exported to Britain is shown as a broken line (data unavailable after 1869) and total guano exported is shown as a solid line (data from Cushman, 2003; Hollett, 2008). The lack of exports around 1880 is the result of the War in the Pacific (1879-1883).

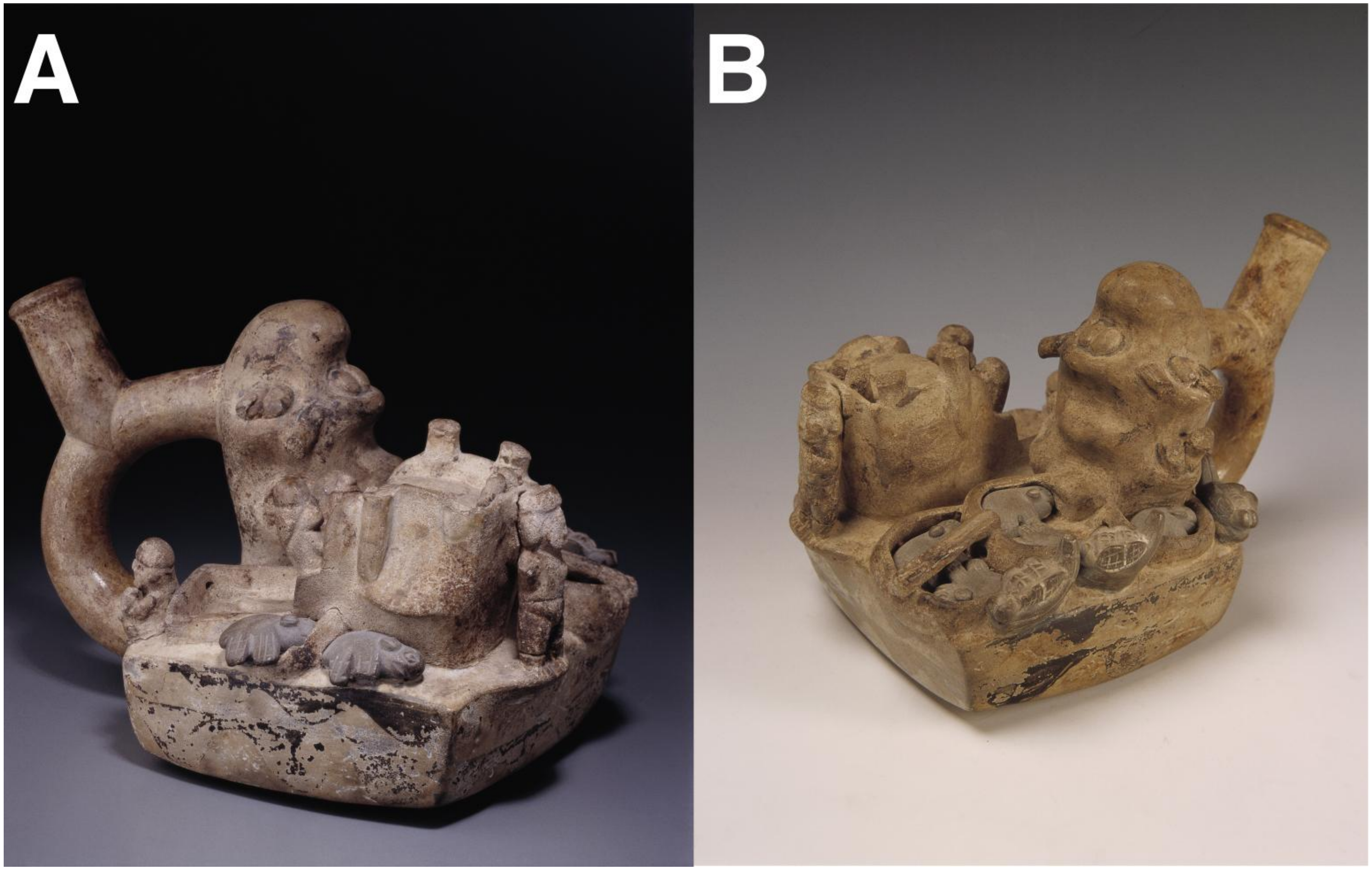

Figure 4.10. Moche vessel depicting an island scene (two views of the same object). Sea lions can be seen, along with guano birds, and reed boats loaded with packages (foreground of B). Photographs courtesy of Museo Larco (Catalogue #ML010853).

Figure 4.11. Moche vessel depicting a sea lion hunt. Photograph courtesy of Museo Larco (Catalogue #ML013615).

Figure 4.12. Moche fineline depiction of a sea lion hunt. The object on the right has been interpreted as a guano island. A structure, two individuals, and two sealed containers (usually associated with scenes of ritual practice) can clearly be seen on the island. Drawing by Donna McClelland, courtesy of Don McClelland.

Figure 4.13. Moche vessel depicting a boat containing a captive and an individual paddling. This likely represents the transportation of an individual destined to be ritually killed on one of the guano islands (Steve Bourget, Personal Communication). Photograph courtesy of Museo Larco (Catalogue #ML003202).

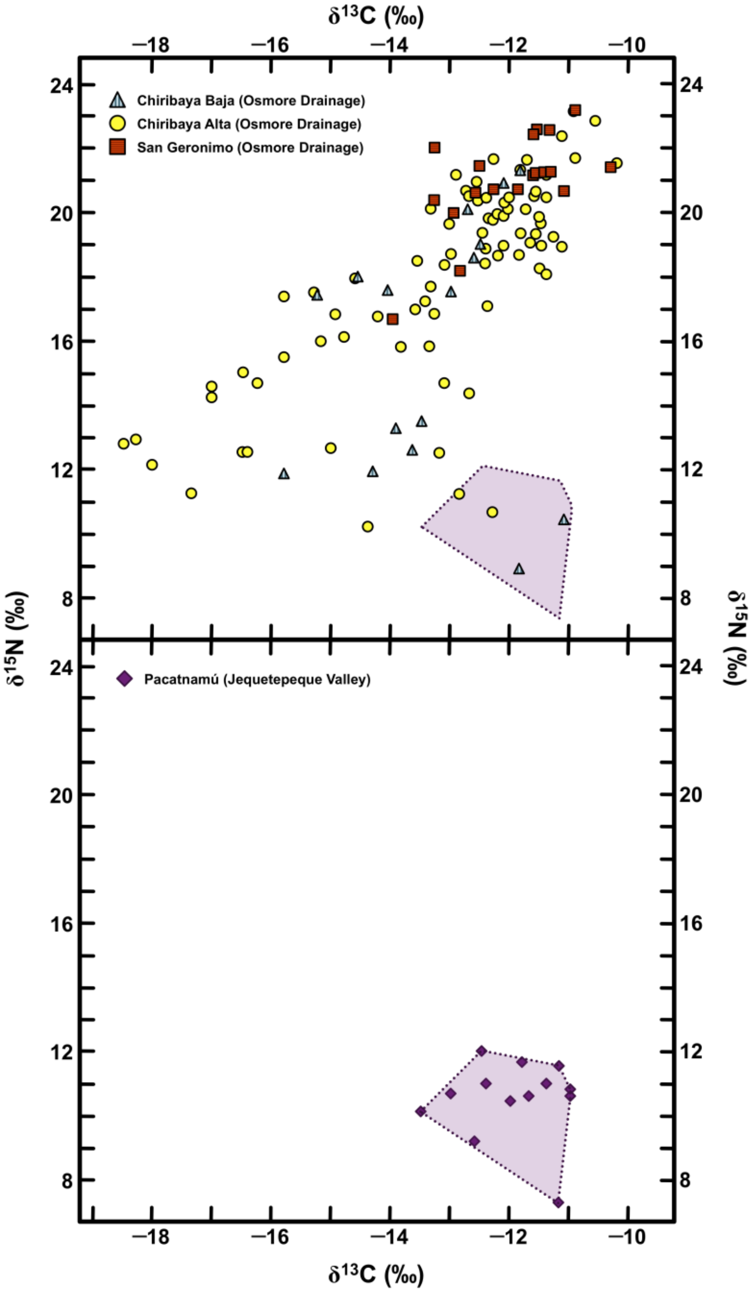

Figure 4.14. Carbon and nitrogen isotopic compositions of human bone collagen. Upper panel: sites from the Osmore Valley on the south coast of Peru (Tomczak, 2003). Lower panel: Pacatnamú, Jequetepeque Valley, north coast of Peru (Verano and DeNiro, 1993; White et al., 2009). The shaded polygon in the lower right portion of the upper and lower panels represents the bivariate isotopic space occupied by the Moche individuals plotted in the lower panel.

5 Human-Camelid Entanglements in the Virú Valley (north coast of Peru): Insight from Stable Isotope Analysis

South American camelids (llamas and alpacas) were of tremendous importance in the Andes in antiquity. Following the arrival of the Spanish, the number and range of camelids was dramatically reduced, with present distributions being primarily restricted to high altitude pasturelands in Peru and Bolivia. This study presents carbon and nitrogen isotopic compositions for bone collagen and serially-sampled hair from a large collection of camelids from two sites (Huaca Gallinazo and Huaca Santa Clara) in the Virú Valley. This paper makes several methodological contributions with respect to the treatment of isotopic data from archaeological contexts, outlining quantitative approaches that can provide considerable insight into isotopic variation (within groups, within individuals, between groups, between individuals), as well as temporal variation in isotopic compositions in incrementally growing tissues. The isotopic compositions of these camelids are consistent with plant isotopic compositions from coastal and low altitude settings, but not from high altitude environments, suggesting that at least some of these animals were raised locally. The results demonstrate a high amount of isotopic variability between individuals and an inconsistent amount of within-individual variation, with no consistent shift in the diet leading up to the time of death for a group of animals from a single ritual event. This suggests that camelid husbandry on the coast of Peru was likely a small-scale activity, with small groups of camelids being managed by families or other small social units. Animals were likely kept primarily in close association to human habitation sites and provided with a diverse array of fodder. These prolonged interactions, occurring at a limited spatial scale, would have allowed a high degree of mutual familiarity to develop between humans and animals. The isotopic analysis of zooarchaeological material derived from livestock has great potential with respect to better understanding animal husbandry practices, and human-animal interactions in the broadest sense.

5.1 Introduction

The interaction between humans and non-human animals is a topic of immense importance in anthropology. Shipman (2010) has proposed that the manner in which humans interact with other animals (the ‘animal connection’) can be placed alongside tool making, symbolism, and language as those behaviors that define humans as a species. Until very recently, anthropologists and archaeologists have viewed animals primarily through two lenses: subsistence and symbolism (Mullin, 1999; Shanklin, 1985); the same is true for zooarchaeologists, but with a much greater emphasis on the former (but see deFrance, 2009; Russell, 2012). In recent years, there has been increased interest in the study of human-animal interactions, not just by anthropologists (Abbink, 2003; Knight, 2003, 2012; Kohn, 2007; Nadasdy, 2007; Shir-Vertesh, 2012; Willerslev, 2004) and archaeologists (Argent, 2010; Herva and Salmi, 2010; Jones, 2009; Oma, 2010; Salmi, 2012), but by cultural geographers (Bear and Eden, 2011; Philo and Wilbert, 2000; Riley, 2011; Wolch and Emel, 1998), sociologists (Franklin, 1999; Jerolmack, 2007; Wilkie, 2005), and primatologists (Fuentes, 2006; Fuentes, 2010; Fuentes and Hockings, 2010; Riley and Priston, 2010). A growing trend has been to move beyond the symbolic importance of animals wherein they are passive *reflections of* human society (i.e. animals are good to think with, following Lévi-Strauss, 1962), and see animals instead as active agents that are *part of* human society (Knight, 2005) − in other words, animals are good to live with (following Haraway, 2008).

As part of this turn in human-animal studies, there has been a call to move away from strictly anthropocentric studies of animals, towards what Kohn (2007::4) has called an “anthropology of life”, one that is explicitly concerned with human entanglements with other living beings. Parallels have been drawn between early attempts to integrate gender into anthropological and archaeological discourses (e.g. Gero and Conkey, 1991) and the current surge seeking to bring non-human voices into anthropology (Birke et al., 2004; Chang, 2012). In sociocultural anthropology, the practice of multispecies ethnography has emerged, which attempts to examine the lives of various beings or selves (both human and non-human), how they interact with, shape, and are shaped by, one another, within larger cultural, economic, and political contexts (Kirksey and Helmreich, 2010).

An important aspect of human-animal studies relates to scale. Most studies focus on various aggregations of animals (herds, entire species or other folk/taxonomic classifications), although several authors have discussed the importance of accounting for the lived experiences of *individual* animals (Alger and Alger, 2003; Argent, 2010; Bear, 2011). The recognition of the very individualized nature of human-animal relationships has primarily been discussed within the context of companion animals (Haraway, 2003, 2006, 2008; Kohn, 2007; Power, 2008), and such approaches have not been extensively applied to livestock (but see Abbink, 2003; Dwyer and Minnegal, 2005). Speaking of livestock, Knight (2005:5) points out that, "a preoccupation with the outcome of the relationship (slaughter for meat) is apt to conceal the protracted relationship of nurturance and care that precedes it." Traditional zooarchaeological research tends to emphasize exactly this aspect of human animal relationships: slaughter, butchery, and the incorporation of the carcass into the archaeological record. It therefore gives primacy to a very limited number of interactions that occur within the context of a much larger and more complex relationship between humans and livestock (Knight, 2012). This is not to suggest that the economic role of animals be discounted, but it must be recognized that there may be a significant ontological distinction between a living animal and an animal carcass, whereby the treatment of the latter does not necessarily reflect the human-animal intersubjectivity prior to the animal's death (Herva and Salmi, 2010). There has been some recognition of individual variation in companion animals in archaeological contexts, with several studies examining the differential treatment of dogs in mortuary contexts (Byrd et al., 2013; Losey et al., 2011; Prummel, 2006). Several studies have examined the importance of livestock, particularly in ritual and mortuary contexts (Goepfert, 2012; Jones, 1998; Marciniak, 2005; Ray and Thomas, 2003; Russell and During, 2006; Salmi et al., 2011; Yuan and Flad, 2005), although this research tends to be largely focused on symbolic aspects of animals (but see Whittle, 2003). Relatively little attention has been paid to the importance and meaning of individual variation in livestock lifeways in archaeological contexts. This variation may be discussed in terms of environmental variation (e.g. Atahan et al., 2011; Bocherens et al., 2000; di Lernia et al., 2013; Richards et al., 2006; Thompson et al., 2005; Towers et al., 2011) or vaguely in terms of differences in animal husbandry (Fisher and Thomas, 2012; Oelze et al., 2011b;

van der Plicht et al., 2012). In both cases, however, there is a lack of robust assessments of isotopic variation.

An important question arises as to how, in a practical sense, to move beyond the study of the roles of animals in prehistoric subsistence economies (economic reductionism) and their discursive representations (symbolic reductionism) to one that focuses on the nature of lived interspecies entanglements. Such an approach should do more than simply layer social theory onto zooarchaeological data, and instead, there must be a real connection between theory and data that has the potential to produce a better understanding of the nature of human-animal interactions. Additional difficulties arise in archaeological contexts, where these interactions cannot be observed directly, and the basis for interpretation must necessarily start with the remains of the animal carcass and the context associated with its disposal. To circumvent this problem, we must look to indirect evidence or 'traces' to better understand animal lives. An analogous approach outside of archaeology was employed by Hinchliffe et al. (2005) who examined water vole tracks, droppings, and other 'traces' in a study of human and non-human ecologies in urban wild spaces in England. Among the most common applications for isotopic analysis in modern ecological studies is to reconstruct the diet or foraging ecology of animal species, many of which cannot be observed directly for a variety of reasons. Similarly, isotopic analysis has proven to be an extremely valuable tool for similar reasons in archaeological contexts.

The isotopic signature recorded in biological tissues is representative of events in the life history of individual organisms. Because certain tissues (teeth, hair, nail, whisker) grow at discrete intervals or continuously, diachronic isotopic analyses of these tissues can provide high-resolution life histories of individuals, reflecting temporal shifts in diet, residence, and potentially health (Balasse et al., 2001; Knudson et al., 2007; White et al., 2009). Within the context of bioarchaeology, most analyses have been concerned with issues at the population or regional level, but a more detailed understanding of larger social processes may be reached through a concerted focus on individuals as well as populations, rather than strictly populations (Knudson and Stojanowski, 2008). Somewhat analogously, there has been a recent trend in ecological research to recognize the importance of variation at the individual level (e.g. foraging specialization) (Bolnick et al., 2002; Bolnick et al., 2003; Svanbäck and Persson, 2004), which has been addressed via isotopic analysis in a number of studies (Matich et al., 2011; Matthews and Mazumder, 2004; Newsome et al., 2009; Szpak et al., 2012c). This has led to the development of a number of methodological techniques that can be used to assess and compare variation both between and within groups and/or individuals (Jackson et al., 2011; Layman et al., 2007a; Layman and Post, 2008; Martínez del Rio et al., 2009; Matich et al., 2011), which have, to date, not been employed in archaeological contexts.

A number of studies have utilized isotopic techniques in the assessment of camelid herding in the Andes (DeNiro, 1988; Finucane et al., 2006; Thornton et al., 2011; Yacobaccio et al., 2009), but little attention has been paid to the significance of within-group variation. Aside from the novelty of these approaches, the extremely small sample size (often $n<5$ for individual sites) in most of these cases is also a significant obstacle. The analysis of large numbers of individual animals of a single species from well-constrained contexts can provide considerable insight into animal husbandry practices (Pearson et al., 2007). In this paper, we utilize isotopic analysis of camelid tissues recovered from two archaeological sites in the Virú Valley of northern Peru to better understand animal husbandry practices and the variation in human-animal interactions at this time. In a more general sense, we discuss the importance of considering isotopic variation within groups, and the potential interpretative power of comparative studies of within-group isotopic variability, drawing on methods utilized in ecology.

5.2 South American Camelids

The South American camelids (hereafter simply camelids) include two domestic species (llama and alpaca) and two wild species (vicuña and guanaco). The differentiation of camelid species on the basis of postcranial skeletal morphology is very difficult. Accordingly, throughout this paper, discussion focuses generally on 'camelids', except in cases where dental and/or soft tissue preservation allow for the assignation of individual animals at the species level (Wheeler et al., 1995).

It is widely recognized that camelids were of tremendous economic, social, political, and ritual significance to various groups throughout the prehispanic Andes (Bonavia, 2008; Dransart, 2002; Mengoni Goñalons, 2008). Views of camelids and camelid herding in the region have been largely shaped by ethnographic and ethnohistoric accounts of camelid pastoralism, which have been limited to high altitude pasturelands (e.g. Flores-Ochoa, 1979; McCorkle, 1987; Murra, 1965, 1980; Orlove, 1977b; Tomka, 1992). The introduction of European domesticates (e.g. cattle, sheep, pig, donkey) beginning in the sixteenth century drastically reduced the geographic range and number of camelids in the Andes (Bonavia, 2008). Several authors have suggested that camelids were herded in a much wider variety of environments prior to the arrival of the Spanish (Goepfert, 2012; Goepfert et al., 2013; Pozorski, 1976; Shimada and Shimada, 1981; Thornton et al., 2011), including the arid coastal region of northern Peru (Shimada and Shimada, 1985). Many questions remain, however, regarding the nature of camelid herding outside of the high altitude zones of the Andes.

Traditional models of camelid husbandry in the Andean region have discussed fairly large herds that graze on high altitude pasturelands in the *puna* (3,800 to 5,000 masl; Flannery et al., 1989; Flores-Ochoa, 1979; Kuznar, 1991a; Markemann and Valle Zárate, 2010; Orlove, 1977b, 1982; Postigo et al., 2008) or high sierra (2,500 to 3,800 masl; Kuznar, 1990, 2001), with the notable exception of Dransart's extensive work in the Salar de Atacama in Chile (2,300 masl; Dransart, 1991; 2002). In the vast majority of cases today, herds are of mixed composition, typically consisting of alpacas, sheep, goats, and in some cases cattle (at lower altitudes). Herding strategies in recent times are thus heavily influenced by the presence of European domesticates. Accordingly, we have no readily applicable Andean analogues of camelid husbandry in (1) coastal or low altitude environments (although there are accounts of camelid husbandry in very arid environments), or (2) in more urbanized settings. This study attempts to examine camelid husbandry in the Virú Valley (north coast of Peru) through the isotopic analysis of faunal material derived from two sites: Huaca Gallinazo and Huaca Santa Clara.

5.3 Archaeological Context

Materials analyzed in this study are derived from two Early Intermediate Period (EIP, ca. 100 BC to AD 700) sites in the Virú Valley (Figure 5.1). The Virú Valley will be familiar to most archaeologists as the location of Gordon Willey's groundbreaking analysis of settlement patterns (Willey, 1953). The culture history of the Peruvian north coast was extremely dynamic, particularly during the EIP, and is only beginning to be understood in light of recent excavations, re-evaluations of ceramic chronologies, and radiocarbon dating programs (Millaire and Morlion, 2009; Millaire, 2010b; Quilter and Castillo, 2010). During the EIP in Virú, there were significant increases in population size and agricultural productivity, the emergence of urban settlements, and a unified political command over the entire Virú Valley (Fogel, 1993; Millaire, 2010b; Willey, 1953) with its capital at the Gallinazo Group (Millaire and Eastaugh, 2011). This polity (Virú) is associated with a distinctive resist-painted ceramic style (Gallinazo Negative), which is largely restricted to the Virú Valley (Figure 5.2). Previously, this style was considered one part of a larger ceramic tradition (including Gallinazo domestic wares that were very widely distributed on the Peruvian north coast) and was considered to be characteristic of the 'Gallinazo culture', a contemporary of the people associated with Moche material culture (Bennett, 1950; Fogel, 1993; Strong and Evans, 1952). In light of recent reappraisals of the nature of this material culture (Millaire and Morlion, 2009), we use the term Virú to refer to the political entity associated with the Virú Negative material culture (sensu Larco Hoyle, 1945). In this schema, Virú is one of several EIP political entities on the north coast roughly contemporaneous with Moche, and the Gallinazo incised and appliqued domestic wares do not correspond with one political entity or cultural group, but are simply a regional domestic ceramic tradition.

The first site from which material was collected, Huaca Gallinazo (V-59), is the largest of the central group of mounds that comprise the Gallinazo Group, covering over 40 ha and located ca. 5 km from the coast. It is estimated that the population of the Gallinazo Group during the EIP may have been between 10,000 and 14,400 (Millaire and Eastaugh, 2011). Several authors have proposed that the Gallinazo Group functioned as the capital or central administrative center for a political entity of varying sizes (depending largely upon the interpretation of ceramic styles) (Bennett, 1950; Fogel, 1993; Millaire, 2010b). Intensive excavations were carried out at the Gallinazo Group in the middle part of the twentieth century (Bennett, 1950; Strong and Evans, 1952), revealing a long history of occupation. More recent excavations and associated radiometric dating have demonstrated that the occupation of the main residential sector at the site dates back to at least 50 BC and may have continued for seven centuries (Millaire, 2010b). The most salient structure at Huaca Gallinazo is a very large civic building, which was likely constructed around AD 50 (Millaire, 2010b). Camelid material sampled from this site is derived primarily from fills associated with building construction, many of which display cut marks associated with butchery. Material from Architectural Complex 1 (AC-1) was recovered at the foot of the main ceremonial platform. The vast majority of elements sampled were first phalanges.

The second site (Huaca Santa Clara, V-67), located about 15 km inland from V-59, has been interpreted as functioning as a regional administrative center (Millaire, 2010a). A mid-sized site, Huaca Santa Clara is comprised of a number of adobe buildings constructed on a natural hill. On the basis of a series of radiocarbon dates, the occupation of the site dates from 160 BC to AD 780 (Millaire, 2010a) and it is contemporaneous with the main period of occupation at Huaca Gallinazo. The administrative nature of the site was suggested on the basis of substantial agricultural storage facilities, as well as by the elite character of the material culture associated with the large adobe platform atop the hill (Sector I) and the storage facilities (Sectors II, IV, VI). The storage facilities were built on the lower terraces along the edges of the mound; small residential structures were constructed at the base of the mound (Figure 5.3). Following the abandonment of Huaca Santa Clara towards the end of the EIP, the site was later reused for the purpose of a ritual event that appears to have been a somewhat widespread phenomenon on the north coast of Peru in the late Middle Horizon to early Late Intermediate Period (ca. AD 800 to 1200) (Millaire and Surette, 2011; Millaire, In Press). This ritual event involved the burial of a young female wrapped in an elaborate textile bundle, accompanied by five other young individuals, as well as 28 immature llamas (Table 5.1). In this case, because the remains of the animals were (in most cases) complete or nearly complete (Figure 5.4), it is possible to identify them as llamas.

Similar ritual events have been described at other sites in the Virú and Moche Valleys (Figure 5.1). At Huancaco (V-89), fifteen immature llamas were buried in what appears to be a single ritual event, in some cases with various objects (turquoise and shell) inserted into some of the llamas' esophagi (Millaire, In Press). At Huaca Negra (V-71), four immature, complete llamas were found interred in the vicinity of an Early Horizon (Guañape Period) structure, apparently buried long after the structure had ceased to be used (Strong and Evans, 1952). Willey (1953) provides limited details on a sacrificial event involving llamas at a rockshelter site in the Virú Valley (Cerro de Huarpe, V-313), again occurring after the site had been abandoned. A number of similar ritual events have also been recorded in the Moche Valley. At Huanchaco, Donnan and Foote (1978) report seventeen child burials, each of which was associated with one or more immature llamas. The burials date to the Late Intermediate Period, but were associated with a previously abandoned structure of unknown provenance. At Cerro Blanco, a large number (MNI=59) of camelids, most of which were immature (80% < six months old) were found near a large building, in association with what has been interpreted as a specialized cemetery (Millaire, In Press). Additional sacrificial events in the area involving camelids have also been described by Goepfert and Prieto (2012) and Kent et al. (2012).

5.4 Stable Isotope Ecology of the Northern Peruvian Andes

The carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic compositions of an animal's tissues reflect a weighted average of the foods consumed during the period at which the tissues formed (DeNiro and Epstein, 1978, 1981). In terrestrial ecosystems, $\delta^{13}C$ and $\delta^{15}N$ values at the base of the food web (in plants and soils) vary with respect to a number of environmental parameters, several of which are particularly relevant to the western slope of the Andes (reviewed by Szpak et al., 2013b). The importance of altitude on structuring human populations in the Andean region has been discussed at length, and various models have addressed the potential significance of ecological variation (Murra, 1968, 1975; Rostworowski, 1977, 1978), although the regional and temporal generality of these models with respect to modeling complex human behaviour has been called into question (Jamieson, 2005; Santoro et al., 2010; Van Buren, 1996). Large changes in mean annual temperature and rainfall occur moving from the Pacific coast in the west into the highlands, with annual precipitation increasing and temperature decreasing with altitude (Bush et al., 2005). The environmental changes that occur with altitude in the Andes have important isotopic consequences, which are explored in more detail below.

The $\delta^{13}C$ values of the two main types of terrestrial plants (C_3 and C_4) are distinct, with mean $\delta^{13}C$ values of ca. −12‰ for C_4 plants (mainly grasses adapted to hot, arid conditions) and ca. −26‰ for C_3 plants (the majority of terrestrial plants) (O'Leary, 1981). In the Andean region of South America, C_4 plants are relatively rare at high altitude locations (Boom et al., 2001; Szpak et al., 2013b), which tend to be cooler and wetter than the low altitude and coastal regions (Sandweiss and Richardson, 2008). C_3 plant carbon isotopic compositions tend to become less depleted of ^{13}C in arid environments (Vitousek et al., 1990), although the effects of altitude on plant leaf morphology and associated changes in photosynthetic capacity counter this effect in the Andes (Szpak et al., 2013b); a similar effect has been observed further south in the Chilean Andes (Tieszen and Chapman, 1992).

The trend of increasing temperature and precipitation with altitude in the region influences the nitrogen isotopic composition of soils and plants (Szpak et al., 2013b). Hot and arid ecosystems are characterized by relatively high $\delta^{15}N$ values due to various biogeochemical processes that favor the loss of the lighter isotope (^{14}N), driven by the 'openness' of these ecosystems (Handley et al., 1999a). Several authors have suggested that arid conditions directly cause relatively high $\delta^{15}N$ values in animal tissues due to various metabolic processes associated with N excretion and water conservation (Ambrose and DeNiro, 1986a, 1987; Gröcke et al., 1997). More recently, however, a much clearer link between plant (and presumably soil) nitrogen isotopic compositions and rainfall has been found (Hartman, 2011; Murphy and Bowman, 2006), suggesting that the ^{15}N-enriched herbivore tissues that have been observed are largely, or wholly, driven by isotopic variation in the diet. Overall then, there is a general pattern of higher carbon and nitrogen isotopic compositions in plant tissues (on average) at coastal and low altitude sites relative to high altitude sites (Szpak et al., 2013b).

Agricultural plants may be less sensitive to these environmentally-mediated effects on tissue isotopic compositions, although direct empirical support for this notion is lacking. Specifically, because agricultural plants may be supplied with supplemental water through irrigation (especially on the coast), the effects of water-availability on plant $\delta^{13}C$ and $\delta^{15}N$ values may be minimized. For example, wild plants (leaves) sampled from coastal sites in the Moche River Valley had $\delta^{15}N$ values as high as 17 ‰ (Szpak et al., 2013b), while the highest $\delta^{15}N$ values observed for unfertilized maize leaves grown under irrigation agriculture in the nearby Virú Valley were 6.4 ‰. Additionally, agricultural plants may be treated with a number of organic fertilizers, which can have moderate (2 to

4 ‰) to extreme (>20 ‰) impacts on plant nitrogen isotopic compositions (Szpak et al., 2012a; Szpak et al., 2012b), and several authors have suggested that one or more fertilizers were utilized in agriculture on the north coast of Peru (Netherly, 1977; Nordt et al., 2004). The nitrogen isotopic compositions of agricultural plants grown on the coast are therefore difficult to predict with a high degree of precision in the absence of isotopic measurements of contextually-associated archaeobotanical material. Nevertheless, the range of possible isotopic compositions for these plants at the very least added to the isotopic complexity of the local food web.

5.5 Materials and Methods

5.5.1 Materials

For comparative purposes, modern camelid specimens (hair and bone) were collected from five locations in northern Peru, primarily at high altitude sites. The majority of the samples collected were hair rather than bone, since the vast majority of camelids in the Andes today are alpacas (rather than llamas), which are raised primarily as fiber-producers. Accordingly, these animals are not butchered for meat, and access to bones is relatively difficult.

Archaeological camelids were sampled from EIP contexts at Huaca Santa Clara and Huaca Gallinazo. These materials were recovered during excavations conducted at these two sites between 2008 and 2012 as part of the Proyecto Arqueológico Virú and Proyecto de análisis isotópica de camélidos y textils precolombinos del norte del Perú. In addition to these EIP materials, later camelids associated with the sacrificial event at Huaca Santa Clara were also sampled from material recovered in these recent excavations. For these animals, as well as a smaller number of butchered animals, high levels of organic preservation facilitated the collection of hair samples with adhering skin, allowing for the diachronic analysis of isotopic compositions.

5.5.2 Isotopic Methodology

Bone collagen was extracted using a modified Longin (1971) method, as described previously (Szpak et al., 2010). Bone samples were cleaned with a brush under deionized water, and small portions were removed using a Dremel ® (3000 model) rotary tool equipped with a diamond-tipped cutting accessory (diamond wheel #545). Cortical bone was specifically targeted, and in cases where any trabecular bone remained, this material was removed by manual abrasion with a dental pick. In the vast majority of cases, central portions of phalanges were sampled, which contained little or no trabecular bone. Cortical bone was ground to a coarse powder (0.018 to 2 mm fragments) using a steel mortar and pestle. All chemical treatments were performed at room temperature (ca. 20°C) unless otherwise noted. Bone fragments were soaked for 24 h in 2:1 chloroform:methanol and occasionally agitated to remove lipids (Folch et al., 1957). After drying, samples were soaked in 0.1 M HCl for 24 h before being soaked in 0.5 M HCl with periodic changes of the acid for a variable amount of time (until the bone was fully demineralized), typically 10 to 20 days. The initial soak (0.1 M HCl) is most effective in demineralizing samples that have relatively low organic preservation. These samples produce profuse quantities of CO_2 if placed initially in 0.5 M HCl and are problematic in terms of separation by centrifugation. After the bone was demineralized (judged subjectively by the translucency and density of the bone fragments), samples were rinsed to neutrality with deionized water (typically 5 to 6 rinses), and soaked in 0.1 M NaOH for successive 20 min treatments until the solution became clear (to remove humic contaminants). The presence of humic compounds appeared to be minimal in these samples. Samples were then rinsed to neutrality with deionized water (typically 5 to 6 rinses), and placed in ~4 ml 10^{-3} M HCl at 90°C for 18 h in sealed glass tubes to solubilize the collagen. The solution containing the collagen was transferred into 4 ml glass vials and air-dried at 90°C. Approximately 0.4 to 0.5 mg of collagen was weighed into tin capsules for elemental and isotopic analysis.

Hair samples were cleaned carefully of adhering particulate matter and loose hairs with fine forceps and a dental pick. Hair was sampled at 1 cm increments wherever possible – hair that was either too short (< 2 cm), or could not be definitively associated with skin was not sampled incrementally, but was sampled in bulk. Hair samples (incremental and bulk) were placed into glass tubes and sonicated in deionized water for 20 min to remove any additional adhering particulate matter. Samples were spun down and air-dried at 60°C, and treated with 2:1 chloroform:methanol to remove lipids and other contaminants

(Webb et al., 2013). Samples were air-dried at 60°C and then minced as finely as possible. Hair (0.4 to 0.5 mg) was then weighed into tin capsules for elemental and isotopic analysis.

Williams et al. (2011) have discussed the importance of errors associated with sampling human scalp hair at various stages of growth (actively growing and dormant hair). Growth cycle determinations were not made for these camelid hair samples for three reasons. First, hair follicle morphology associated with different growth phases has not been studied in camelids as it has been in humans (Antonini, 2010). Second, and more importantly, camelids (like many other fiber-producing mammals) are characterized by highly synchronized hair growth, such that hairs will not occur in multiple growth phases simultaneously as is the case in humans (Ebeling et al., 1991; Galbraith, 2010). Third, the length of time spent in the active growth phase (anagen) in camelids is typically quite long, and the transition into the inactive (telogen) phase is typically associated with shedding (Galbraith, 2004). Given that both llamas and alpacas were utilized as fiber-producing animals (Bonavia, 2008), it is highly unlikely that these animals would be allowed to go unshorn for any appreciable amount of time after the hair was not actively growing. Moreover, the animals that produced the majority of the hair samples were all juveniles that had likely never been shorn.

Isotopic and elemental compositions were determined using either a Thermo Finnigan Delta^{PLUS} XL or Thermo Finnigan Delta V continuous flow mass spectrometer coupled to a Costech Elemental Analyzer at the Laboratory for Stable Isotope Science (The University of Western Ontario). Samples analyzed using the Delta^{PLUS} XL were calibrated to VPDB with NBS 22 (oil, accepted δ^{13}C value = −30.03 ‰) and IAEA-CH-6 (sucrose, accepted δ^{13}C value = −10.45 ‰), and to AIR with IAEA-N-1 (ammonium sulfate, accepted δ^{15}N value = 0.4 ‰) and IAEA-N-2 (ammonium sulfate, accepted δ^{15}N value = 20.3 ‰). Samples analyzed with the Delta V were calibrated to VPDB and AIR with USGS40 (glutamic acid, accepted values δ^{13}C = −26.39 ‰, δ^{15}N = −4.52 ‰) and USGS41 (glutamic acid, accepted values δ^{13}C = 37.63 ‰, δ^{15}N = 47.6 ‰). In addition to these calibration standards, international and internal standard reference materials were analyzed in all runs to monitor analytical accuracy and precision (summarized in

Appendix E). Furthermore, 10 % of samples were analyzed in duplicate. For bone collagen, the mean differences between duplicate pairs (25 duplicates) were: 0.07 ‰ (δ^{13}C), 0.11 ‰ (δ^{15}N), 0.75 % (% C), 0.44 % (% N). For hair, the mean differences between duplicate pairs (34 duplicates) were: 0.09 ‰ (δ^{13}C), 0.10 ‰ (δ^{15}N), 0.57 % (% C), 0.23 % (% N).

5.5.3 Quantification of Between-Individual Isotopic Variability

Many of the recent quantitative methods that have been applied to isotopic data have been concerned primarily with reconstructing diet composition (Froehle et al., 2012; Kellner and Schoeninger, 2007; Moore and Semmens, 2008; Parnell et al., 2010; Semmens et al., 2009; Ward et al., 2010). These methods can be extremely useful and have been significant advances with respect to accounting for uncertainty in source isotopic compositions, tissue-diet fractionations, and source elemental compositions. More recently, however, ecologists have become interested in quantifying isotopic variation within groups (e.g. species, trophic guilds, entire communities) as a means of examining niche width or niche breadth (Eloranta et al., 2013; Fink et al., 2012; Grey and Jackson, 2012; Guzzo et al., 2013; Hayden et al., 2013; Inger et al., 2006; Jackson et al., 2011; Jackson et al., 2012; Lavoie et al., 2012; Layman et al., 2007a; Layman et al., 2007b; Layman and Allgeier, 2012; Llewellyn and Peyre, 2011; Lloret and Marín, 2009; Martínez del Rio et al., 2009; Matich et al., 2011; Navarro et al., 2013; Ruokonen et al., 2012; Syväranta et al., 2013; Szpak et al., 2012c; Thomson et al., 2012; Vander Zanden et al., 2013). On this basis, a number of metrics have been proposed that are reflections of some aspect of niche width, all of which are based primarily on Euclidean approaches to bivariate data.

Isotopic data that are used primarily in ecological and archaeological studies (δ^{13}C, δ^{15}N) are most commonly plotted as points (x, y) in bivariate space because the relationships between isotopic data (relative to one another, or relative to food sources) are qualitatively meaningful when plotted this way. Indeed, most archaeological studies take this approach (and go no further) to interpret their isotopic data. The metrics outlined in this portion of the paper take advantage of this visually or qualitatively meaningful way of plotting bivariate isotopic data, and further provide a number of quantitative measures that follow the same logic.

The metrics used to compare variation (between individuals within groups) in this paper can be divided into three broad categories: extreme value metrics, density or packing metrics, and mixed metrics. The extreme value metrics are all affected in the same way by sample size. For a given isotopic dataset, as *n* decreases, these metrics will decrease or remain unchanged – they can never increase as sample size decreases. As the name implies, these metrics will be strongly influenced by outliers or extreme values. These metrics are as follows:

1. CR ($\delta^{13}C$ range): the difference between individuals with the highest and lowest $\delta^{13}C$ values ($\delta^{13}C_{max} - \delta^{13}C_{min}$) (Layman et al., 2007a).

2. NR ($\delta^{15}N$ range): the difference between individuals with the highest and lowest $\delta^{15}N$ values ($\delta^{15}N_{max} - \delta^{15}N_{min}$) (Layman et al., 2007a).

3. CHA (convex hull area): the minimum area convex polygon that encloses all of the data in bivariate space (also known as total area or TA; Layman et al., 2007a).

The density metrics relate information about how evenly packed the isotopic data are in two-dimensional space, or δ space (Newsome et al., 2012). These metrics will respond inconsistently with decreasing sample size, the effects of which will be highly dependent on the overall distribution and level of variation of the isotopic dataset. These metrics are as follows:

4. CD (mean distance to centroid): the mean Euclidean distance between each individual and the centroid of the polygon defined above. Note that the centroid is not the mean of all data, but the mean of the points that form the vertices of the CHA polygon (Layman et al., 2007a).

5. MD (mean distance to the mean): the mean Euclidean distance between each individual and the mean of the entire group. This metric will slightly differ from CD,

especially in cases where the CHA is composed of bivariate data that are substantially different than the majority of other data.

6. NND (nearest neighbor distance): the mean Euclidean distance between each individual and its nearest neighbor (Layman et al., 2007a).

7. SDNND: (standard deviation of nearest neighbor distance): the standard deviation of the nearest neighbor distance for all individuals (Layman et al., 2007a).

8. MND (mean neighbor distance): the mean Euclidian distance between each individual and every other individual within the group.

9. SDMND (standard deviation of mean neighbor distance): the standard deviation of the neighbor distance for all individuals.

The final set of metrics (mixed metrics) attempt to quantify the same properties as the convex hull, but recognize the sensitivity of convex hull to sample size and extreme values. These metrics use the standard ellipse, which is defined in the most basic sense on the basis of the mean and standard deviation of the two sets of data (in this case δ^{13}C and δ^{15}N) as well as their correlation coefficient (Batschelet, 1981::129-158).

10. SEA (standard ellipse area): the area of the bivariate ellipse with its centroid at the mean x (δ^{13}C) and y (δ^{15}N) values (Jackson et al., 2011).

11. SEA$_c$ (standard ellipse area corrected for small sample size): the area of the bivariate ellipse with its centroid at the mean x and y values that is corrected for small sample size according to the method provided by Jackson et al. (2011) where SEA$_c$ = SEA(n−1)[(n−2)$^{-1}$].

12. SEA$_b$ (standard ellipse area Bayesian): the area of the bivariate ellipse generated using a Bayesian framework, where a defined number of iterative draws (typically between 10^4 and 10^6) from a Markov chain Monte Carlo method are used to generate a robust number of areas. The series of SEA$_b$ values generated for a given dataset can be easily compared to other similar datasets, and Jackson et al. (2011) suggest that for

comparative purposes, SEA_b is the most robust metric and in fact better accounts for small sample sizes than does SEA_c.

With respect to archaeological data, SEA_b and SEA_c should be most appropriate for making comparisons between groups (e.g. between sites) rather than CHA because archaeological sample sizes tend to be rather small. Even in modern ecological contexts where sample sizes are often small − but still appreciably larger than in archaeological contexts − and from a much more constrained temporal context, CHA is extremely sensitive to sample size. SEA is also sensitive to sample size, although less so than CHA (Jackson et al., 2011; Syväranta et al., 2013).

For camelids analyzed in this study, within group variation was compared between groups using the SEA_b metric. For the Markov-chain Monte Carlo, posterior draws were set at three different levels (10^4, 10^5, 10^6) to examine any potential differences that might be generated in the posterior Bayesian ellipse areas or in the posterior credible intervals generated using SIAR (stable isotope analysis in R; Parnell et al., 2010). Similarity between groups was assessed using the extent of overlap between the CHA and SEA_c.

All analyses described in this section were performed in the open source statistical computing package R (R Development Core Team, 2007) for Mac, utilizing the SIBER (stable isotope Bayesian ellipses in R) scripts (Jackson et al., 2011) within the SIAR package (Parnell et al., 2010).

5.5.4 Quantification of Within-Individual Isotopic Variability

A number of studies have employed isotopic analysis of incrementally growing tissues such as hair (Knudson et al., 2007; Webb et al., 2013; White et al., 2009; Williams and Katzenberg, 2012; Wilson et al., 2007) to examine temporal variation in diet and habitat use. The interpretation of these data has been largely qualitative, relying on a visual interpretation of plots of carbon and nitrogen isotopic composition with time. This approach is problematic in that it often treats bivariate isotopic data (for $\delta^{13}C$ and $\delta^{15}N$ specifically) as two distinct sets of univariate data. Moreover, it is difficult to compare the magnitude and directionality of dietary shifting between individuals quantitatively.

To compare within-individual isotopic variation (differences between long-term [bone collagen] and short-term [hair]) dietary signals, circular statistics were employed to quantify the magnitude and direction of dietary change (Schmidt et al., 2007). This approach provides an attractive alternative in that it generates metrics both for the direction of change (the angle of the change, a) and the dispersion of that change (the mean vector length for all paired data, r, and the angular deviation, s). Several recent ecological studies have utilized similar approaches to examine changes in specific community components (e.g. individual species, trophic guilds) or entire communities (Bartels et al., 2012; Dekar et al., 2009; Duyck et al., 2011; Hobson et al., 2012; Jackson et al., 2012; Lloret and Marín, 2009; Martínez del Rio et al., 2009; Mauna et al., 2011; Reum and Essington, 2013; Schmidt et al., 2009; Turner et al., 2010b). For additional detail on circular statistics, the reader is referred to Batschelet (1981) and Zar (2010::605-668).

The representation of paired isotopic data in bivariate space generates unit vectors. These data cannot be analyzed statistically according to a normal Gaussian distribution, but instead follow the von Mises (or circular normal) distribution (Zar, 2010). For example, the arithmetic mean of the three angles (2°, 358°, 0°) is 120°, although 0° is intuitively the correct mean (Figure 5.5). For a sample consisting of n angles ($a_1 \ldots a_n$), the mean angle ($\bar{a}$) and mean vector length (r) are defined as follows:

$r = \sqrt{X^2 + Y^2}$ Equation 5

$X = \frac{\sum_{i=1}^{n} \cos a_i}{n}$ Equation 6

$\boldsymbol{Y} = \frac{\boldsymbol{\sum_{i=1}^{n} \sin a_i}}{\boldsymbol{n}}$ Equation 7

$\mathbf{sin}\, \bar{a} = \frac{\boldsymbol{Y}}{\boldsymbol{r}}$ Equation 8

The mean vector length (r) is not equivalent to the mean length of the Euclidean distance between points. Instead, it is a representation of the concentration of angles and varies between 0 and 1. An r of 1 indicates that all angles are concentrated in the same direction, while r of 0 indicates no consistent pattern in the concentration of angles. When r=0, there is too much dispersion in the data for a mean angle ($\bar{a}$) to be defined.

Several metrics have been proposed to quantify angular dispersion. The angular deviation (s) is the circular metric that is most analogous to the standard deviation:

$$s = \frac{180°}{\pi}\sqrt{2(1-r)} \qquad \text{Equation 9}$$

The minimum possible value for s is 0° and the maximum value is 81.03°. While s does not provide additional information (as it is derived directly from r), it does provide a useful graphical representation of the angular dispersion in space.

These data are represented as arrow diagrams, which are modified from those produced by the circular statistics package Oriana (Kovach, 2013). On these diagrams, solid arrows represent the change between each individual hair segment and the bone collagen for specific individuals, treating the collagen isotopic compositions as point of origin. The angle of this change represented on this arrow diagram is derived from the angle of change between the two points in bivariate space after accounting for tissue-specific differences in fractionation (discussed below). On the bivariate plot with δ^{13}C on the x axis and δ^{15}N on the y axis, angles of change (a) are defined as follows: 0°/360° positive change in δ^{15}N, no change in δ^{13}C; 90° positive change in δ^{13}C, no change in δ^{15}N; 180° negative change in δ^{15}N, no change in δ^{13}C; 270° negative change in δ^{13}C, no change in δ^{15}N. The broken line emanating from the center of the graph represents the mean angle of change ($\bar{a}$) and the mean vector length of change (r), with the radius of the solid circle representing r=1. The shaded area represents the angular deviation (s).

For direct comparisons of isotopic compositions derived from different tissues, it is important to account for potential changes in tissue-diet fractionation (denoted with a capital delta, Δ). For mammalian bone collagen, the following tissue-diet fractionations were used: +3.7 ‰ for Δ^{13}C and +3.6 ‰ for Δ^{15}N (Szpak et al., 2012c). For mammalian hair keratin, a review of published literature yielded the following tissue-diet fractionation factors: +2.4 ± 1.2 ‰ for Δ^{13}C (n=14) and +3.5 ± 1.0 ‰ for Δ^{15}N (n=9)

(Table 5.2). On this basis $\Delta^{15}N_{keratin-diet}$ and $\Delta^{15}N_{collagen-diet}$ were assumed to be the same, but the unusually high value for $\Delta^{13}C_{collagen-diet}$, driven by the high glycine content of collagen (Hare et al., 1991; Koch, 1998) meant that an adjustment was necessary to directly compare carbon isotopic compositions of hair and bone collagen. To this end, when hair and bone collagen isotopic compositions were plotted together, $\delta^{13}C_{keratin}$ values were increased by +1.3‰.

5.6 Results

5.6.1 Modern Camelids and the 'Highland Pattern'

In order to determine whether or not the isotopic compositions of prehispanic coastal camelids are distinct from those of modern camelids herded in the high-altitude regions of the Andes, it is first necessary to establish what is expected (isotopically) of camelids herded at high altitudes. Carbon and nitrogen isotopic compositions from modern highland animals are presented in Figure 5.6 as standard ellipse areas corrected for sample size (SEA_c). These data are derived from bone collagen, bulk hair, and serially sampled hair. The use of convex hulls for isotopic compositions of incrementally growing tissues such as hair is likely reasonable as well, but because of the different number of segments analyzed at the individual level, SEA_c is more appropriate for comparative purposes.

These modern camelids are characterized by low $\delta^{13}C$ and $\delta^{15}N$ values, consistent with a diet comprised largely or entirely of C_3 vegetation. There is also relatively little isotopic variability both between and within individuals (Figure 5.6). On this basis, therefore, animals raised in the Andean highlands should be characterized by low carbon and nitrogen isotopic compositions, and a relatively low amount of inter- and intra-individual isotopic variability.

The low isotopic variation in these camelids is driven by two factors. First, there are few C_4 plants in high altitude pasturelands — with the exception of *Muhlenbergia* sp. (Bryant and Farfan, 1984), and accordingly — there is a relatively low amount of baseline variation in plant $\delta^{13}C$ (Szpak et al., 2013b). Figure 5.7 depicts the mixing polygons formed for five different ecological zones in northern Peru (Moche Valley region), demonstrating the lower baseline isotopic variability (TA in Figure 5.7) in plants from high altitude (relative to low altitude and coastal) contexts. Second, animals tend to graze together in relatively large groups, even though these groups may consist of camelids owned by numerous families (Murra, 1965; Tomka, 1992). Camelid diets therefore tend to be fairly consistent between individuals. The entire suite of Layman and SIBER metrics for groups of modern camelids from this study and from published literature are presented in Table 5.3 (bulk hair and bone collagen) and Table 5.4 (serially sampled hair for individual camelids).

5.6.2 Archaeological Camelid Bone Collagen

Carbon and nitrogen isotopic compositions, as well as associated elemental data and preservation criteria (%C, %N, C:N, collagen yield) for all archaeological camelids sampled are presented in Table 5.5. Only collagen samples that met *all* of the following criteria were included in summary plots and statistical analyses (following recommendations of Ambrose, 1990; DeNiro, 1985; Harbeck and Grupe, 2009; Szpak, 2011; van Klinken, 1999): collagen yield > 1%, %C ≥ 13%, %N ≥ 4.8%, 2.9 < C:N ratio < 3.6.

Collagen was generally well preserved (Figure 5.8), which is not surprising given the levels of organic preservation at the sites. In all, acceptable carbon and nitrogen isotopic compositions for camelids were generated from the following number of individuals: *n*=43 from EIP contexts at Huaca Gallinazo (V−59), *n*=33 from EIP contexts at Huaca Santa Clara (V−67), and *n*=24 sacrificed individuals from the late Middle Horizon context at Huaca Santa Clara.

In addition to carbon and nitrogen isotopic compositions, standard ellipse areas corrected for small sample size (SEA$_c$) are presented in Figure 5.9 and convex hull areas (CHA) are presented in Figure 5.10. For the sake of clarity, the SEA$_c$ (without individual isotopic data) for these archaeological camelids from Virú are plotted alongside the SEA$_c$ for modern highland camelids in Figure 5.11. Carbon isotopic compositions for modern animals have been adjusted by +1.5 ‰ to account for the Suess Effect (Keeling, 1979; Keeling et al., 1979; Yakir, 2011) and carbon isotopic compositions derived from hair keratin have been adjusted by +1.3 ‰ on this figure as discussed previously. To generate the modern camelid ellipse, mean $\delta^{13}C$ and $\delta^{15}N$ values were used for individuals with serially-sampled hair. The Virú camelids are characterized by a great range of carbon and nitrogen isotopic compositions, with a more-or-less continuous distribution of points in bivariate space between −20 ‰ and −10 ‰ for $\delta^{13}C$. Because of this, these groups do not lend themselves being characterized as consuming predominantly C_3 or C_4 plants. While it is true that there are more individuals with diets consisting of a high proportion of C_4 plants relative to modern highland animals, this does not adequately compare the complexity and extreme variability in these data.

The ellipses for the Virú camelids are of comparable sizes to one another, but much larger than the modern camelid ellipse (even though this modern dataset is derived from llamas, alpacas, and vicuñas drawn from both northern and southern Peru). The Huaca Santa Clara sacrificed camelids have slightly higher carbon and nitrogen isotopic compositions than the EIP camelids, although there is considerable overlap between the two groups. This is likely caused by the very young age of these camelids, which were still largely or wholly dependent on their mother's milk (Brown, 2000; Koford, 1957; Sharpe et al., 2009), creating a slight suckling offset. This effect has been observed in mammalian species and occurs because the infant is essentially consuming the tissues of the mother, rather than the normal adult diet (Balasse et al., 2001; Knoff et al., 2008; Newsome et al., 2006; Polischuk et al., 2001; Prowse et al., 2008).

Isotopic variation metrics for the Virú camelids, as well as for other archaeological and camelid groups from the Peruvian Andes are presented in Table 5.6. Because of the sensitivity of these metrics to sample size, it is very difficult to compare the camelids from this study to other archaeological camelid groups that have been analyzed to date. Syväranta et al. (2013) suggested a minimum number of samples for reasonable comparison of the Layman (2007a) and SIBER (Jackson et al., 2011) metrics to be around n=30. With respect to the comparisons generated on the basis of SEA_b, Jackson et al. (2011) recommend a minimum of n=10 for each group being compared. Two of the three camelid groups exceed these minimum numbers, while the third (V-67 sacrifices) does not (n=23), but is still larger than other archaeological camelid groups, most of which are smaller than n=10 (Table 5.6). At these very low sample sizes, high values for many of the metrics (e.g. SEA) for groups of archaeological camelids are as much (if not more) a reflection of the *uncertainty* in generating these metrics as they are a reflection of the real variation expected in a given group. Thus, comparisons between the camelid groups presented in this study, and other archaeological camelid groups are highly problematic. In addition to this, it is not meaningful to group individual camelids from the same site together when the contexts from which they were derived span several thousand years. While archaeological contexts will always be associated with comparatively poor temporal resolution, at the very least, an attempt must be made to restrict comparative groups to some kind of meaningful spatial *and* temporal context. In other words, large groups at the site level that span several chronological periods should be avoided even if this means that a sufficiently large sample cannot otherwise be produced.

The posterior probability distributions of SEA_b for the Virú camelids are plotted in Figure 5.12, with three different numbers of posterior draws (10^4, 10^5, 10^6). No difference was evident between these three analyses, suggesting that 10^4 draws are sufficient to describe the SEA of each of these sets of data. At much smaller sample sizes ($n \leq 10$), this may not be the case, and 10^6 draws may be more desirable due to increased uncertainty of SEA created by small sample size. The ellipse areas of the three Virú camelids groups are generally very similar, although the Huaca Santa Clara sacrifice group is of smaller size than the two EIP groups. This is likely driven by: (1) the slightly smaller sample size in the sacrifice group compared to the other two, and (2) the extremely restricted age range of these animals.

The extent of dietary similarity between these groups can be best assessed by comparing the SEA and CHA metrics, which are broadly analogous to the trophic niche of a particular group (Fink et al., 2012). Most studies have compared carbon and nitrogen isotopic compositions between groups separately (e.g. ANOVA, Student's t-test, Mann-Whitney U test). This approach is problematic since it treats bivariate data as two sets of univariate data that are unrelated and in the majority of instances (where carbon and nitrogen isotopic compositions are being compared) this is not the case; carbon and nitrogen isotopic compositions in plant or animal tissues may often be strongly correlated (usually positively for animals).

The extent of overlap, expressed as a percentage of overlapping area between the two polygons or ellipses, for the three groups of archaeological camelids from Virú are summarized in Table 5.7. Additionally, direct comparisons can made between each of the areas generated using the bootstrapping procedure in the calculation of SEA_b (typically between 10^4 and 10^6). This generates a proportion of the areas of Group 1 that are larger than the areas of Group 2, where 0.5 indicates complete similarity, and values closer to 0 or 1 indicate increasingly greater dissimilarity in elliptical areas. These metrics are presented in Table 5.7 as $SEA_{1>2}$.

In ecological studies of niche width, 60% overlap between two groups is considered to be significant, based both on observational (Schoener, 1968) and isotopic (Guzzo et al., 2013) data. The isotopic approach will tend to overestimate the extent of dietary overlap because some foods may be functionally different but isotopically similar. There is considerable overlap between each of these camelid groups, suggesting very similar diets for each of these groups. There tends to be less overlap between CHAs relative to SEAs, which is due to the fact that CHA is more sensitive to extreme values. Based on the various assessment of similarity discussed above, both with respect to the extent of isotopic variation, and the extent of overlap between polygons or ellipses in bivariate space, these three groups do not significantly differ from one another.

5.6.3 Archaeological Camelid Hair

Carbon and nitrogen isotopic compositions, as well as associated elemental data (%C, %N, C:N) for camelid hair are presented in Table 5.8. Incrementally-sampled hair carbon and nitrogen isotopic compositions are plotted in Figure 5.13; SEA_c for each of these individuals camelids are also presented in the far right panel of Figure 5.13. Layman and SIBER metrics for each of the individual camelids with incrementally-sampled hair are presented in Table 5.9.

Hair is a composite tissue, but is composed primarily of the protein keratin. Unlike bone collagen, there are no widely agreed-upon criteria to assess the preservation of archaeological hair. While the C:N ratio of archaeological keratin has been utilized as a means of assessing preservation, O'Connell and Hedges (1999) warn that these values must be viewed cautiously due to the very large variation observed in hair C:N ratios, which they report to be 2.9 to 3.8. By way of comparison, the observed range in mammalian bone collagen C:N ratios is much more restricted, 3.16 to 3.32 (Szpak, 2011). A literature review revealed a range of 3.02 to 3.68 for mammalian hair/wool keratin, with a tendency for hair C:N ratios derived from wool producing mammals to be between 3.5 and 3.7 (table 5.10). These values are derived from reported amino acid compositions of keratin specifically, and may therefore not faithfully reflect the expected C:N ratios for bulk hair due to its composite nature. Hair segments sampled from modern camelids presented in this study had C:N ratios between 3.09 and 3.39, with a mean value of 3.25±0.07 (*n*=87). Therefore, while C:N ratios are reported, they act as only very general indicators of preservation (following O'Connell and Hedges, 1999). In this study, isotopic data derived from hair keratin were considered to be unreliable if the sample produced low % C (<30 %) and/or % N (<10 %), values that correspond to approximately 2σ below the mean values for the archaeological hair. These criteria are much more stringent than those recommended by Ambrose (1990) as minimum values for bone collagen % C (13%) and % N (4.8 %), respectively. On this basis, only two hair segments from one individual produced unacceptable data (Table 5.8), although the carbon and nitrogen isotopic compositions of these segments are not unusual. Following the logic of DeNiro (1985), these data could be considered acceptable, but erring on the side of caution, they are not included in subsequent analyses.

For comparative purposes, serially-sampled tail hairs from cattle that were subjected to a diet switching experiment (pure C_4/pure C_3/pure C_4) are depicted in Figure 5.14. What is significant here is that the cattle tail hairs did not immediately reflect the switch between two diets with carbon isotopic compositions that differed by approximately 14 ‰. Instead, a period of 60 to 75 d that represented a more gradual change or equilibration between the two diets was required before a pure C_3 or C_4 signal was recorded in the hair. This is noteworthy in the context of the Huaca Santa Clara camelids, since some of these animals are characterized by 5 ‰ changes in $\delta^{13}C$ along the length of the hair sample. Given many of these animals only lived six months, or many cases less than three months, this implies an extremely significant change in the diet of these animals during their short lives. Surprisingly, the sacrificed animals with the greatest changes in diet tend to have lower $\delta^{13}C$ values leading up to the time of death, discounting the possibility that these animals may have been ceremonially fed maize or maize beer in preparation for this sacrificial event. Conversely, other animals are characterized by little or no change throughout the course of the hair sampling. Overall, there is no clear trend among these individuals in carbon or nitrogen isotopic compositions leading up to the time of death. Some individuals are characterized by very large isotopic variation, while others are characterized by almost none. Similarly, in the three butchered EIP animals from Huaca Santa Clara, there is no clear trend in isotopic compositions overall, or leading up to the time of death. Again, there is a range in isotopic variation from extremely small (AIS 395) to very large (AIS 578).

The comparison of the isotopic compositions of tissues that represent different periods in an animal’s life (either due to incremental growth or different residence/turnover times) allows for further comparison of temporal variation in diet and habitat use. For individual camelids for which bone and hair (with adhering skin) were both available, the carbon and nitrogen isotopic compositions of these two tissues were compared directly using the angular/circular approaches discussed previously (Figure 5.15). Adjustments for different trophic-level fractionation were made to directly compare the isotopic compositions of these two tissues as discussed previously. In these angular diagrams, the center represents the isotopic composition of the bone collagen of that individual animal. Each arrow emanating from the central point represents a distinct hair segment sampled from that individual. The lengths of the arrows represent the Euclidean distance between the bone collagen and hair isotopic compositions in bivariate space — longer arrows reflect larger isotopic differences between the hair segment and the collagen. The angle of these arrows reflects the direction of the difference between the hair and the collagen. The broken line emanating from the center represents the mean vector length (*r*) as defined previously. Similarly, the shaded area represents the angular deviation (*s*). Therefore as *s* becomes smaller and *r* becomes longer, the angles of change between the hair and the collagen are more similar to one another. For the circular diagrams, the circles with broken lines (within the larger circle) signify: 0.25 units for *r*, 1.5 ‰ (in bivariate space, not for δ^{13}C or δ^{15}N individually).

All nine camelids for which data are presented in Figure 5.15 are sacrificed animals from the later context at Huaca Santa Clara. There are no consistent patterns of isotopic differences between the hair and the bone both between and within these individuals. Some (e.g. Llamas 5 and 6) are associated with minimal differences between the hair and collagen isotopic compositions. Others (e.g. Llamas 19 and 26) are associated with very large differences between the hair and collagen isotopic compositions. Additionally, there is no consistent trend in the direction or consistency of isotopic difference between the hair and the collagen. Some individuals (e.g. Llamas 19, 22, 25, 26) are characterized by very consistent differences between hair and collagen isotopic compositions, indicated by the high value for *r* and small angular variance (*s*). Even among these individuals, however, the direction of these differences is not consistent. Finally, some individuals (e.g. Llamas 5, 8, 17) have no consistent difference between hair and collagen isotopic compositions (those with small *r* and large *s* values).

5.7 Discussion

5.7.1 Local/Coastal Camelid Herding

Previously, relatively high δ^{13}C and δ^{15}N values have been interpreted as evidence of camelid herding in the low sierra or coastal regions, due possibly to a reliance on marine algae (DeNiro, 1988) or *lomas* plants (Thornton et al., 2011). In this study, relatively high δ^{13}C and δ^{15}N values were observed for camelids recovered from coastal sites in relation to animals herded in high altitude areas of the Andes (Figure 5.11). When the camelid isotopic data are considered in relation to plants sampled along an altitudinal transect in northern Peru, the variation observed in camelid isotopic compositions can be satisfactorily explained by the consumption of local terrestrial vegetation. Figure 5.16 depicts the convex polygons formed by the carbon and nitrogen isotopic compositions for modern plants sampled in five major ecological zones along an altitudinal transect in northern Peru. Transposed onto these polygons are the convex hulls for the three groups of camelids analyzed in this study. Following the basic principles of isotopic mixing, the isotopic composition of a consumer in bivariate space must fall within the polygon formed by the sources (foods); if this condition is not met, these sources cannot explain the consumer isotopic composition (Phillips and Gregg, 2003; Schwarcz, 1991). The area of overlap between the camelid (consumer) and plant (source) polygons represents the relative percentage of consumer isotopic data that can be produced by the consumption of the plants making up the source polygon. Table 5.11 summarizes the percent area of overlap between the two polygons, with a higher percentage overlap being associated with a higher probability that a given consumer polygon can be associated with a given source polygon. In this case, the coastal polygon explains 100 % of the isotopic variation observed for each of the consumer (camelid) polygons, while the source (plant) polygons in each of the other ecological zones never explains more than 72 % of this variation. This is true for all three groups of Virú camelids. On this basis, it is reasonable to suggest that at least some of these animals were raised on local vegetation, and were not imported from high altitude contexts. In other words, some of these camelids have tissue isotopic compositions that are not consistent with the isotopic variation observed in non-coastal vegetation.

The extremely restricted age range of the sacrificed camelids from the Late Middle Horizon context at Huaca Santa Clara is worthy of additional discussion within the context of coastal herding. The variation in carbon and nitrogen isotopic compositions in these sacrificed animals is very similar to that observed in the early camelids from Huaca Santa Clara and Huaca Gallinazo (Figure 5.9), with a high degree of overlap between these groups (Table 5.7). There is slightly less variation in these sacrificed animals, but this is likely a product of the extremely restricted age range and slightly smaller sample size for this group. Moreover, there is a high degree of within-individual variation in some of the sacrificed camelids, as well as the EIP camelids, although for both groups the general pattern is an *inconsistent* amount of variation within individuals. On this basis, it is reasonable to suggest that the pattern of animal husbandry associated with these sacrificed camelids was very similar to that associated with the earlier EIP camelids. Alternatively, it is possible that the type of isotopic ‘signature’ observed for these camelids is the product of a group of camelids derived from disparate geographic areas, some being imported from long-distance, possibly from high altitude locations. Aside from the incompatibility of this explanation with the isotopic variation in plants previously discussed, there are several biological aspects of camelid reproductive biology that make this suggestion extremely unlikely, as is discussed next.

Taking into account the ages of these sacrificed camelids (Table 5.1), if they were ‘imported’ from elsewhere but killed at <6 months of age, they would need to traverse the distance to the site as a very young animal. There is no record of caravans including pregnant female camelids, or juveniles that have not been fully weaned, which usually occurs between seven and nine months (Brown, 2000; Koford, 1957; Sharpe et al., 2009). Caravan llamas begin training after two years of age (Browman, 1990a), with caravans consisting of castrated males between two and eight years old (Nielsen, 2001). For the first few months of life, camelids consume 10 % of their body weight in milk every day, suckling for several minutes between every two hours and several times per hour between 6:00 and 20:00 (Fowler, 1998). Moreover, neonatal and pre-weaned camelids are associated with high morbidity and mortality rates (as high as 70 % mortality in the Andes), with the highest mortality rates associated with animals <6 months of age (Davis et al., 1998; Sharpe et al., 2009; Wright et al., 1998). Accident and injury may be a major cause of mortality in pre-weaned camelids (Davis et al., 1998). Combined, these factors make it extremely unlikely that these juvenile animals would have traversed any significant distances prior to being killed as part of this ritual event. It may also be suggested that some of the butchered animals from EIP contexts are in fact caravan animals that died while traveling from the highlands to the coast. Following this logic, some of the individual animals with bone collagen $\delta^{13}C$ and $\delta^{15}N$ values that are intermediate between animals with predominantly C_3 or C_4 diets are caravan animals that feed in a diverse range of environments. While this is a possibility, the fact that many of the juvenile sacrificed camelids also fall within this intermediate range demonstrates the presence of such an isotopic pattern for local animals.

Although the notion that these animals were imported from distant, ecologically distinct locations is not supported by the isotopic data, this does not imply that these animals were herded in the immediate vicinities of the sites from which they were eventually recovered. These animals may have been herded in the vicinity of any of the numerous settlements in the Virú Valley (Willey, 1953), but the dearth of vegetation at a regional scale, combined with the isotopic variability observed within these camelid groups points to a scale and mode of husbandry that differs from what has traditionally been associated with highland environments in modern and historic accounts — herds moving between large highland pastures.

5.7.2 Small-Scale Camelid Husbandry

Aside from the isotopic compositions of camelid groups and their relation to source (plant) isotopic compositions discussed previously, it is important to consider the isotopic variation both within groups and within individuals. As discussed in the introduction, the quantification of dietary (isotopic) *variation* rather than an attempt at a precise reconstruction of diet *composition* has excellent potential to provide insight into the nature of animal husbandry practices and human-animal interactions in prehistoric contexts.

Camelids are generally very adaptable in terms of their diet. Since llamas and alpacas have become more common on farms outside of the Andes in the last fifty years, they have been raised in a great diversity of environments, and on nearly every type of pasture in North America, Europe, Australia, and New Zealand (Bakker et al., 1998; Dumont et al., 1995; Fowler, 1998; Fraser and Gordon, 1997; Fraser, 1998; Liesegang et al., 2005; McGregor, 2002; Pinares-Patiño et al., 2003). Moreover, isotopic evidence from archaeological camelids suggests that foddering with agricultural products or byproducts (maize specifically) occurred outside of the *puna* (Finucane et al., 2006; Thornton et al., 2011; Verano and DeNiro, 1993). This practice has also been recorded ethnographically (Gade, 1992; Godoy, 1984; Godoy, 1991; Goland, 1993; McCorkle, 1987; Mitchell, 1991; Nielsen, 2001; Orlove, 1977a) and ethnohistorically (Nielsen, 2009), with maize being the only cultigen specifically mentioned. Accordingly, that camelids would have varied diets is not surprising, but in most cases, the large dietary variation that has been observed occurs at the group level over time, rather than between individuals within groups. For instance, the grazing of field stubble after harvest is a seasonal activity that is often part of transhumant movement of pastoral groups, but all camelids within these groups feed on the same kinds of food throughout the year. Although the proportions of these different foods may vary somewhat between individuals, this scale of variation is unlikely to manifest itself to a significant degree in the isotopic composition of a tissue like bone collagen. These smaller variations will most likely be dampened by the slow turnover rate of collagen, which reflects dietary intake over the last several years of an animal's life (Hedges et al., 2007; Riofrío-Lazo and Aurioles-Gamboa, 2013; Stenhouse and Baxter, 1979; Wild et al., 2000).

At the site level, there is a relatively high amount of isotopic variation at both Huaca Gallinazo and Huaca Santa Clara (Table 5.6), although it is important to keep in mind that other archaeological camelid groups subjected to isotopic analysis to date are too small for many of the statistical comparisons outlined here. Even with the small sample sizes of the comparative groups, the Virú camelids still tend to have among the highest, or the highest, values for metrics that indicate dietary variation (extreme value and mixed metrics) such as: CR, NR, CHA and SEA (Table 5.6).

At the level of individual camelids, there is no clear pattern in isotopic variation. Both the magnitude and directionality of change in isotopic compositions over time varies greatly between individual camelids (Figure 5.15). In comparison to modern animals from high altitude contexts, the archaeological animals are characterized by an extremely wide range of isotopic variation (measured as SEA_b) and evenness (measured as MND) (Figure 5.17). These patterns have important implications with respect to the scale of camelid husbandry.

This pattern of very high between-individual variation and variable within-individual variation is inconsistent with the type of camelid husbandry that has been described for *puna* and high sierra environments in the Andes (Flannery et al., 1989; Flores-Ochoa, 1979; Kuznar, 1991a; Kuznar, 1990, 2001; Markemann and Valle Zárate, 2010; Orlove, 1977b, 1982; Postigo et al., 2008). Instead of the relatively large herds associated with this classic model of Andean pastoralism, the patterns observed for these archaeological camelids suggest a smaller-scale variety of camelid husbandry may have occurred in the low altitude and coastal areas of the Andes. Specifically, small groups of camelids may have been kept by individual families or other small social units. In this case, the large amount of isotopic variation for these Virú camelids may have been driven by differences in management strategies by individual herders for any number of reasons: (1) access to particular kinds of forage (either as crops, or wild pasture) may have varied between kin groups, (2) considerable variability existed surrounding the notion of the ‘proper way’ to raise one’s camelid, and what it should be fed, (3) certain individual camelids or groups of camelids exhibited strong preferences for particular types of forage. The last possibility seems relatively unlikely due to the ability of South American camelids to consume a wide variety of fodder, in many cases of much lower quality than would be acceptable for sheep or goats (López et al., 1998). The first two options, however, are extremely plausible. In support of the first, there is large isotopic variation in both wild and domestic local plants, and considerably more variation with respect to other ecological zones along the western slopes of the Andes (Figure 5.7). With respect to the second, for camelids that are provided with fodder, there is a great diversity in the attitudes of modern owners in terms of the appropriate foddering method (Fowler, 1998). The tending of small herds provided with distinct types of forage may have been further necessitated by the unique nature of the environment in the coastal valleys, with sparse vegetation outside of the lush cultivated zones in close proximity to rivers and irrigation networks. More extensive wild vegetation, specifically dry hardwood forests (*Prosopis* sp.) may have been more extensive in antiquity, possibly due to a combination of long-term environmental and anthropogenic disturbances (Beresford-Jones, 2005; Beresford-Jones et al., 2009). Leaves and/or pods gathered from these nitrogen-fixing trees could have provided additional fodder for camelids living in coastal settings; seeds in archaeological camelid dung have been recovered supporting this assertion (Shimada and Shimada, 1985).

The practice of grazing camelids on field stubble in the context of coastal husbandry merits further discussion for several reasons. The nitrogen isotopic composition of plant tissues is determined primarily by the nitrogen isotopic composition of source nitrogen. In turn, this is influenced by a variety of processes in the soil, and within the plant after uptake and assimilation (Szpak et al., 2012b; Szpak et al., 2013b). In general, plant organs that serve as nitrogen sources (leaves and stalks) tend to be enriched in ^{15}N relative to plant organs that are nitrogen sinks (grains) (Szpak et al., 2012a). Therefore, animals consuming variable proportions of grains and leaves/stalks following harvest could have significantly different tissue nitrogen isotopic compositions; these effects have been observed in maize specifically, and in some cases, may be very large (>10‰; Szpak et al., 2012a; Szpak et al., 2012b). If particular groups of animals grazed consistently on harvested fields and others did not (perhaps because camelids herded by certain families had more limited access to agricultural fields and/or were situated on the valley margin with limited access to water), this may have served as a further source of variation in source isotopic compositions, potentially contributing to the high inter-individual variation observed for the Virú camelids.

Related to the above point is the potential importance of the fertilization of agricultural fields with camelid dung, either purposefully and/or coincidentally during the grazing of field stubble. The extent to which plant δ^{15}N values are influenced by animal manure fertilization will depend on a variety of factors, including: the type of manure applied, the amount of manure applied, the frequency with which manure is applied (both in the short and long term), and local environmental conditions (Bogaard et al., 2007; Choi et al., 2002; Fraser et al., 2011; Szpak et al., 2012a; Szpak et al., 2012b). With respect to environmental conditions, processes such as water availability (due to variable access to irrigation water), light intensity, and physical properties of the soil may all vary at small scales, and could influence the relative importance of various soil processes (nitrification, denitrification, ammonification, ammonia volatilization, runoff) and in turn the nitrogen isotopic composition of manure-derived nitrogen in the soil, and the plants utilizing this nitrogen. While there may be no predictable and consistent means with which to model the relative importance of these effects, the significant point here is that they may serve to increase the source isotopic variation (increase the area of the mixing polygon) and contribute to high levels of isotopic variation among consumers.

Differences in ownership (or at least management responsibilities) of camelids combined with the lack of large local pastures at coastal and low altitude locations may have necessitated the spatial segregation of small groups of animals. In the highlands, individual families typically own two to several hundred animals, although all of the animals owned by a single community will graze together in a much larger aggregation with ownership being physically ascribed to the animals (often on their ears) (Murra, 1965; Tomka, 1992). The scale of settlement and subsistence patterns (with respect to agriculture and water management techniques specifically) was markedly different on the north coast of Peru (Hayashida, 2006; Netherly, 1977, 1984; Nordt et al., 2004; Willey, 1953) than what exists in present day and historic highland environments utilized by herders (Flannery et al., 1989; Flores-Ochoa, 1979). In this context, it is noteworthy that at Conchopata, a relatively large (ca. 20 ha) Wari (Middle Horizon) urban settlement in Ayacucho (ca. 2,700 masl), Finucane et al. (2006) found two divergent camelid foddering practices, focused on C_3 and C_4 (presumably maize) plants respectively. Although each of these two groups are still characterized by modest amounts of isotopic variation (Table 5.6), the bimodal distribution of camelid carbon isotopic compositions suggests some physical separation between two types of camelids — most likely llamas (beasts of burden/meat producers) and alpacas (fiber producers). The extreme variation, but fairly even spacing of camelid isotopic compositions in bivariate space for the Virú camelids (Figure 5.9) may very well be indicative of a large diversity of animal management strategies, rather than the more straightforward division described by Finucane et al. (2006).

5.7.3 Regional Significance

The management of livestock and, accordingly, the interactions that occur between humans and animals is often strongly influenced by a range of social and political factors (Comaroff and Comaroff, 1990; Holloway, 2001; Kirksey and Helmreich, 2010). The organization and scale of north coast polities during the EIP and Middle Horizon are widely debated, and a clear picture of the development of states in the region is only beginning to emerge. On the basis of four-tiered hierarchical settlement structure, the extensive and complex irrigation networks, the presence of urbanized settlements, and increase in population size, the Virú polity appears to have developed the political structure associated with archaic states (Fogel, 1993; Millaire, 2010b). While the importance of this ruling polity in directing large-scale public works projects (most notably the expansion of irrigation networks), and the presence of large storage facilities at Huaca Santa Clara suggests the collection of some form of tribute from the local populace (Millaire, 2010a), it is not clear to what extent this polity may have exerted control over animal husbandry.

The most extensive comparative data available come from Murra (1965, 1968, 1980), who summarizes a number of ethnohistoric accounts to develop a detailed picture of how camelid husbandry operated (primarily in southern Peru) under Inka control and immediately following the Spanish conquest. In these accounts, herding takes place primarily in the *puna*. Generally herds that were controlled either by the state or by the church were very large, while community herds were of extremely variable size. There are numerous instances in these accounts in which camelids are segregated into distinct groups, not only with respect to ownership and management, but also physical segregation of particular herds. For instance, there were herds controlled by the state or ‘crown’ and the ‘church’, both of which were large, and physically separated from one another. Additionally, state herds in different counties (e.g. Lupaca and Pasca in the southern Lake Titicaca area) were assigned to particular pastures, with animals from one area being restricted from grazing in the pastures assigned to another (Polo de Ondegardo, 1571). There is also evidence that church herds were segregated by color, with particular colors of llama or alpaca being sacrificed in associated with particular events: one hundred brown animals when maize is newly planted, one hundred white animals several weeks into the growing season to ensure rain, and one hundred of all colors during the harvest (Polo de Ondegardo, 1559). Conflicting accounts exist as to whether or not community animals were provided in the form of tribute to the state, and whether or not state or community animals were destined for sacrificial events. No details are available with respect to the specifics of different management practices of these animals, at least none that might manifest themselves isotopically. For instance, although Webster (1972) describes a modern llama sacrificial ritual that first involves the force-feeding of *chicha* (maize beer) to llamas, this occurs briefly and very close to the time of the animal’s death.

Murra (1965) notes that in the southeastern portion of the Inka empire, despite frequent wars and the appearance of a series of ruling polities with different sociopolitical structures, the activity of camelid herding itself remained largely organized at the kin group level. Along the same lines, even though animals that were part of state or church herds may have been destined for tribute or to serve as sacrifices, it appears as though the management of these animals occurred in accordance with local herding practices. The similarities in carbon and nitrogen isotopic compositions, and isotopic variation between the EIP and late MH camelids in Virú may have been driven by similar forces. Specifically, it is possible that the traditional north coast mode of camelid management involved highly differentiated herding of small groups of animals by kin groups, and in Virú at least, this continued unchanged with the rise and fall in the influence of the EIP polities, and with the introduction of new ritual practices during the MH. That herding appears to have continued at this small scale does not imply that the ruling elites did not impact camelid husbandry in a broad sense. They may have required new levels of tribute in the form of whole camelids for ritual or of camelid products. They may also have altered the nature of the ownership of camelid herds. There is, however, no evidence of the expansion of the scale of camelid herding to anything equivalent to what is observed in the highlands, or of the large-scale importation of animals raised in high altitude contexts. It is possible that local environmental conditions did not allow for the maintenance of the very large herds that were associated with later Andean polities, such as the Inka (Murra, 1965). Even when comparing herds in the *puna* and low/high sierra today, herd sizes are often on the order of 100 to 300 animals in the former, but typically between much smaller (15 to 100) in the latter (Dransart, 2002; Kuznar, 1990). Accordingly, the small herds of coastal settlements may represent a continuation of this pattern.

Additional comparative isotopic data from other areas along the Peruvian coast will be instrumental in developing a better understanding of camelid husbandry at a regional level. It is possible that the patterns described here for Virú in the EIP and late MH are anomalous, or that animal management practices varied strongly depending on both the local environment and the degree of influence of the ruling polity. Much potential exists in this area, especially with respect to the sacrificial camelids, as several similar ritual events have been documented along the north coast, both in Virú and elsewhere.

5.7.4 Human-Animal Interactions

Provided the interpretation of small-scale husbandry is correct, it is important to consider this in terms of the interactions that may have occurred between humans and animals. Given the relative lack of vegetation, the maintenance of local camelid herds would almost certainly have required that these animals' diets be supplemented by agricultural products and/or byproducts. Ethnohistoric accounts describe caravan animals on the coast being provisioned with maize, and not simply maize stalks and leaves (Zárate, 1555). As discussed previously, isotopic evidence from other sites suggests that this may have been a fairly common practice. In this case, rather than animals being brought to a particular pasture, fodder would have been brought to the animals, and their diet would be further constrained by the choices of the herders. The fact that both wild and domestic vegetation was concentrated in the vicinity of rivers and associated irrigation networks, it stands to reason that these animals would have been kept for a significant portion of time in the vicinity of settlements, which were similarly concentrated in these areas. Some evidence for small corrals exists along the coast (Bawden, 1982; Shimada, 1994; Wilson, 1988). Although these structures have not been identified to date in Virú, significant camelid dung deposits have been recorded at several sites (Millaire, Personal Communication). In this scenario, where animals are kept close to human habitation sites and food is (at least on some occasions) gathered and brought to animals in corrals, there is a great chance for close, face-to-face interactions between people and camelids, much more than would occur if animals spent significant periods of time away from human settlements, grazing on distant pastures. These conditions (limited spatial and extended temporal) are precisely the type that allow for complex relationships to develop between *individuals* of each species (Dwyer and Minnegal, 2005; Knight, 2012).

Thinking back to Kohn's (2007) notion of an 'anthropology of life' that examines the entanglements between humans and other species, a much different mode of interaction existed between coastal and highland camelid herders, at least on the basis of their diets. It is entirely possible that additional differences exist between the traditional high altitude mode of Andean pastoralism and that which occurred along the prehistoric north coast of Peru. Additional lines of evidence that are able to provide insight into how animals lived should shed further light on these issues, but zooarchaeologists and their collaborators must prioritize their research accordingly. Such lines of evidence include, but are not limited to: paleopathology, ancient DNA, tooth wear, molecular and microscopic coproscopy, and additional isotopic or elemental markers. Primary zooarchaeological data (Reitz and Wing, 2008) obviously remain of immense importance, and none of the above-mentioned techniques would be meaningful and/or feasible without these data.

In summation, the large amount of isotopic variation that is observed between individual camelids, combined with the inconsistent isotopic variation within individual camelids reflects a wide range of interactions between humans and the animals they herded. Returning to one of the issues raised in the introduction of this paper, focusing solely on the circumstances surrounding the deaths of these animals obscures this variation. For instance, the large group of juvenile camelids that were part of the ritual sacrifice at Huaca Santa Clara may have died under generally similar circumstances, but the isotopic data demonstrate that these animals lived very separated lives prior to this event.

5.8 Conclusion

The methodologies outlined here for quantifying isotopic variation have great potential in the broadest sense for archaeological data. They offer quantitative and robust means with which to compare groups across space and time; however, the problem of small sample size must be considered. Wherever possible, investigators must seek to maximize the number of individuals that are analyzed while avoiding sampling multiple elements from the same individual. In a more general sense, if the subfields of isotopic archaeology or isotopic anthropology are to make a meaningful contribution to the field, it is important for investigators to explore such quantitatively-grounded methodologies in their interpretations. The basic principles of these methods that rely on Euclidean metrics and other measures in bivariate space make use of the same logical spatial principles that anthropologists and archaeologists presently use in a strictly descriptive or qualitative sense to interpret their data. Finally, considering the extreme uncertainty associated with source isotopic compositions in archaeological contexts, more attention must be paid to interpretive methods that do not only or primarily seek to reconstruct diet composition, but also consider the importance of isotopic variation. All of this is not to suggest that the methods outlined take the place of any other that may be applied to isotopic data. Instead, they represent one tool in an ever-expanding interpretive toolkit that may serve to provide new insight into isotopic data.

The groups of camelids from Huaca Gallinazo and Huaca Santa Clara are characterized by high levels of inter-individual isotopic variation, as well as inconsistent levels of within-individual isotopic variation. Taking into account the isotopic compositions of sources from different ecological zones in the Andes, only plants growing in the low altitude and coastal regions adequately explain the isotopic variation observed among these individuals, suggesting that at least some of these animals were raised locally. Further, for the late MH sacrificed camelids, there are comparable levels of isotopic variation and a high degree of similarity in isotopic compositions, suggesting these animals were managed in a similar manner to those from the EIP contexts. These data imply a high degree of variation in the way in which camelids were managed, fitting with a small-scale type of husbandry where small groups of animals are kept relatively close to human habitation sites and fed a highly variable diet. This may be due to a combination of environmental (availability of adequate forage or differential access to different types of forage) and social (different perceptions about ‘proper’ camelid husbandry practices) factors.

Isotopic analysis is one of several methods that provide a means with which to better understand how animals lived, in addition to reconstructing the conditions under which they died. Isotopic analysis specifically has great potential to contribute to reconstructing human-animal relationships in prehistoric contexts.

Table 5.1. Estimated ages for sacrificed camelids from Huaca Santa Clara (Millaire, In Press).

Specimen ID	Estimated Age	Notes
Llama 2	<3 months	
Llama 3	<3 months	
Llama 4	<3 months	
Llama 5	<3 months	
Llama 6	3 to 6 months	
Llama 7	<3 months	
Llama 8	<3 months	
Llama 9	<3 months	
Llama 12	<3 months	
Llama 13	Juvenile	Crania missing
Llama 14	Juvenile	Crania missing
Llama 15	<3 months	
Llama 16	<3 months	
Llama 17	Juvenile	Crania missing
Llama 18	<3 months	
Llama 19	<3 months	
Llama 20	3 to 6 months	
Llama 21	<3 months	
Llama 22	<3 months	
Llama 24	<3 months	
Llama 25	3 to 6 months	
Llama 26	<3 months	
Llama 27	<3 months	

Table 5.2. Tissue−diet fractionations ($\Delta^{13}C$ and $\Delta^{15}N$) for hair keratin derived from published literature.

Species	**$\Delta^{13}C$**	**$\Delta^{15}N$**	**Notes**	**Reference**
Cattle	+2.7±0.4	−	−	(Sponheimer et al., 2003a)
Goat	+3.2±0.1	−	−	(Sponheimer et al., 2003a)
Alpaca	+3.2±0.1	−	−	(Sponheimer et al., 2003a)
Llama	+3.5±0.2	−	−	(Sponheimer et al., 2003a)
Rabbit	+3.4±0.3	−	−	(Sponheimer et al., 2003a)
Cattle	+2.7	−	−	(Schwertl et al., 2005)
Cattle	+2.6	−	−	(De Smet et al., 2004)
Cattle	−	+2.9	−	(Sutoh et al., 1987)
White−tailed deer	+0.3	+5.2	−	(Darr and Hewitt, 2008)
Various herbivores	+3.5	+5.2	Field data	(Kohzu et al., 2009)
Deer mouse	+0.3	+3.3	−	(Miller et al., 2008)
Rat	−	+3.4±0.5	−	(Ambrose, 2000)
Pig	+0.2	+2.7	−	(Nardoto et al., 2006)
Various Pinnipeds	+3.0	+2.8	Field data	(Hobson et al., 1997)
Red fox	+2.6±0.1	+3.2±0.1	−	(Roth and Hobson, 2000)
Bonobo	+2.8	+3.2	Field data	(Oelze et al., 2011a)
Japanese macaque	+2.8±0.3	+3.4±0.2		(Nakashita et al., 2013)

Table 5.3. Layman and SIBER variability metrics for modern camelids (bulk hair and bone collagen).

Type	**Elevation (masl)**	***n***	**CR**	**NR**	**CD**	**MD**	**NND**	**SDNND**	**MND**	**SDMND**	**CHA**	**SEA**	**SEA$_c$**	**SEA$_b$**	**Reference**
Bulk Hair[1]	3,182 to 3,595	7	5.4	2.6	1.7	1.0	1.7	1.1	1.4	0.9	2.7	4.9	6.2	7.4	This study
Bone collagen	3,388 to 3,595	3	0.7	1.0	0.5	0.2	0.4	0.3	0.6	0.2	0.8	0.2	<0.1	<0.1	This study
Bone collagen	Unknown	5	0.5	0.8	0.3	0.1	0.3	0.1	0.3	0.1	0.5	0.1	0.2	0.2	(Schoeninger and DeNiro, 1984)
Bone collagen	4,850	5	0.8	1.9	0.9	0.3	0.9	0.3	0.9	0.7	1.4	0.4	0.8	1.6	(Thornton et al., 2011)

1. Two llamas, two vicuñas, three alpacas.

Table 5.4. Layman and SIBER variability metrics for modern camelids (serially-sampled hair for individual camelids).

Sample ID	Species	Elevation (masl)	Segments	CR	NR	CD	MD	NND	SDNND	MND	SDMND	CHA	SEA	SEA_c	SEA_b
AIS 203	Alpaca	3,469	7	1.1	0.9	0.4	0.3	0.4	0.3	0.2	0.2	0.6	0.2	0.3	0.2
AIS 204	Alpaca	3,469	16	1.5	1.4	0.4	0.3	0.4	0.3	0.2	0.2	0.6	0.2	1.0	0.4
AIS 205	Alpaca	3,469	11	1.4	0.6	0.4	0.3	0.5	0.2	0.2	0.1	0.7	0.2	0.4	0.3
AIS 210	Alpaca	3,388	11	2.9	0.8	0.8	0.5	0.8	0.5	0.2	0.1	1.2	0.3	1.2	0.7
AIS 212	Alpaca	3,388	5	0.7	0.8	0.4	0.2	0.4	0.2	0.3	0.2	0.6	0.1	0.3	0.3
AIS 227	Alpaca	3,388	7	0.7	0.2	0.3	0.1	0.2	0.1	0.1	0.1	0.4	0.1	0.1	0.0
AIS 228	Alpaca	3,388	6	0.8	0.6	0.3	0.2	0.3	0.2	0.3	0.1	0.5	0.1	0.3	0.2
AIS 520	Llama	3,595	4	0.8	0.5	0.3	0.1	0.3	0.1	0.4	0.1	0.5	0.1	0.2	0.2
AIS 521	Alpaca	3,595	11	1.7	1.5	0.6	0.3	0.6	0.3	0.3	0.3	0.8	0.3	1.3	0.7

Table 5.5. Isotopic and elemental compositions, collagen yields, and associated contextual information for all camelids (bone collagen) analyzed in this study.

Sample ID	Sector	AC[1]	Room	Unit	δ^{13}C (‰, VPDB)	δ^{15}N (‰, AIR)	%C	%N	C:N	Collagen Yield
Huaca Gallinazo, V-59 (Early Intermediate Period)										
AIS 624	A			31	-12.81	7.32	48.32	17.58	3.21	14.4
AIS 622	A			25	-14.45	7.11	36.22	13.02	3.25	16.6
AIS 623	A			26	-12.76	7.60	39.60	14.74	3.13	19.1
AIS 620	B	1	1	10	-17.57	6.49	48.50	17.45	3.24	12
AIS 621	B	1	1	10	-12.49	9.45	45.16	16.53	3.19	17.3
AIS 625	B	1	1	16	-10.95	6.47	37.49	13.47	3.25	4.4
AIS 618	B		2007-3		-19.92	5.79	41.67	15.28	3.18	17.5
AIS 2595	H	2	11	108	-16.16	6.21	42.96	15.61	3.21	8.4
AIS 2596	H	2	11	108	-15.71	6.14	44.59	16.27	3.20	15.8
AIS 2599	H	2	11	110	-12.77	8.20	43.43	15.82	3.20	3.3
AIS 2600	H	2	11	110	-16.29	7.27	44.88	16.28	3.22	15.1
AIS 2602	H	2	11	110	-19.07	5.11	43.19	15.83	3.18	11.2
AIS 2603	H	2	11	110	-17.55	6.48	45.19	16.44	3.21	10.2
AIS 2605	H	2	11	110	-9.37	9.16	42.68	15.52	3.21	7.8
AIS 2609	H	2	14	115	-13.91	8.89	41.27	15.04	3.20	7.7
AIS 2594	H			33	-20.00	6.20	46.41	16.93	3.20	14.4

Sample ID	Sector	AC[1]	Room	Unit	δ^{13}C (‰, VPDB)	δ^{15}N (‰, AIR)	%C	%N	C:N	Collagen Yield
AIS 2606	H	2	13	113	-13.00	8.87	43.66	15.84	3.22	11.2
AIS 2616	A			122	-12.58	6.22	44.71	16.30	3.20	21.1
AIS 2617	A			122	-12.35	6.67	45.61	16.59	3.21	18
AIS 2618	A			122	-19.33	5.83	44.75	16.38	3.19	22.5
AIS 2620	A			122	-13.00	6.94	44.74	16.24	3.21	19.8
AIS 2621	A			122	-18.96	5.17	42.34	15.38	3.21	12.4
AIS 2622	A			122	-19.59	6.95	46.49	17.00	3.19	17.3
AIS 2624	A			122	-16.16	5.28	44.44	16.14	3.21	16.5
AIS 2625	A			122	-16.46	5.91	45.01	16.45	3.19	15
AIS 2627	A			122	-19.10	5.07	45.83	16.71	3.20	16.4
AIS 2628	A			122	-18.17	5.38	44.46	16.14	3.21	19.5
AIS 2629	A			122	-17.40	6.91	44.61	16.30	3.19	20.3
AIS 2630	A			122	-19.52	6.98	38.30	13.30	3.36	1.6
AIS 2631	A			122	-18.64	5.16	44.77	16.21	3.22	16.3
AIS 2632	A			122	-13.82	5.46	44.92	16.44	3.19	19.4
AIS 2634	A			122	-18.57	6.46	44.80	16.38	3.19	18.1
AIS 2635	A			123	-19.79	6.95	45.66	16.70	3.19	17.7
AIS 2637	A			124	-17.45	7.52	44.79	16.31	3.20	20.7
AIS 2638	A			124	-17.40	7.43	39.56	14.36	3.21	16.9
AIS 2639	A			124	-17.52	7.69	45.96	16.62	3.23	22.5

Sample ID	Sector	AC[1]	Room	Unit	$\delta^{13}C$ (‰, VPDB)	$\delta^{15}N$ (‰, AIR)	%C	%N	C:N	Collagen Yield
AIS 2640	A			124	-17.24	7.32	44.31	16.19	3.19	19.8
AIS 2641	A			125	-19.99	5.92	45.48	16.46	3.22	16.2
AIS 2643	A			126	-9.89	8.08	41.76	15.14	3.22	15.4
AIS 2644	A			126	-13.77	6.01	40.83	14.85	3.21	17.9
AIS 2646	A			126	-13.77	7.15	43.00	15.38	3.26	14.4
AIS 2647	A			126	-14.52	4.88	42.80	15.67	3.19	18.4
AIS 2648	A			126	-13.59	8.33	41.56	15.18	3.19	18.4
Huaca Santa Clara, V-67 (Early Intermediate Period)										
AIS 377	II		1		-15.55	6.51	43.20	15.91	3.17	19.1
AIS 381	II		19		-14.90	6.74	41.41	15.16	3.19	13.4
AIS 378	II		2		-17.12	5.45	38.82	14.27	3.17	13.2
AIS 382	II		22		-14.41	6.59	44.19	16.18	3.19	20.7
AIS 383	II		24		-10.89	5.65	43.13	16.07	3.13	18.4
AIS 379	II		3		-11.77	4.98	42.32	15.42	3.20	20.5
AIS 380	II		7		-13.32	8.38	40.99	15.23	3.14	10.1
AIS 386	II		S Ext.		-13.29	5.77	44.38	15.87	3.26	16.3
AIS 399	VI		102		-15.25	6.14	41.31	15.08	3.20	22.8
AIS 400	VI		102		-16.95	5.93	43.17	16.02	3.14	13
AIS 401	VI		104		-14.65	6.61	43.35	15.82	3.20	22.5

Sample ID	Sector	AC[1]	Room	Unit	δ^{13}C (‰, VPDB)	δ^{15}N (‰, AIR)	%C	%N	C:N	Collagen Yield
AIS 402	VI		105		-15.24	6.87	34.68	12.65	3.20	14.1
AIS 403	VI		106		-16.24	7.33	32.26	11.21	3.36	1.1
AIS 404	VI		108		-19.10	5.73	39.35	14.12	3.25	15.9
AIS 405	VI		110		-17.05	6.81	46.80	17.21	3.17	17.7
AIS 407	VI		117		-15.39	5.81	41.26	14.83	3.24	18.1
AIS 393	VI		97		-15.16	6.06	44.91	16.22	3.23	24.8
AIS 396	VI		97		-17.59	7.49	45.37	15.82	3.35	18.3
AIS 397	VI		97		-15.43	5.74	40.65	15.03	3.16	20.7
AIS 375	I		93		-16.72	8.36	44.67	16.04	3.25	14.9
AIS 376	I				-13.01	7.97	43.27	16.07	3.14	15.3
AIS 394	VI		97		-17.75	11.76	37.76	14.00	3.15	18.7
AIS 387	III				-18.78	5.05	41.30	14.81	3.25	12.4
AIS 388	III				-17.01	5.90	42.49	15.60	3.18	12.9
AIS 389	III				-14.13	7.48	41.61	15.06	3.22	18.8
AIS 390	V				-16.32	6.78	42.38	15.46	3.20	15.4
AIS 391	V				-13.54	6.95	43.43	15.67	3.23	18.2
AIS 392	V				-14.17	8.13	39.33	14.54	3.16	17.1
AIS 412	VII		103		-19.06	4.12	35.33	12.43	3.32	1.9
AIS 411	VII		98		-14.63	8.05	42.01	15.47	3.17	14.3
AIS 409	VII		PC-1		-13.69	6.63	41.76	14.99	3.25	4.3

Sample ID	Sector	AC[1]	Room	Unit	δ^{13}C (‰, VPDB)	δ^{15}N (‰, AIR)	%C	%N	C:N	Collagen Yield
AIS 410	VII		PC-1		-13.60	6.87	47.47	17.54	3.16	11.0
AIS 408	VII				-21.88	5.45	44.40	16.08	3.22	19.5
Huaca Santa Clara, V-67 (Late Middle Horizon Sacrifices)										
Llama 2	VI				-15.19	5.03	45.07	16.67	3.15	16.3
Llama 3	VI				-17.04	4.97	45.33	16.38	3.23	13.3
Llama 4	VI				-13.44	6.15	44.66	16.18	3.22	20.2
Llama 5	VI				-13.57	10.14	37.18	13.22	3.28	6.3
Llama 6	VI				-15.54	6.61	36.22	13.08	3.23	14.1
Llama 7	VI				-14.49	7.96	42.80	15.67	3.19	21.3
Llama 8	VI				-16.41	6.51	40.85	15.23	3.13	10.6
Llama 9	VI				-12.20	6.97	44.31	16.36	3.16	19.8
Llama 12	VI				-11.96	8.73	40.22	14.44	3.25	21.8
Llama 13	VI				-17.08	6.94	44.04	15.10	3.40	18.7
Llama 14	VI				-15.69	7.34	42.49	14.23	3.48	11.7
Llama 15	VI				-10.30	7.64	44.31	16.12	3.21	19.1
Llama 16	VI				-10.82	7.57	38.94	14.26	3.19	18.3
Llama 17	VI				-15.97	7.31	42.33	14.12	3.50	19.2
Llama 18	VI				-15.83	7.19	46.72	16.65	3.27	20.8
Llama 19	VI				-13.39	7.03	46.16	17.04	3.16	13.5

Sample ID	Sector	AC[1]	Room	Unit	δ^{13}C (‰, VPDB)	δ^{15}N (‰, AIR)	%C	%N	C:N	Collagen Yield
Llama 20	VI				-13.05	7.92	46.87	17.03	3.21	23.6
Llama 21	VI				-11.22	7.21	40.65	15.06	3.15	16.4
Llama 22	VI				-15.95	5.74	38.19	13.41	3.32	9.2
Llama 24	VI				-18.30	7.05	36.09	13.05	3.23	6.3
Llama 25	VI				-16.99	5.04	43.28	15.79	3.20	19.5
Llama 26	VI				-10.72	9.12	42.26	15.14	3.26	17.8
Llama 27	VI				-16.39	8.40	41.24	13.63	3.53	19.4

1. AC=architectural complex

Table 5.6. Layman and SIBER variability metrics for archaeological camelids (carbon and nitrogen isotopic compositions from bone collagen).

Site	~Age (Years BP)	Elevation	*n*	CR	NR	CD	MD	NND	SDNND	MND	SDMND	CHA	SEA	SEA_c	SEA_b	Reference
V-59	2,000 to 1,350	Coastal	43	10.6	4.6	2.9	2.9	0.5	0.3	3.9	0.9	30.1	9.4	9.6	9.5	1
V-67	2,000 to 1,350	Coastal	33	11.0	7.6	2.2	2.1	0.7	0.7	3.2	1.2	45.9	9.8	10.1	9.7	1
V-67	1,000 to 800	Coastal	23	8.0	5.2	2.4	2.4	0.8	0.5	3.4	0.7	24.1	8.4	8.8	8.4	1
V-89	1,150 to 1,000	Coastal	9	4.6	3.6	1.8	1.8	0.9	0.5	2.7	0.4	10.7	6.3	7.1	5.0	2
Caylan	2.800 to 2,000	Coastal	15	8.3	5.4	2.6	2.2	0.7	0.9	3.3	1.3	17.8	7.2	7.8	7.5	2
Cerro Baul	1350 to 950	2,500	11	9.3	10.0	3.6	3.6	1.5	0.8	5.2	1.8	24.4	13.9	15.4	14.0	3
Yaral	950 to 750	1,000	6	3.2	3.3	1.6	1.5	1.3	0.8	2.3	0.5	6.8	4.8	6.0	5.2	3
Torata Alta	450 to 250	2,500	9	3.2	2.8	1.1	1.1	0.8	0.8	1.7	0.8	4.5	2.5	2.8	3.1	3
Pacatnamú	1,350 to 1,050	Coastal	4	5.9	5.4	2.7	2.7	2.7	1.1	4.6	1.2	8.8	11.3	16.9	11.1	4
Pacatnamú	850 to 550	Coastal	5	6.5	4.6	3.0	2.9	1.4	0.9	4.3	0.9	9.8	9.0	12.0	9.6	4
Conchopata^A	1,450 to 1,000	2,700	6	2.7	3.9	1.8	1.8	0.9	0.5	2.6	0.4	5.0	4.0	5.1	5.0	5
Conchopata^B	1,450 to 1,000	2,700	11	3.9	5.0	1.8	1.7	0.8	0.7	2.5	0.7	11.4	6.0	6.6	6.0	5
Paloma	5,800 to 1,200	Coastal	3	8.1	7.7	3.9	3.9	5.4	0.6	7.4	1.6	3.2	5.6	11.3	13.5	6
Chilca	2,100 to 260	Coastal	5	5.1	7.9	3.3	3.3	3.0	1.4	5.3	1.0	9.8	17.7	23.6	16.1	6
Pucara	2,800 to 1,800	>3,000	18	3.2	4.0	1.4	1.3	0.4	0.3	1.9	0.4	8.8	3.4	3.6	3.6	6
Tiwanaku	550 to 418	3,800	9	2.8	2.5	1.2	1.2	0.6	0.3	1.7	0.3	3.4	2.1	2.4	2.9	2

References: 1. This study, 2. Szpak Unpublished Data, 3. Thornton et al. (2011), 4. Verano and DeNiro (1993), 5. Finucane et al. (2006), 6. DeNiro (1988).

For Conchopata, A=alpaca, B=llama. The carbon isotopic compositions for Conchopata camelids are distributed bimodally, which Finucane et al. (2006) interpret as being caused by different foddering strategies for llamas (fed primarily maize) and alpacas (grazing on highland pastures dominated by C_3 grasses). Following this, and the requirement of the SIBER metrics for data to be normally distributed, camelids from this site are divided into ‘llama’ and ‘alpaca’.

Table 5.7. Similarity in isotopic niche between groups of archaeological camelids from Viru.

Site (Site 1 / Site 2)	SEA_c % Overlap[1]	CHA % Overlap[1]	$SEA_{1>2}$[2]
V59 (EIP) / V67 (EIP)	80.0	73.6	0.54
V59 (EIP) / V67 (Late MH)	62.9	70.2	0.27
V67 (EIP) / V59 (EIP)	76.2	48.3	0.46
V67 (EIP) / V67 (Late MH)	58.9	36.3	0.24
V67 (Late MH) / V59 (EIP)	71.5	87.9	0.63
V67 (Late MH) / V67 (EIP)	70.3	69.1	0.76

1. Defined as (% overlapping area/total area for Site 1)
2. Defined as proportion of ellipse areas for Site 1 (generated through Markov Chain Monte Carlo with 10^5 iterations) that are larger than ellipse areas for Site 2

Table 5.8. Isotopic and elemental compositions, and associated contextual information for all camelids (hair) analyzed in this study.

Sample ID	**Sector**	**Room**	**Llama**	**δ^{13}C (‰, VPDB)**	**δ^{15}N (‰, AIR)**	**%C**	**%N**	**C:N**
Huaca Santa Clara, V-67 (Early Intermediate Period)								
AIS 374-0	I			-20.14	8.57	41.27	13.60	3.54
AIS 389-0	III			-15.19	9.08	38.95	13.04	3.48
AIS 395-1	VI	97		-19.14	7.79	39.39	14.02	3.28
AIS 395-2	VI	97		-19.26	7.88	39.10	13.85	3.29
AIS 395-3	VI	97		-19.27	7.77	39.61	14.15	3.27
AIS 395-4	VI	97		-19.16	7.76	38.53	13.73	3.27
AIS 395-5	VI	97		-18.90	7.75	38.50	13.71	3.28
AIS 579-01	II	18		-13.66	10.80	38.31	12.75	3.51
AIS 579-02	II	18		-13.67	10.86	36.75	12.02	3.57
AIS 579-03	II	18		-13.91	11.07	37.17	12.45	3.48
AIS 579-04	II	18		-14.34	11.02	39.22	12.88	3.55
AIS 579-05	II	18		-13.79	11.18	38.42	13.05	3.44
AIS 579-06	II	18		-13.51	10.92	36.83	12.52	3.43
AIS 579-07	II	18		-13.53	10.77	37.41	12.52	3.48
AIS 579-08	II	18		-13.90	11.24	32.40	10.81	3.50
AIS 579-09	II	18		-13.86	10.85	36.88	12.46	3.45
AIS 579-10	II	18		-12.58	9.66	36.34	12.35	3.43

Sample ID	**Sector**	**Room**	**Llama**	**δ^{13}C (‰, VPDB)**	**δ^{15}N (‰, AIR)**	**%C**	**%N**	**C:N**
AIS 579-11	II	18		-12.12	9.13	37.47	12.73	3.43
AIS 578-01	II	5		-17.01	9.36	42.59	14.16	3.51
AIS 578-02	II	5		-20.66	8.89	35.24	11.63	3.53
AIS 578-03	II	5		-20.85	8.69	42.38	14.20	3.48
AIS 578-04	II	5		-20.73	8.25	42.20	14.06	3.50
AIS 578-05	II	5		-20.63	7.51	41.57	13.95	3.48
AIS 578-06	II	5		-20.12	7.05	41.12	13.65	3.51
AIS 578-07	II	5		-19.40	6.81	40.88	13.58	3.51
AIS 578-08	II	5		-19.04	6.68	40.16	13.46	3.48
AIS 578-09	II	5		-19.11	6.82	40.91	13.71	3.48
Huaca Santa Clara, V-67 (Late Middle Horizon Sacrifices)								
AIS 371-01	VI		26	-13.79	11.18	38.42	13.05	3.44
AIS 371-02	VI		26	-13.51	10.92	36.83	12.52	3.43
AIS 371-03	VI		26	-13.53	10.77	37.41	12.52	3.48
AIS 371-04	VI		26	-13.90	11.24	32.40	10.81	3.50
AIS 371-05	VI		26	-13.86	10.85	36.88	12.46	3.45
AIS 371-06	VI		26	-14.07	8.06	38.52	12.60	3.57
AIS 371-07	VI		26	-15.10	7.69	39.35	12.60	3.64
AIS 371-08	VI		26	-15.20	8.15	38.68	12.62	3.57
AIS 371-09	VI		26	-14.76	8.59	36.84	11.78	3.65

Sample ID	Sector	Room	Llama	δ^{13}C (‰, VPDB)	δ^{15}N (‰, AIR)	%C	%N	C:N
AIS 371-10	VI		26	-14.92	8.87	37.04	11.88	3.64
AIS 327-1	VI		4	-14.80	8.50	42.15	14.63	3.36
AIS 327-2	VI		4	-17.67	8.32	41.46	14.64	3.30
AIS 327-3	VI		4	-16.71	6.99	40.95	14.47	3.30
AIS 327-4	VI		4	-15.40	6.29	39.82	14.22	3.27
AIS 327-5	VI		4	-14.59	6.59	38.49	13.73	3.27
AIS 327-6	VI		4	-15.11	7.13	40.21	14.25	3.29
AIS 330-1	VI		5	-15.06	9.95	41.41	14.64	3.30
AIS 330-2	VI		5	-15.04	10.04	40.35	14.35	3.28
AIS 330-3	VI		5	-14.86	9.76	38.88	13.94	3.25
AIS 330-4	VI		5	-14.64	10.19	38.29	13.86	3.22
AIS 334-1	VI		6	-18.06	7.26	40.81	14.47	3.29
AIS 334-2	VI		6	-17.30	6.88	40.58	14.61	3.24
AIS 334-3	VI		6	-16.65	7.04	40.21	14.63	3.21
AIS 334-4	VI		6	-16.09	7.32	38.63	14.18	3.18
AIS 334-5	VI		6	-16.57	6.75	39.05	14.20	3.21
AIS 339-1	VI		8	-18.91	6.86	40.13	14.77	3.17
AIS 339-2	VI		8	-18.76	6.89	39.91	14.72	3.16
AIS 339-3	VI		8	-16.92	6.24	39.97	14.83	3.14
AIS 339-4	VI		8	-14.21	7.24	38.86	14.39	3.15

Sample ID	Sector	Room	Llama	δ^{13}C (‰, VPDB)	δ^{15}N (‰, AIR)	%C	%N	C:N
AIS 352-1	VI		17	-18.36	11.42	41.14	13.61	3.53
AIS 352-2	VI		17	-17.54	9.42	41.20	14.17	3.39
AIS 352-3	VI		17	-15.60	7.81	41.24	14.47	3.32
AIS 352-4	VI		17	-14.78	6.70	40.89	14.36	3.32
AIS 352-5	VI		17	-14.45	7.09	40.45	14.35	3.29
AIS 352-6	VI		17	-13.82	7.40	39.75	14.22	3.26
AIS 352-7	VI		17	-14.01	7.60	36.29	13.00	3.26
AIS 358-01	VI		19	-20.08	7.68	33.31	10.99	3.54
AIS 358-02	VI		19	-20.41	7.85	33.71	11.22	3.50
AIS 358-03	VI		19	-19.53	8.55	33.11	11.18	3.46
AIS 358-04	VI		19	-19.51	8.67	35.47	11.99	3.45
AIS 358-05	VI		19	-18.01	9.26	35.08	11.83	3.46
AIS 358-06	VI		19	-18.47	9.39	36.20	11.87	3.56
AIS 358-07	VI		19	-16.86	9.89	34.07	11.55	3.44
AIS 358-08	VI		19	-17.15	9.82	34.28	11.50	3.48
AIS 358-09	VI		19	-16.60	9.83	35.02	11.90	3.43
AIS 358-10	VI		19	-16.80	9.83	35.47	11.91	3.48
AIS 358-11	VI		19	-16.63	9.84	34.81	11.68	3.48
AIS 358-12	VI		19	-17.98	9.78	**13.58**	**4.26**	**3.72**
AIS 358-13	VI		19	-17.66	9.74	34.57	11.64	3.47

Sample ID	**Sector**	**Room**	**Llama**	**δ^{13}C (‰, VPDB)**	**δ^{15}N (‰, AIR)**	**%C**	**%N**	**C:N**
AIS 358-14	VI		19	-17.94	9.15	33.72	11.56	3.40
AIS 358-15	VI		19	-17.87	9.14	31.89	11.06	3.36
AIS 358-16	VI		19	-19.17	8.98	**24.51**	**8.34**	**3.43**
AIS 358-17	VI		19	-18.27	8.73	32.25	11.12	3.38
AIS 364-01	VI		22	-18.84	6.34	36.51	14.42	2.95
AIS 364-02	VI		22	-18.24	7.16	39.37	12.19	3.77
AIS 364-03	VI		22	-18.07	6.69	41.52	12.89	3.76
AIS 364-04	VI		22	-17.92	6.99	41.16	13.06	3.68
AIS 364-05	VI		22	-18.05	7.22	40.67	12.92	3.67
AIS 364-06	VI		22	-18.23	7.68	41.04	13.19	3.63
AIS 364-07	VI		22	-18.12	7.62	39.98	13.13	3.55
AIS 364-08	VI		22	-18.02	7.49	40.55	13.63	3.47
AIS 369-01	VI		25	-18.92	7.28	38.92	13.16	3.45
AIS 369-02	VI		25	-18.54	7.28	37.93	12.84	3.45
AIS 369-03	VI		25	-18.04	7.45	37.94	12.86	3.44
AIS 369-04	VI		25	-17.47	7.77	37.91	12.94	3.42
AIS 369-05	VI		25	-17.80	7.36	37.72	12.82	3.43
AIS 369-06	VI		25	-18.39	6.90	37.39	12.73	3.43
AIS 369-07	VI		25	-19.11	6.48	45.49	15.66	3.39

Data for samples in boldface are considered unreliable (as discussed in the text).

Table 5.9. Layman and SIBER variability metrics for archaeological camelids (carbon and nitrogen isotopic compositions of serially sampled hair).

Sample ID	**Segments**	**CR**	**NR**	**CD**	**MD**	**NND**	**SDNND**	**MND**	**SDMND**	**CHA**	**SEA**	**SEA$_c$**	**SEA$_b$**
Huaca Santa Clara (EIP)													
AIS 395	5	0.4	0.1	0.1	0.1	0.1	0.1	0.2	0.1	2.2	2.6	3.4	4.5
AIS 579	11	2.2	2.1	0.7	0.7	0.3	0.2	1.0	0.5	2.5	1.7	1.9	3.8
AIS 578	9	3.8	2.7	1.4	1.4	0.7	1.0	2.0	0.7	12.9	9.1	10.5	9.8
Huaca Santa Clara (Sacrifices)													
Llama 4	6	3.1	2.2	1.3	1.3	1.1	0.4	2.0	0.5	4.2	3.8	4.8	4.4
Llama 5	4	0.4	0.4	0.2	0.2	0.2	0.2	0.3	0.1	0.8	1.1	1.7	4.2
Llama 6	5	2.0	0.6	0.7	0.6	0.5	0.2	1.0	0.3	2.7	2.9	3.9	5.0
Llama 8	4	4.7	1.0	1.7	1.7	1.3	1.4	2.7	0.9	0.7	1.0	1.5	3.5
Llama 17	7	4.5	4.7	2.1	2.0	1.0	0.9	2.8	1.1	8.2	6.4	7.7	6.8
Llama 19	17	3.8	2.2	1.2	1.1	0.2	0.2	1.7	0.5	9.4	5.1	5.5	5.3
Llama 22	8	0.9	1.3	0.4	0.4	0.3	0.2	0.7	0.2	2.2	1.7	1.4	2.1
Llama 25	7	1.6	1.3	0.6	0.6	0.4	0.2	0.9	0.2	0.3	0.2	0.2	1.3
Llama 26	10	3.0	1.4	0.9	0.9	0.4	0.1	1.3	0.3	5.8	4.0	4.5	4.6

Table 5.10. C:N ratios of mammalian hair keratin derived from literature.

Species	C:N	Reference
Horse	3.08	(O'Connell and Hedges, 1999)
Human	3.02	(O'Connell and Hedges, 1999)
Human	3.04	(O'Connell and Hedges, 1999)
Human	3.06	(O'Connell and Hedges, 1999)
Human	3.07	(O'Connell and Hedges, 1999)
Human	3.07	(O'Connell and Hedges, 1999)
Human	3.10	(O'Connell and Hedges, 1999)
Human	3.11	(O'Connell and Hedges, 1999)
Human	3.12	(O'Connell and Hedges, 1999)
Human	3.14	(O'Connell and Hedges, 1999)
Human	3.16	(O'Connell and Hedges, 1999)
Human	3.17	(O'Connell and Hedges, 1999)
Human	3.20	(O'Connell and Hedges, 1999)
Human	3.21	(O'Connell and Hedges, 1999)
Human	3.24	(O'Connell and Hedges, 1999)
Human	3.26	(O'Connell and Hedges, 1999)
Human	3.27	(O'Connell and Hedges, 1999)
Human	3.28	(O'Connell and Hedges, 1999)
Human	3.29	(O'Connell and Hedges, 1999)
Human	3.31	(O'Connell and Hedges, 1999)
Human	3.34	(O'Connell and Hedges, 1999)
Human	3.36	(O'Connell and Hedges, 1999)
Human	3.39	(O'Connell and Hedges, 1999)
Human	3.39	(O'Connell and Hedges, 1999)
Human	3.39	(O'Connell and Hedges, 1999)
Human	3.39	(O'Connell et al., 2001)
Human	3.45	(O'Connell and Hedges, 1999)
Human	3.45	(O'Connell et al., 2001)
Human	3.46	(O'Connell et al., 2001)
Human	3.47	(O'Connell et al., 2001)

Species	**C:N**	**Reference**
Human	3.48	(O'Connell et al., 2001)
Human	3.49	(O'Connell and Hedges, 1999)
Human	3.50	(O'Connell et al., 2001)
Human	3.51	(O'Connell and Hedges, 1999)
Human	3.51	(O'Connell et al., 2001)
Human	3.52	(O'Connell et al., 2001)
Human	3.53	(O'Connell et al., 2001)
Human	3.54	(O'Connell et al., 2001)
Human	3.55	(Robbins and Kelly, 1970)
Human	3.55	(Robbins and Kelly, 1970)
Human	3.55	(O'Connell et al., 2001)
Human	3.55	(O'Connell et al., 2001)
Human	3.56	(Robbins and Kelly, 1970)
Human	3.56	(Robbins and Kelly, 1970)
Human	3.56	(O'Connell et al., 2001)
Human	3.57	(O'Connell et al., 2001)
Human	3.58	(Robbins and Kelly, 1970)
Human	3.59	(O'Connell et al., 2001)
Human	3.61	(O'Connell and Hedges, 1999)
Human	3.62	(O'Connell et al., 2001)
Human	3.62	(O'Connell et al., 2001)
Human	3.63	(O'Connell et al., 2001)
Human	3.63	(O'Connell et al., 2001)
Human	3.67	(O'Connell et al., 2001)
Merino sheep	3.55	(Corfield and Robson, 1955)
Merino sheep	3.59	(Aluigi et al., 2007)
Merino sheep	3.64	(Simmonds, 1954)
Merino sheep	3.68	(Robbins and Kelly, 1970)
Sheep	3.62	(Ward et al., 1955)
Sheep	3.62	(Ward et al., 1955)
Sheep	3.62	(Ward et al., 1955)

Species	C:N	Reference
Sheep	3.63	(Ward et al., 1955)
Sheep	3.63	(Ward et al., 1955)
Sheep	3.64	(Ward et al., 1955)
Sheep	3.65	(Ward et al., 1955)

Table 5.11. Percentage of variation in camelid isotopic compositions explained by variation in plant isotopic compositions in different ecological zones along an altitudinal gradient, expressed as % overlap between plant mixing polygon and camelid convex hull area.

	% Overlap between Camelid Polygon and Plant Polygon				
Site (Context)	**0 to 500 masl**	**500 to 1,800 masl**	**1,800 to 2,800 masl**	**2,800 to 3,700 masl**	**3,700 to 4,000 masl**
V59 (EIP)	100	48	0	54	15
V67 (EIP)	100	59	8	72	31
V67 (Late MH)	100	57	0	45	1

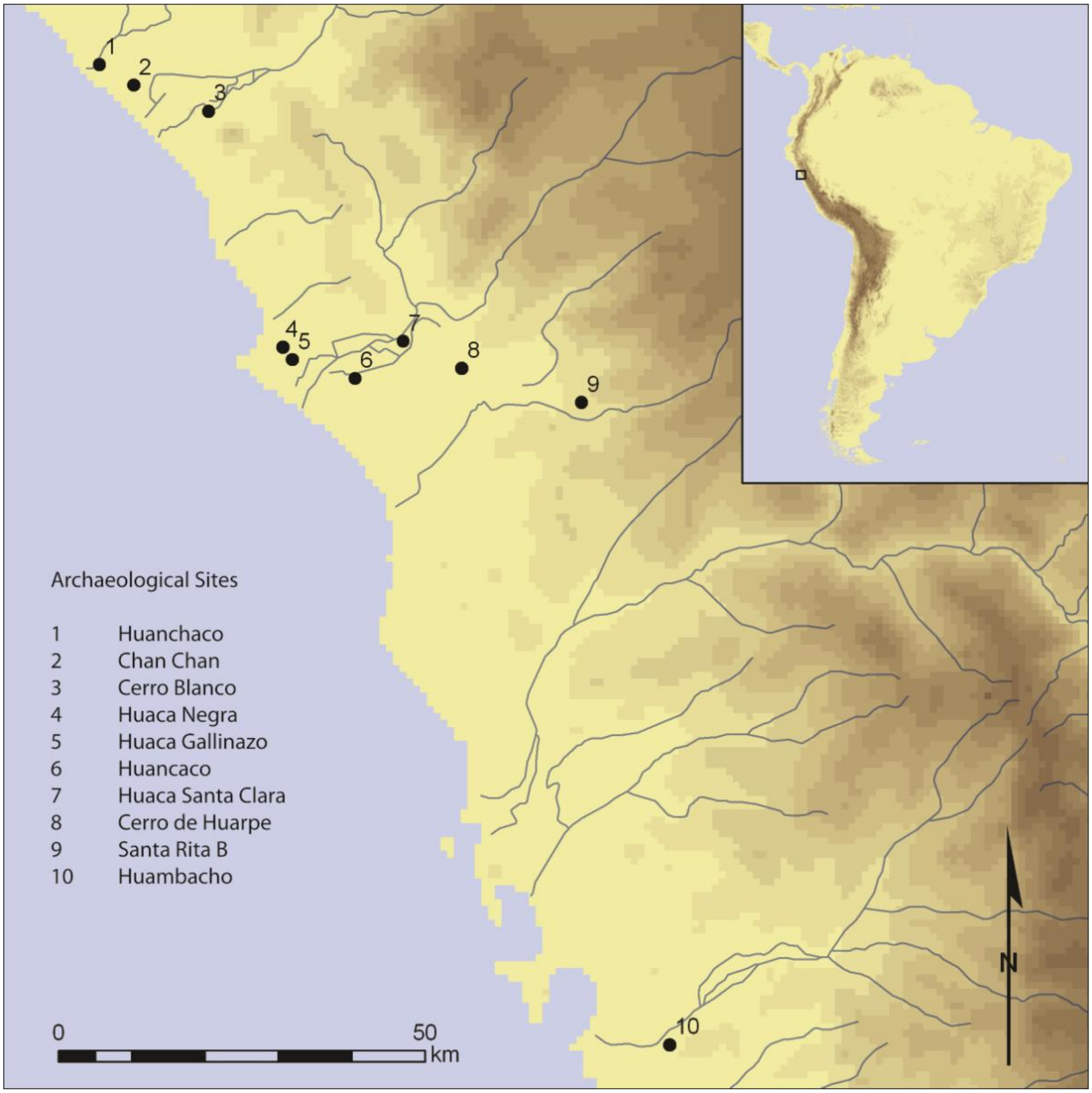

Figure 5.1. Map depicting sites mentioned in the text.

Castillo incised and modeled vessels (Gallinazo)

Moche-style vessels

Virú negative vessels

Figure 5.2. Representations of ceramics typical of the styles discussed in the text.

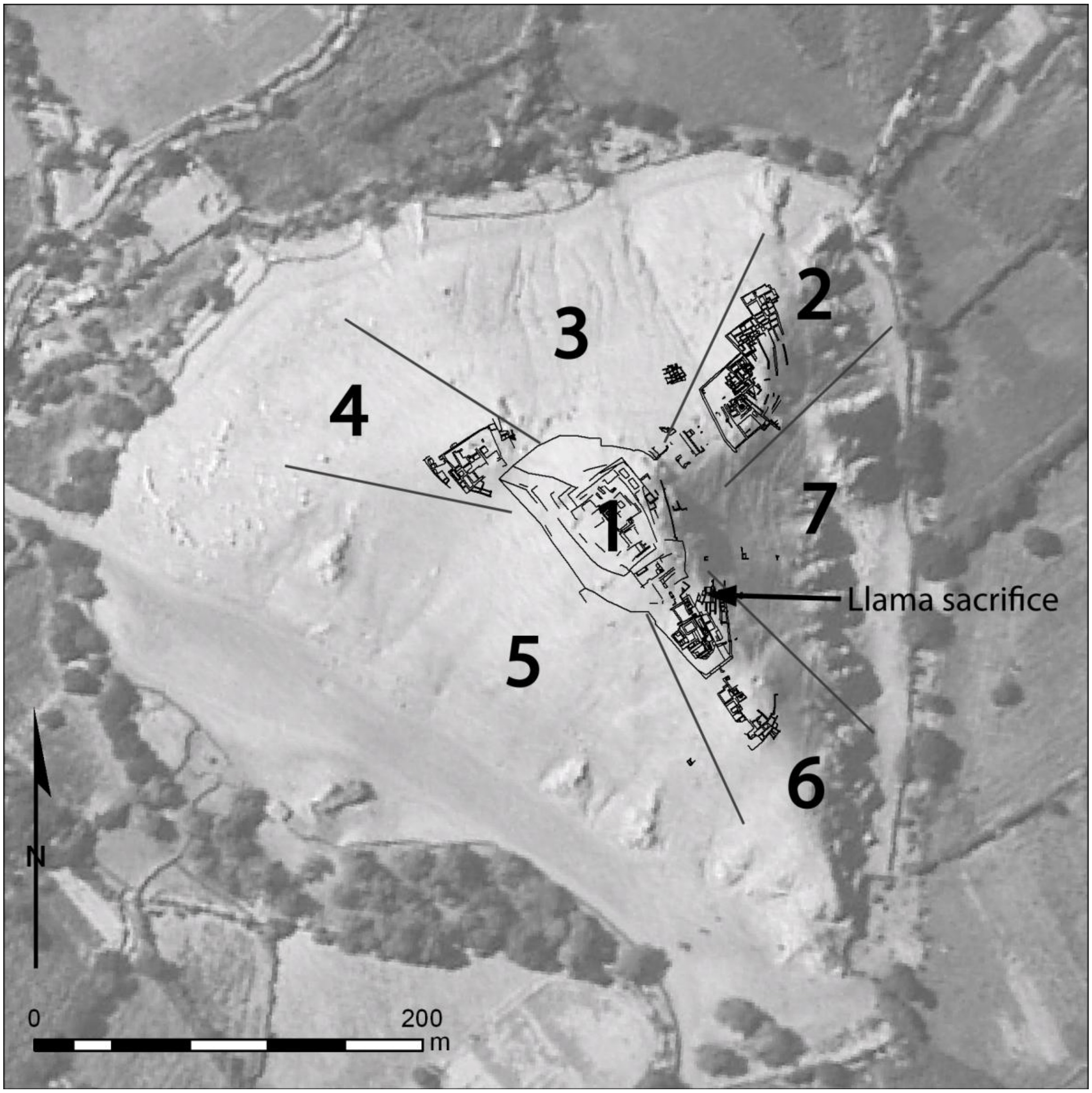

Figure 5.3. Aerial photograph of Huaca Santa Clara showing the sectors discussed in the text and the location of the sacrificial event involving the llamas.

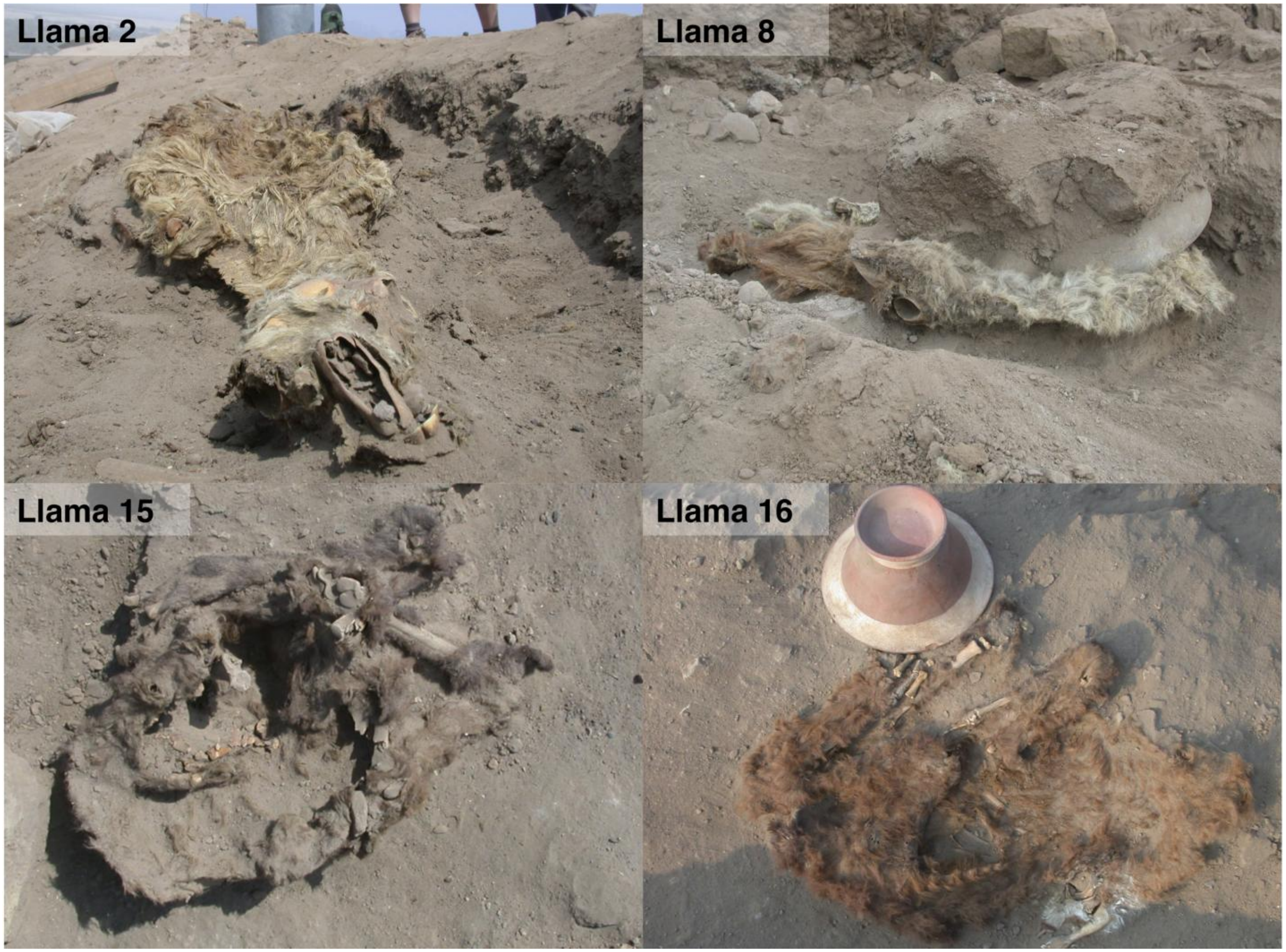

Figure 5.4. Sacrificed llamas from Huaca Santa Clara.

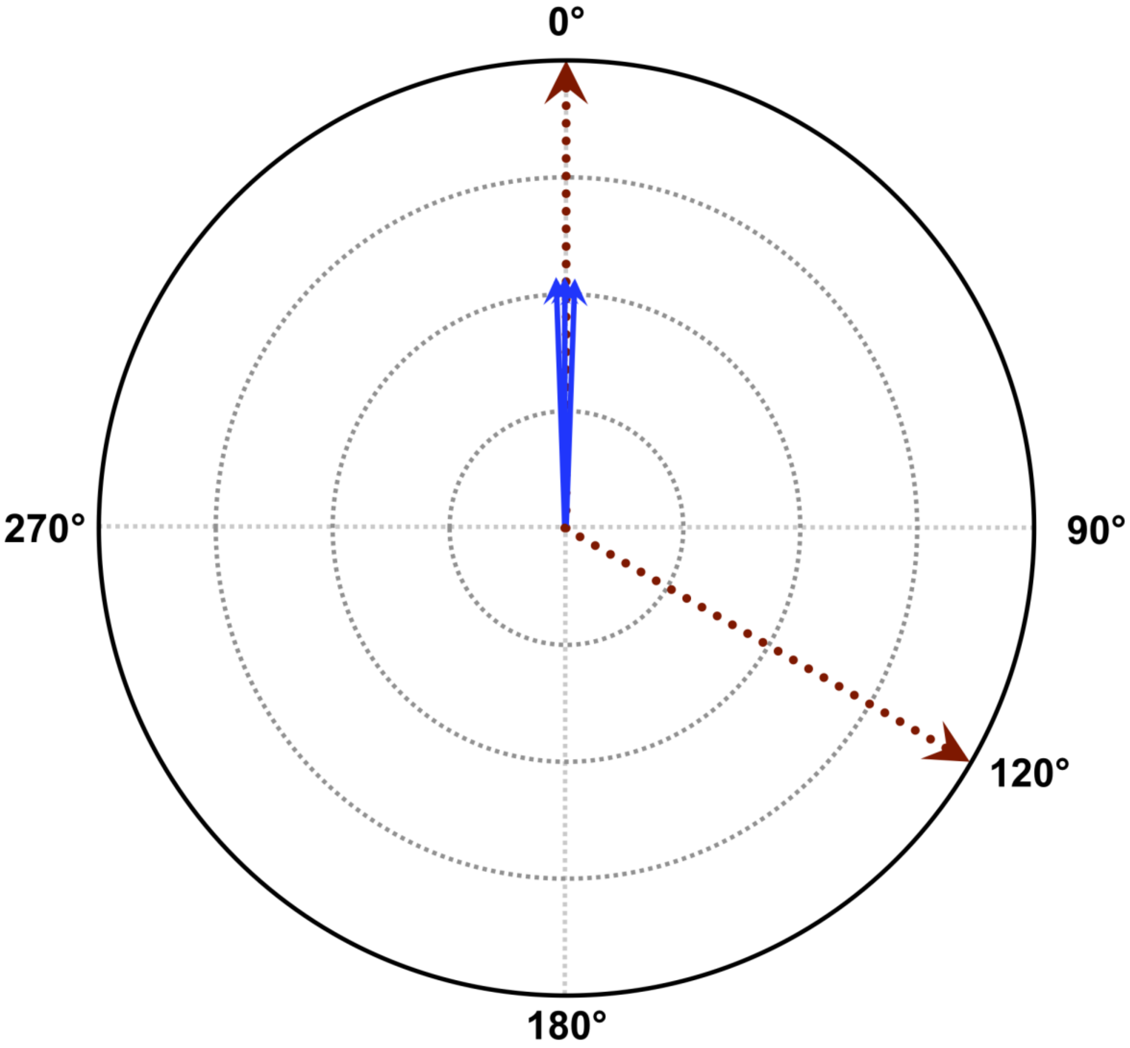

Figure 5.5. Circular diagram showing the mean of three angles (0°, 2°, 358°) represented as solid lines. The incorrect mean (120°) is the simple arithmetic mean of the three angles. The correct mean (0°) is calculated as described in the text.

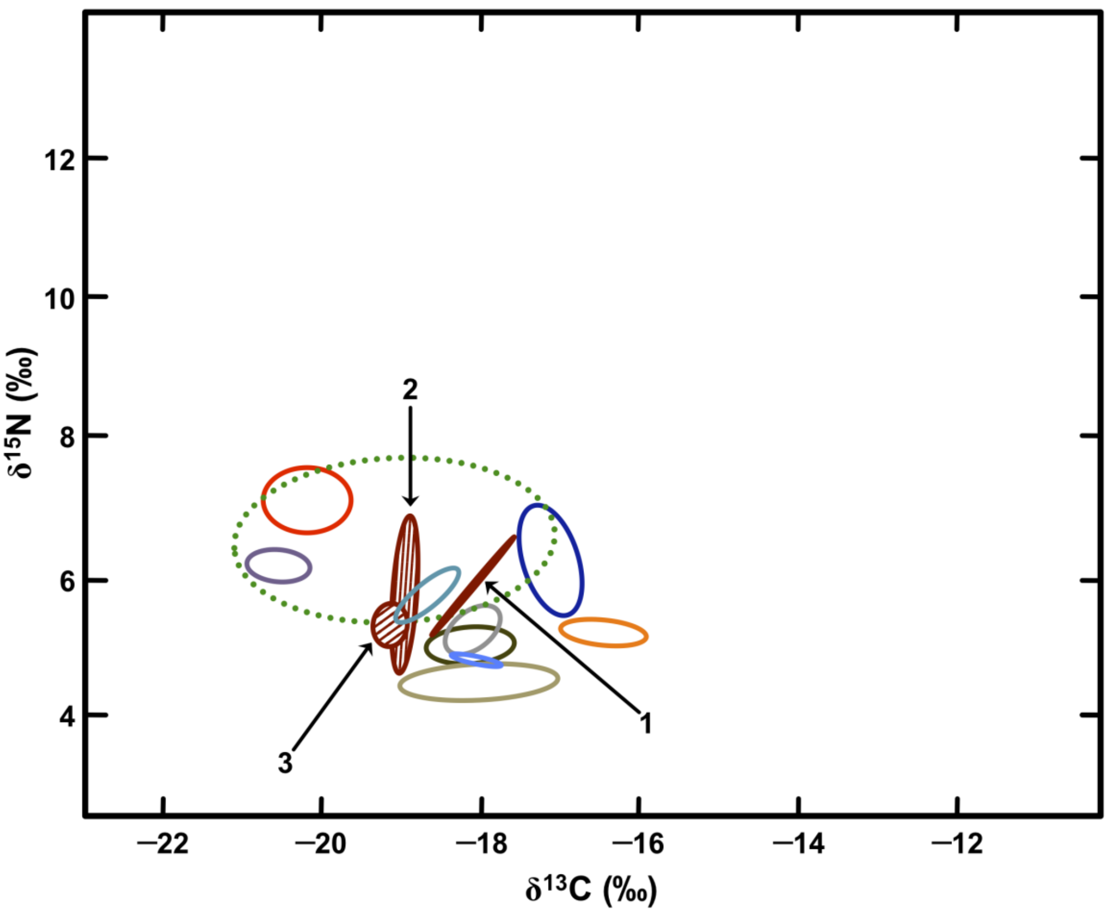

Figure 5.6. SEA$_c$ for modern camelids. Shaded circles represent data for bone collagen: (1) northern Peruvian highlands (this study), (2) unknown Peruvian highlands (Schoeninger and DeNiro, 1984), (3) Upper Mantoro Valley (Thornton et al., 2011). Open ellipses with solid lines each represent serially-sampled hair for individual camelids from the northern Peruvian highlands. The open ellipse with the broken line represents bulk hair sampled from three camelid species (llama, alpaca, vicuña) from the northern Peruvian highlands. Hair δ^{13}C values have been adjusted upwards by +1.3 ‰ as described in the text. Carbon isotopic compositions for modern animals have been adjusted upwards by +1.5 ‰ to account for the Suess Effect (Keeling, 1979; Keeling et al., 1979; Yakir, 2011).

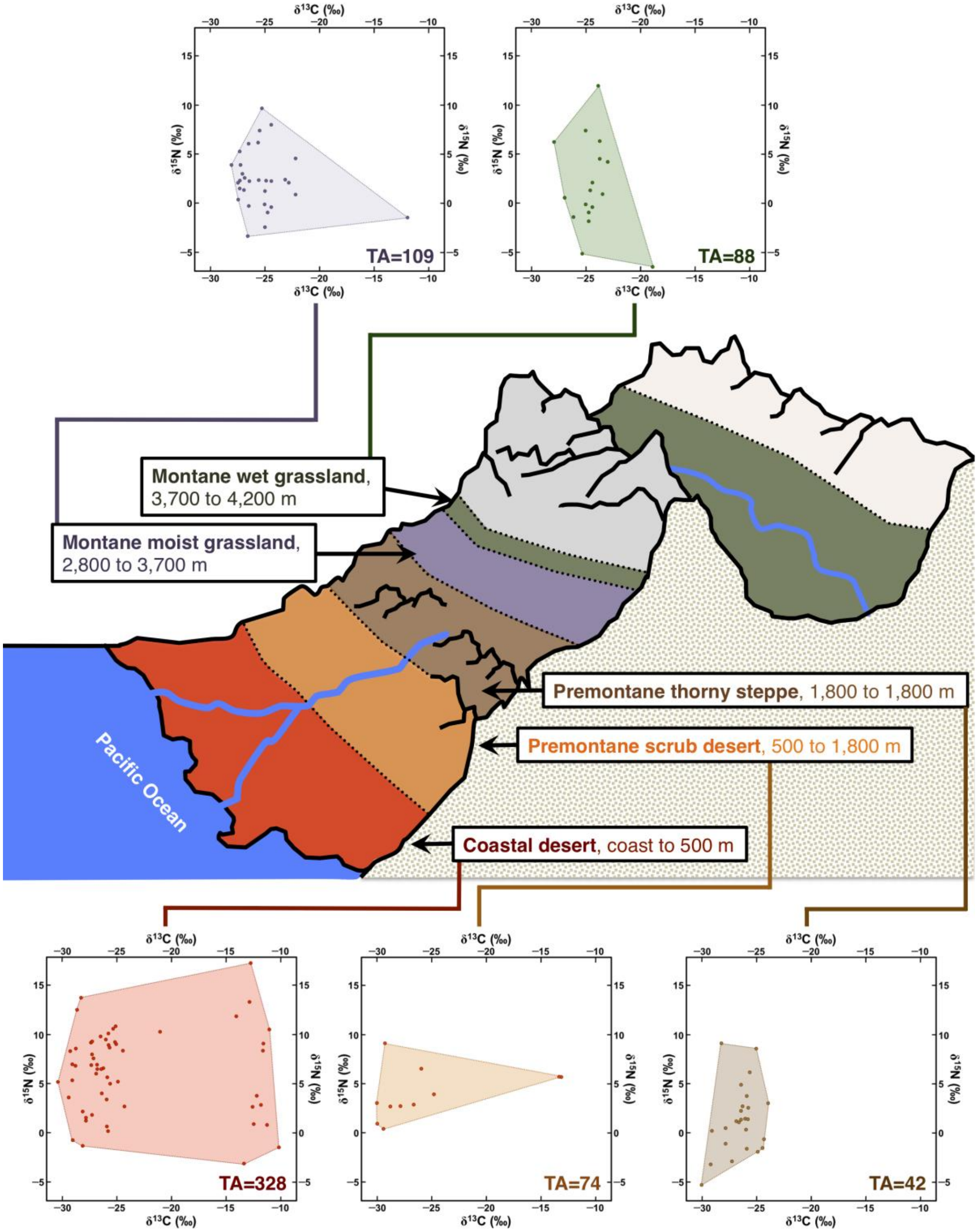

Figure 5.7. Mixing polygons generated for plants (leaves) sampled along an altitudinal transect in northern Peru (Moche Valley region) (data are from Szpak et al., 2013b). The value (TA) in the bottom right of each panel is the total area of the polygon. Plant isotopic compositions have not been adjusted to account for any trophic-level fractionation.

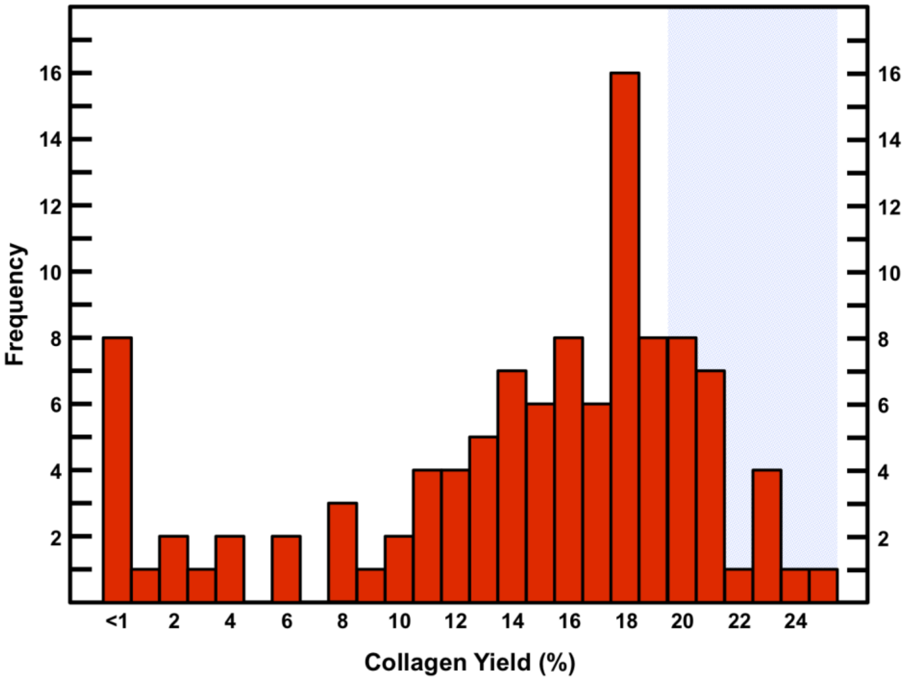

Figure 5.8. Frequency histogram for bone collagen yields (%) for archaeological camelids from Viru analyzed in this study. The shaded range (20 to 25 %) represents typical collagen yields for fresh mammalian bone (Ambrose, 1990; Currey, 2008; Szpak, 2011).

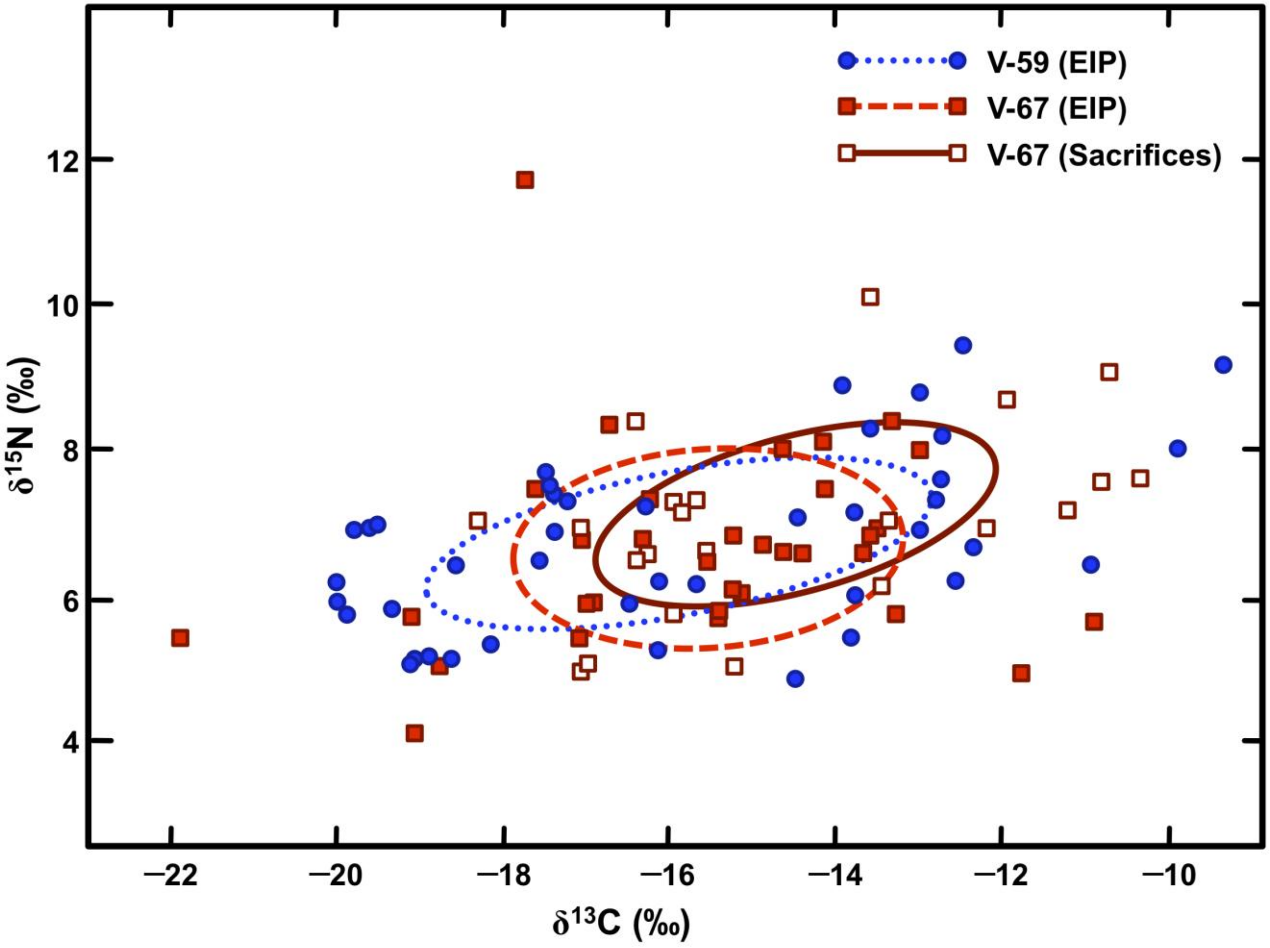

Figure 5.9. Carbon and nitrogen isotopic compositions for archaeological Virú camelid bone collagen: closed circles (V-59, EIP), closed squares (V-67, EIP), open squares (V-67, late MH sacrifices). Ellipses are standard ellipse areas corrected for small sample size (SEA*c*).

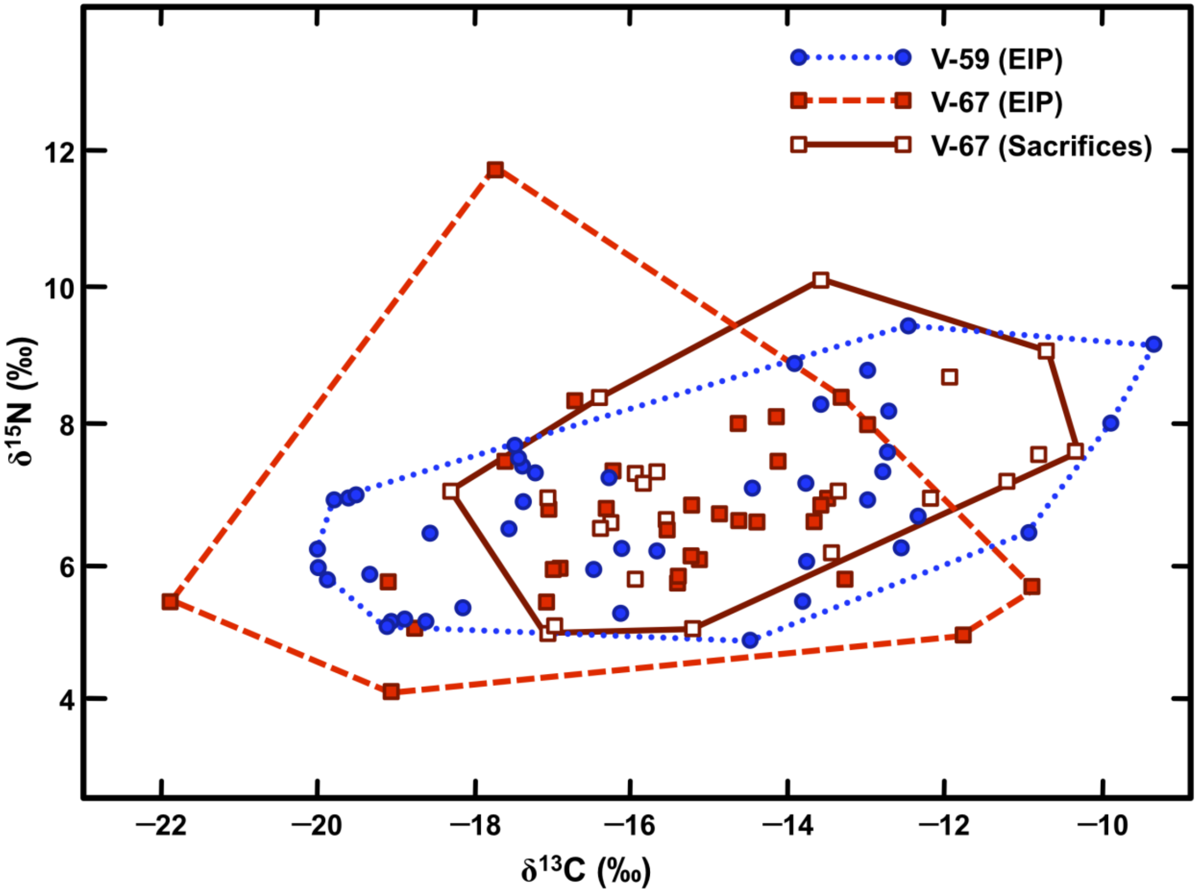

Figure 5.10. Carbon and nitrogen isotopic compositions for archaeological Virú camelid bone collagen: closed circles (V-59, EIP), closed squares (V-67, EIP), open squares (V-67, late MH sacrifices). Polygons are convex hull areas (total areas) for each group (CHA).

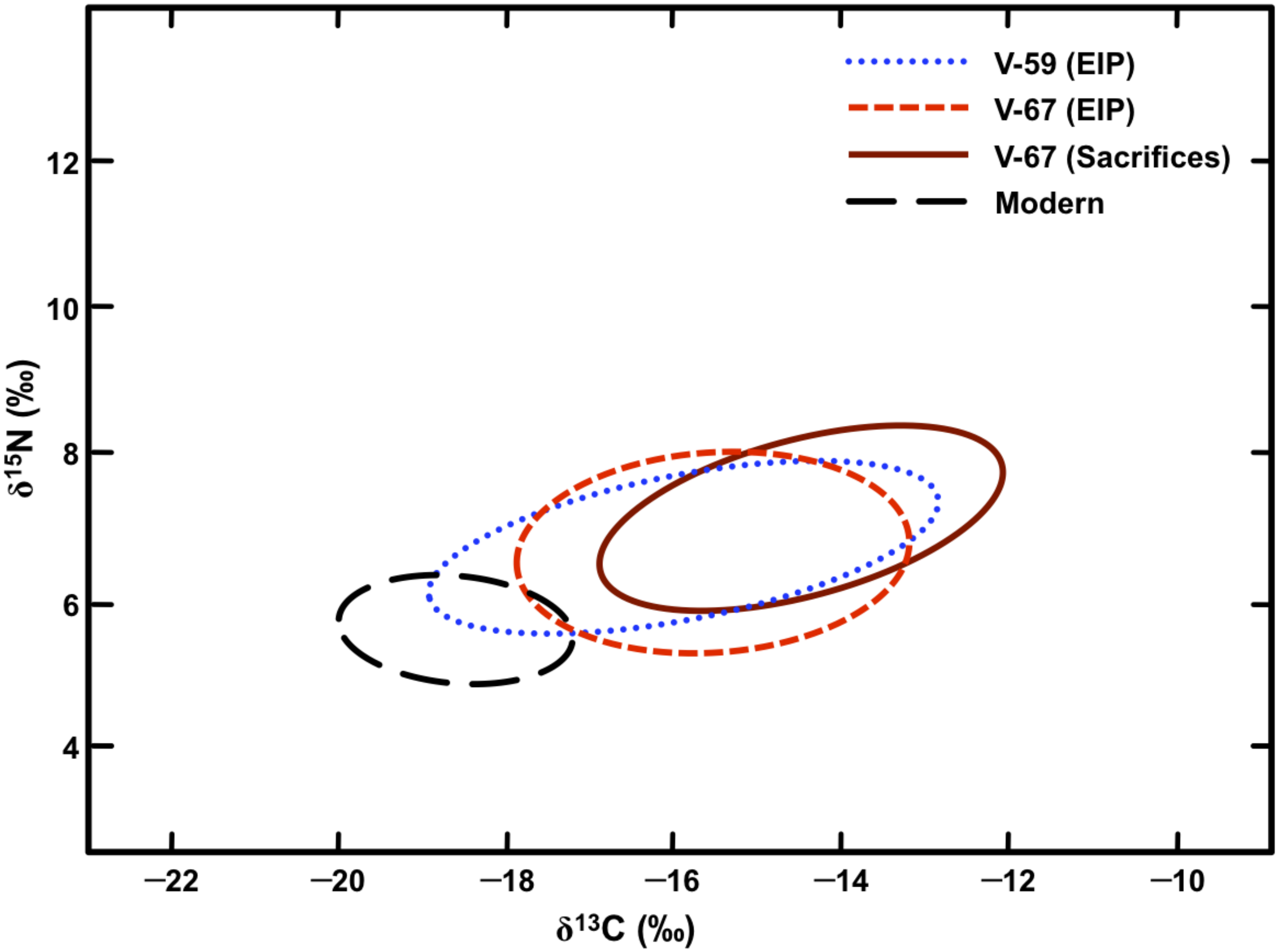

Figure 5.11. SEA$_c$ for archaeological camelids from Virú compared to modern highland camelids.

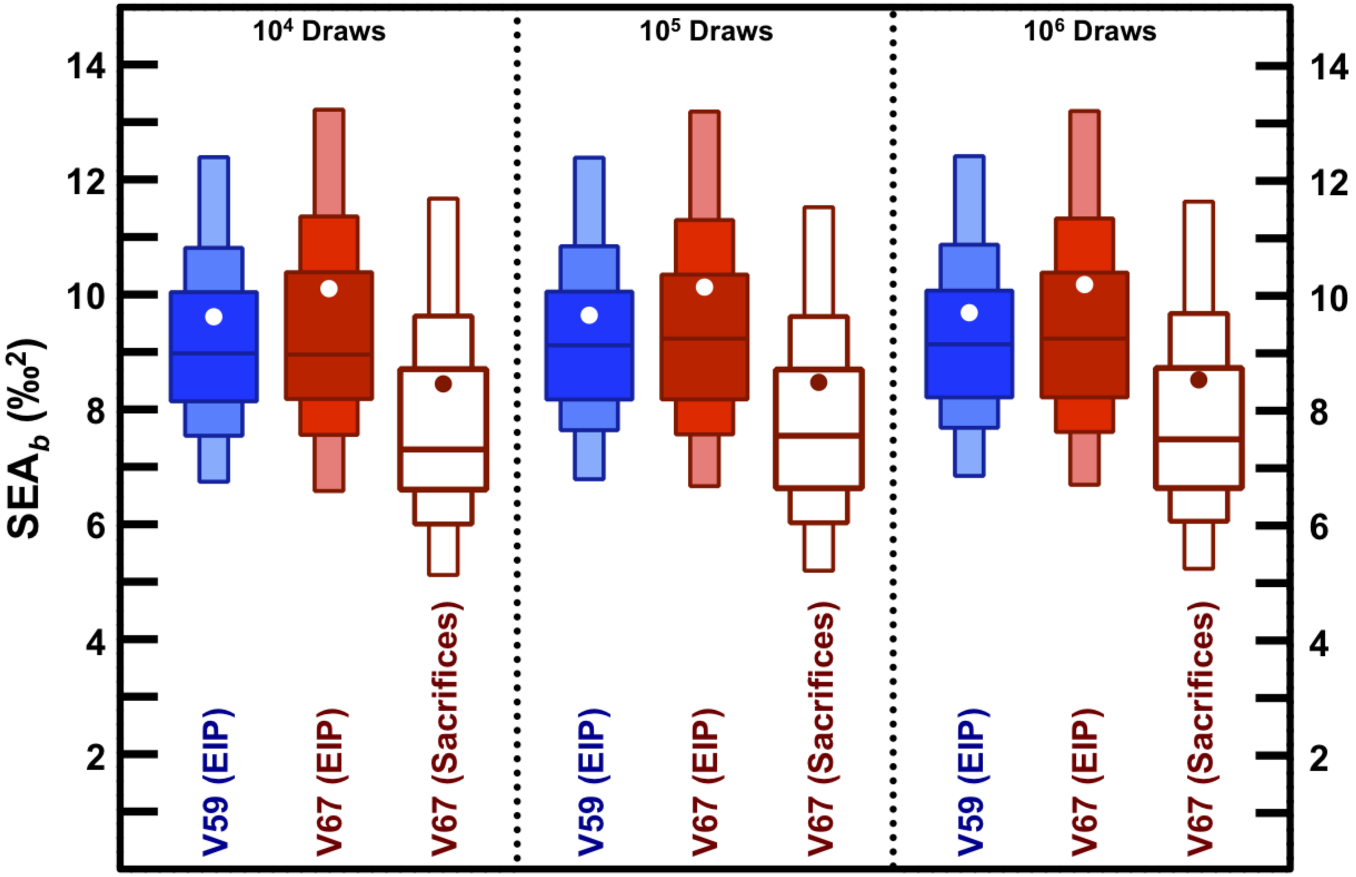

Figure 5.12. Density plot showing the confidence intervals of the standard ellipse areas for three different numbers of posterior draws. Thickest boxes (50% CI), medium-thickness boxes (75% CI), thinnest boxes (95% CI), horizontal line (mean standard ellipse area), circle within boxes (standard ellipse area corrected for small sample size SEA_c).

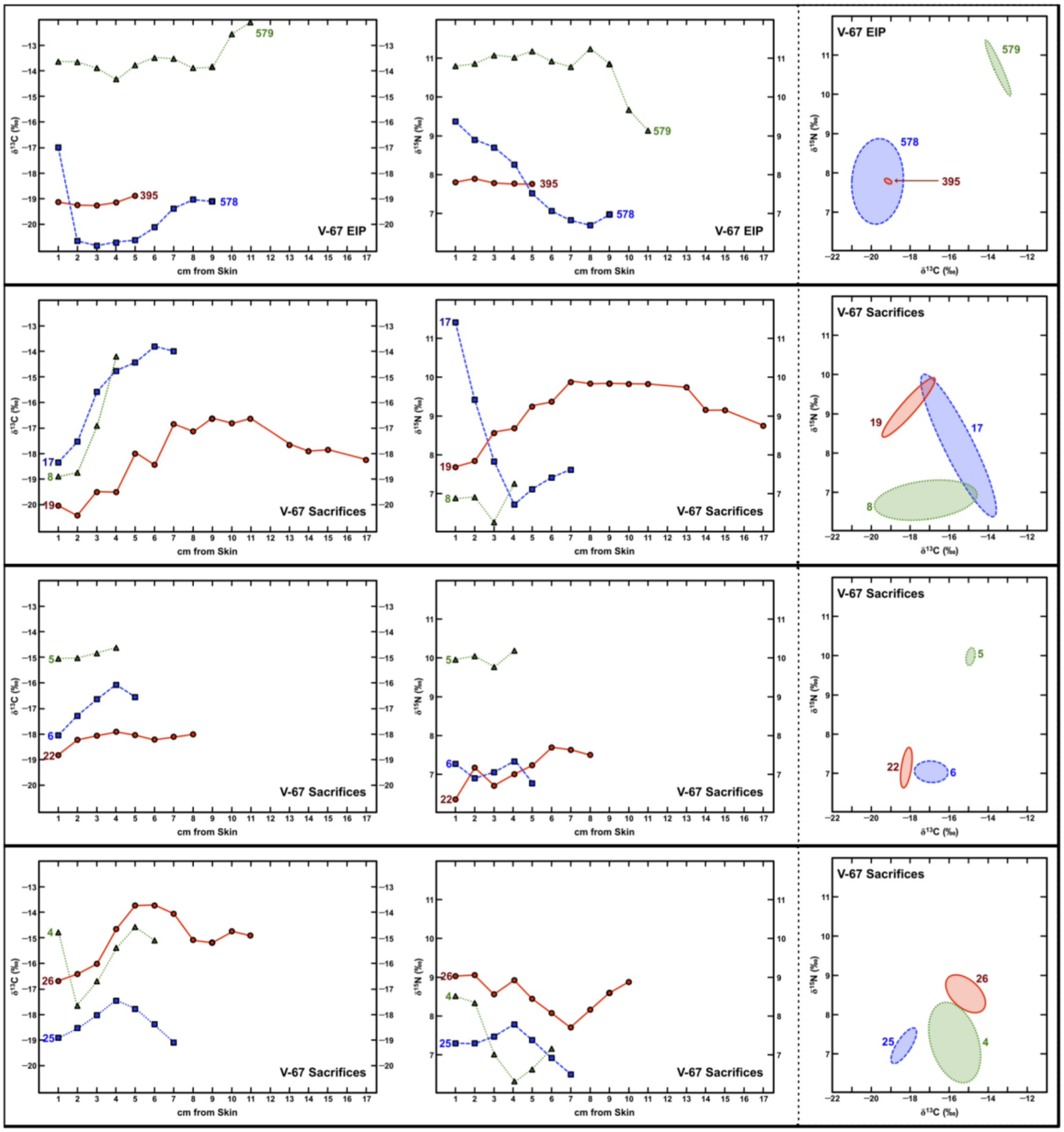

Figure 5.13. Carbon (left panels) and nitrogen (center panels) isotopic compositions of serially-sampled hair and standard ellipse areas corrected for small sample size (right panels) for archaeological camelids from Virú. Hair segments formed closest to the time of the animal's death are towards the left of the *x*-axis on the left and center panels. The top panels are for EIP camelids from Huaca Santa Clara. The bottom three panels are for Late MH sacrificed camelids from Huaca Santa Clara; these have been divided over three panels for the sake of clarity. Numbers correspond to sample IDs as outlined in Table 5.5 and Table 5.8.

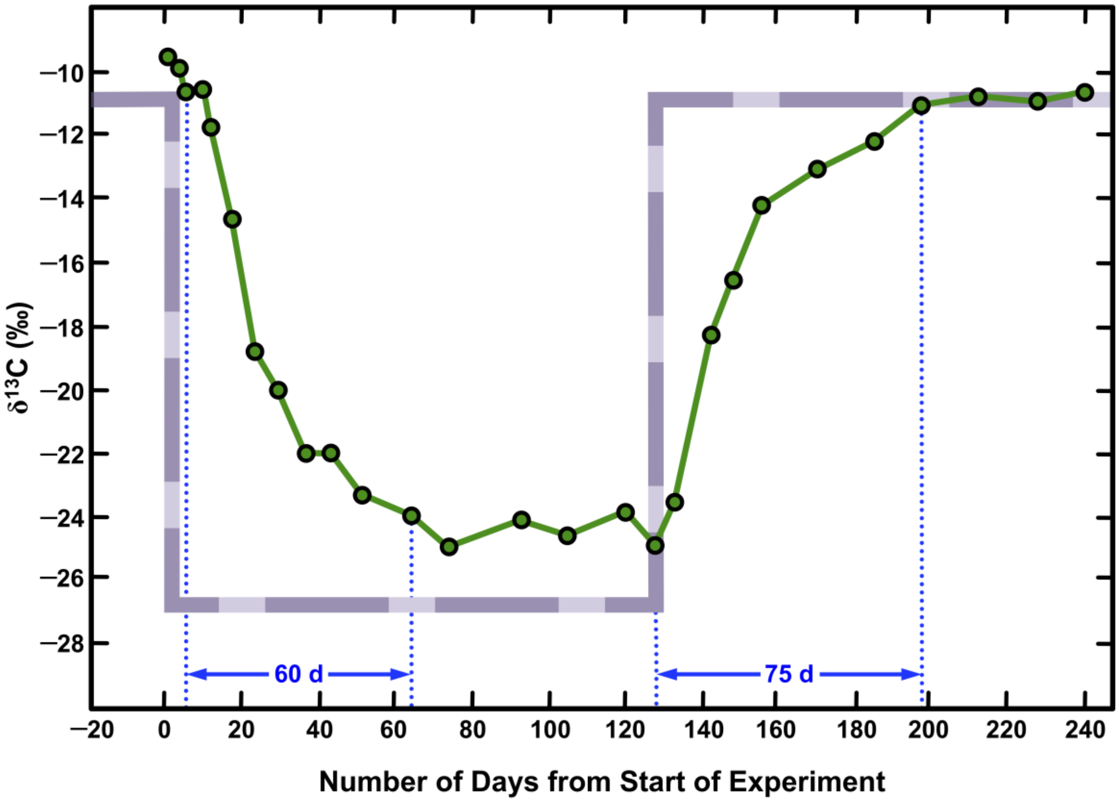

Figure 5.14. Carbon isotopic compositions of serially-sampled cattle hairs. Individual isotopic data from tail hairs are represented as solid circular points. The carbon isotopic composition of the experimental diet is indicated by the thick, faded broken line (purple). The 60 d and 75 d intervals indicated here demonstrate the amount of time after the diet switch for the tail hairs to fully 'equilibrate' to the new diet. Figure is adapted from data in Jones et al. (1981).

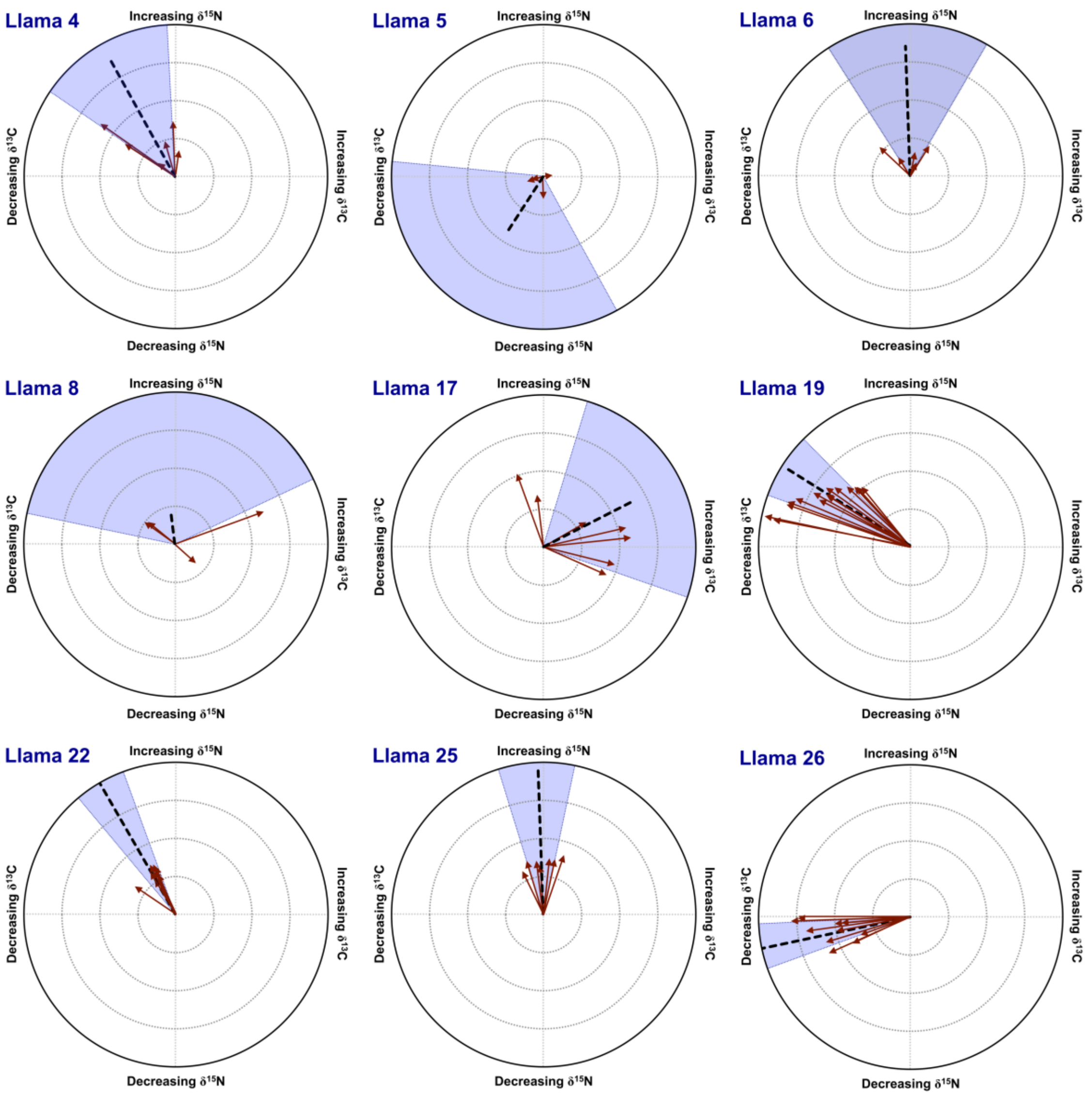

Figure 5.15. Circular diagrams depicting changes in carbon and nitrogen isotopic compositions between hair and bulk bone collagen for individual camelids. The center of each diagram represents the bone collagen isotopic composition. Arrows emanating from the center represent individual hair segments, with the length of the arrows being proportional to the Euclidean distance between the hair and bone collagen isotopic compositions (after accounting for differences in trophic level fractionations between collagen and hair). Broken lines emanating from the center represent the mean angle of change (*r*) and shaded areas around this broken line represent the angular deviation (*s*).

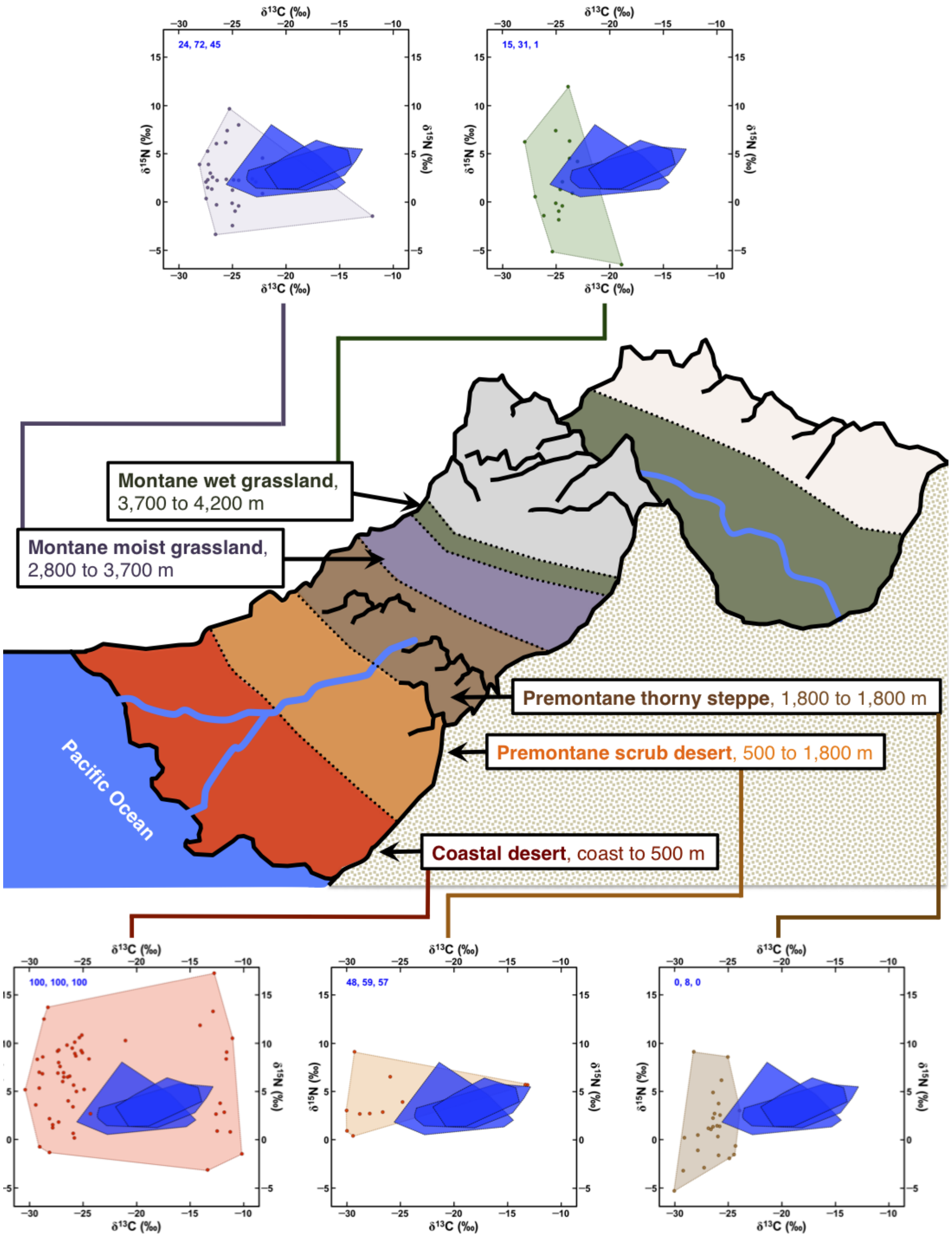

Figure 5.16. Mixing polygons for plants sampled from five major ecological zones along an altitudinal gradient in northern Peru (Szpak et al., 2013b). The three darkly shaded (blue) polygons that appear in every panel represent the convex hull areas for the three groups of Virú camelids discussed in the text (adjusted for trophic level fractionation for bone collagen). The areas of overlap between the plant polygons and the camelid polygons are listed in blue text in the top left of each plot.

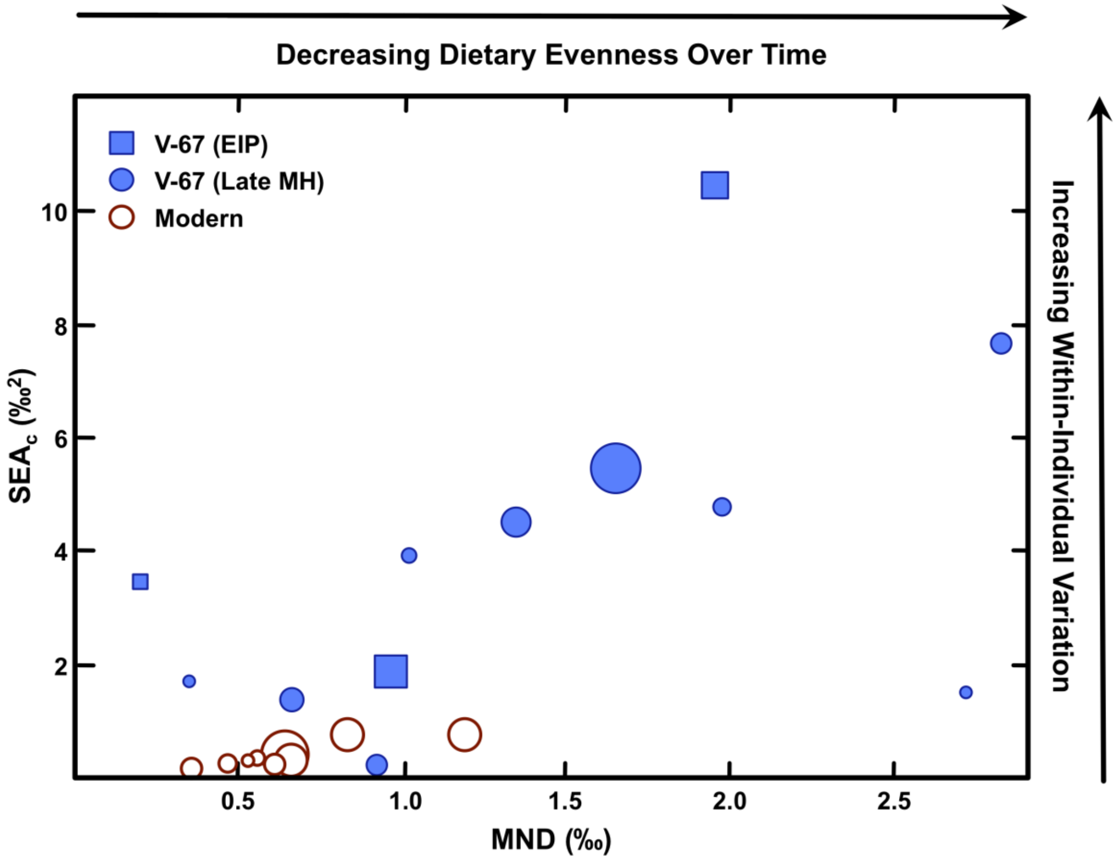

Figure 5.17. Comparison of variation (SEA$_c$) and evenness (MND) metrics within individual modern (high sierra) and archaeological (coastal) camelids generated from serially-sampled hair. Shape sizes are scaled to sample size (number of hair segments sampled).

Chapter 6

6 General Discussion and Conclusions

The papers presented in this dissertation are linked by their methodological (stable isotope analysis) and regional (northern Peruvian Andes) foci. Thematically, each also contributes to the larger goal of better understanding the ways in which humans interacted with other animals and with their environment. To address these questions with stable isotope geochemistry, it is first necessary to understand the isotopic ecology of a particular region in detail. It is only then that we can really begin to address these human-environment interactions in the archaeological past. Within this context, this chapter summarizes the results of the dissertation and discusses related areas for future investigation.

6.1 Isotopic Baselines in Archaeology and Paleoecology

6.1.1 Isotopic Baselines in Archaeology and Paleoecology

While isotopic analysis has the potential to address a broad range of questions, these questions cannot be properly handled without the development of adequate baseline information. It is true that some basic expectations for source isotopic compositions can be made on the basis of very general principles of stable isotope geochemistry: the difference in $\delta^{13}C$ between C_3 and C_4 plants, relatively high $\delta^{15}N$ values in arid ecosystems, stepwise enrichment of ^{15}N with trophic level, relatively low $\delta^{15}N$ values in nitrogen-fixing plants, and so on. Nevertheless, it is crucial to develop detailed baselines at the regional level (as a minimum) − this is true for even the most basic and descriptive approaches to interpreting isotopic data. As interpretive techniques become increasingly refined, they are (theoretically) able to provide increasingly constrained solutions to questions about diet and ecology via isotopic analysis. This is true if *and only if* the model inputs are similarly refined. Considering specifically some of the recently developed techniques involving Bayesian mixing models, there are several reasons why these approaches may produce ineffective solutions, or solutions that are ‘underdetermined’ (Fry, 2013): (1) insufficient isotopic variability exists between functionally significant sources, (2) source parameters (isotopic compositions) are unknown, and (3) there is too much uncertainty in source parameters (e.g. source isotopic compositions, trophic level fractionation estimates). This first issue is simply a reality of the way isotopes are distributed in the biosphere, and little can be done to address this matter while working within the confines of these particular isotope systems. The last two issues, however, can, and in all cases *should* be prioritized areas of investigation, not just for ecologists, but for archaeologists and anthropologists as well. With respect to carbon, nitrogen, and sulfur, regional surveys of plants and animals are critical to the development of these baselines. Such studies may often be paired with other surveys aimed at constructing, for example, strontium, hydrogen, or oxygen isotopic 'isoscapes' through the sampling of similar materials, as well as surface waters and soils. These data are extremely useful for any number of investigators working with isotopic data, and not only ecologists and geologists. For example, there is a rapidly growing number of scholars in the food sciences interested in isotopic data of this nature (Adami et al., 2010; Aghemo et al., 2011; Bontempo et al., 2011; Capuano et al., 2013; Carrijo et al., 2006; Chesson et al., 2010; González-Martin et al., 1999; Li et al., 2011; Maggi et al., 2011; Osorio et al., 2011; Perez et al., 2006; Perini et al., 2009; Piasentier et al., 2003; Schmidt et al., 2005b; Vinci et al., 2013). Additionally, because there may be temporal variation in environmental conditions, and in turn in carbon and nitrogen isotopic compositions in plant and animal tissues (Bump et al., 2007; Burton et al., 2001; Burton et al., 2002; Newsome et al., 2007a; Newsome et al., 2007b; Richards and Hedges, 2003), the analysis of zooarchaeological material is similarly useful in this context of baseline isotopic data, and this approach has become fairly common (Borić et al., 2004; Bösl et al., 2006; Choy and Richards, 2009; Craig et al., 2009; Drucker and Bocherens, 2004; Eriksson, 2004; Eriksson et al., 2008; Fornander et al., 2008; Grupe et al., 2003; Grupe et al., 2009; Jay, 2008; Jones and Quinn, 2009; Jørkov et al., 2010; King et al., 2013; Kusaka et al., 2010; Lillie et al., 2011; Müldner and Richards, 2005; Naito et al., 2010; Nehlich et al., 2010; Reitsema et al., 2010; Szpak et al., 2009). Similarly, the direct isotopic analysis of archaeobotanical material (Aguilera et al., 2008; DeNiro and Hastorf, 1985; Fiorentino et al., 2012; Kanstrup et al., 2012; Lightfoot and Stevens, 2012) has great potential with respect to understanding a number of issues, notably agricultural production techniques.

Put very simply, inadequate baseline data are the rate-limiting step in our interpretations of isotopic data. There is little utility in producing copious quantities of isotopic data from archaeological materials when these data cannot be effectively interpreted. These are, after all, destructive processes and their use should be limited to cases when these methods work well. To do so, we must aim to generate the best isotopic baselines possible. Baseline isotopic work must not be considered incidental or an afterthought, but must be foregrounded into regional isotopic studies.

6.1.2 Influence of Fertilizers on Plant Nitrogen Isotopic Compositions

Fitting within the theme of understanding baseline isotopic variability, the influence of fertilizers on plant nitrogen isotopic compositions is an issue of extreme importance, particularly within the context of human dietary reconstruction. Animal-derived fertilizers have the capacity to significantly impact plant nitrogen isotopic compositions, typically resulting in tissue δ^{15}N values that are 1 to 40 ‰ higher than unfertilized plants (Szpak et al., 2012a). This range is immense, and nearly completely encompasses the range of natural variation in δ^{15}N in living organisms. The data presented in Chapters 3 and 4 demonstrate the potential for seabird guano to have a greater effect on plant δ^{15}N values than any other fertilizer, or any other natural process that influences plant δ^{15}N values (up to +40 ‰), although the results of the field study (Chapter 4) suggest smaller, but still substantial, increases of between 10 and 25 ‰. Significantly, within the context of isotopic dietary reconstruction in the Andes, when maize is fertilized with seabird guano, it has the potential to isotopically resemble a high trophic level marine predator. Interpretations of isotopic data on the basis of bulk collagen δ^{13}C and δ^{15}N values will be insufficient in this context to resolve the importance of marine protein in the diet; additional isotopic (Corr et al., 2005; Styring et al., 2010) or other markers are required (Dolphin et al., 2013). Camelid dung fertilization had more moderate effects on plant δ^{15}N values, similar to what has been observed for other manures derived from terrestrial herbivores (+2 to +4 ‰). This is particularly significant in the high altitudes areas of Peru where the assessment of the important of animal and plant protein in the diet may be confused on the basis of bulk collagen $\delta^{13}C$ and $\delta^{15}N$ values. Once again, additional markers are required to resolve this problem.

6.1.3 Isotopic Baselines in the northern Peru

The results of Chapters 2, 3, and 4 contribute to developing detailed carbon and nitrogen isotopic baselines in northern Peru. Carbon and nitrogen isotopic compositions will not always vary in a systematic way across a given landscape (Hedges et al., 2005; Valenzuela et al., 2011). This may be because there is too much environmental homogeneity across a particular study area, particularly at sub-continental or regional scales. This may hamper the ability to resolve questions such as those concerning animal migrations and the origins of biological materials; isotopic markers that are typically more sensitive to geographic variation at relatively smaller scales ($\delta^{18}O$, $\delta^{2}H$, $^{87}Sr/^{86}Sr$) may be required. The carbon and nitrogen isotopic data presented in Chapter 2 for plants sampled in different ecological zones of the Andes demonstrate significant variation with altitude, which is largely driven by differences in rainfall and temperature. While not being as specific as some of the isoscapes that have been constructed on the basis of, for example, surface water $\delta^{18}O$ or $\delta^{2}H$ (Bowen, 2010), there is potential for examining the movement of people or animals between these different zones, or of assessing the likelihood that a particular human or animal inhabited a particular zone. Generally, plant $\delta^{15}N$ values decrease moving from the coast to higher altitudes. Although C_3 plant $\delta^{13}C$ values increase with altitude, the relative distribution of C_3 and C_4 plants in these zones overwhelms these smaller effects, so that the general trend among all plants is for decreasing $\delta^{13}C$ with altitude. Aside from these general trends, there is much greater isotopic variability in coastal and low altitude plants relative to plants growing at higher altitudes, which has important implications when considering consumer isotopic variability (discussed in greater detail in Chapter 5).

6.1.4 Future Directions in Regional Isotopic Baseline Research

Plants sampled from the different ecological zones outlined in Chapter 2 were characterized by considerable variability, which was related to larger environmental variation. The Andean region as a whole, however, is one of tremendous environmental variability, and much more work is needed to more completely understand this variation. Several possible lines of research are briefly outlined here.

6.1.4.1 N_2 Fixation in Coastal Plants

While there is a trend towards higher $\delta^{15}N$ values in coastal plants, many plants with N_2 fixing capabilities occur on the coast of Peru (*Prosopis*, *Acacia*). Because these plants were more abundant in antiquity than they are today, and may have been significant food sources for camelids, they may have formed crucial components of local food webs. The importance of N acquired through fixation is highly variable in woody perennials (Boddey et al., 2000), and therefore a more intensive survey of these plants would aid in clarifying the relative importance of N_2 fixation on seasonal and long-term bases, and how these processes are influenced by El Niño.

6.1.4.2 Isotopic Consequences of Irrigation Agriculture

The high $\delta^{15}N$ values observed in many of the coastal plants sampled are driven by water availability and the openness of the nitrogen cycle. It is not clear, however, to what extent the $\delta^{15}N$ values of plants would be affected by growth under different water management schemes in the region. While the data are very limited (sampled from a single agricultural field), the unfertilized maize plants in the field study (Chapter 4) had relatively low $\delta^{15}N$ values compared to wild coastal plants. Studies conducted in fields irrigated under different conditions would aid in resolving these issues.

6.1.4.3 Isotopic Ecology of Andean Microenvironments

There are several important microenvironments or microhabitats in the Andes that are particularly significant for humans, animals, or both. On the coast, the *lomas* formations that occur are particularly noteworthy in this regard. Although a limited number of isotopic data (four plant specimens) for *lomas* plants were reported by Thornton et al. (Thornton et al., 2011), who found relatively high $\delta^{15}N$ values, the range of plants found in these habitats (e.g. epiphytes, cacti, grasses, shrubs), and the potential differences in water availability caused by the fog within the *lomas,* are unclear. Additional investigations of the isotopic ecology of *lomas* formations would be extremely useful, particularly one that includes taxa sampled from multiple microhabitats and over multiple years.

The high altitude *puna* in the Andean region is in fact characterized by three different grassland types: moist *puna*, dry *puna*, and salt *puna* (Baied and Wheeler, 1993). Each of these *puna* types is differentiated on the basis of vegetation and water availability, which suggests potential isotopic differences among these types. These habitats are today, and have been for thousands of years, important in camelid herding. Additionally, the *bofedales*, marsh-like formations that form in the highlands, are characterized by a different set of plants and hydrological conditions (Squeo et al., 2006), and are important habitats in camelid herding today. The environmental differences between these habitat types suggest the possibility that there may be isotopic differences between them. This may have significant implications for understanding camelid husbandry patterns in the highlands.

6.1.4.4 Fertilizers

Many questions remain regarding the isotopic effects of fertilization. With respect to seabird guano and camelid dung, it would be useful to understand the effects of fertilizer application at different rates, both in the short and long term. These long-term studies are unlikely to match some of the work that has been conducted in Europe in terms of scale, where long-term agricultural fields were established in the 19th century, providing convenient archival material for sampling (Bogaard et al., 2007; Bol et al., 2005; Fraser et al., 2011; Senbayram et al., 2008). Nevertheless, even studies conducted over five or ten year periods would be valuable.

Of the Peruvian seabird guano analyzed in this study, the range in δ^{15}N values was nearly 15‰. This raises questions as to whether or not particular islands have isotopically distinct guano. Studies of guano sampled from each of the guano islands would be useful in clarifying the geographic variation in guano isotopic compositions. While the ‘traceability’ of guano to particular islands is likely impractical using these techniques, understanding the range in guano δ^{15}N values would aid in addressing the potential magnitude of fertilization effects.

Camelid dung fertilizer was used in an experimental field in the coastal region of Peru that was fed by irrigation water, but it would be useful to examine the effects of camelid dung fertilization in high altitude tuber agriculture, a context in which it is known to have been important. Other fertilizers must also be investigated, both in the Andes and throughout the world. In the Andes, fishmeal is a potentially important fertilizer in coastal agricultural systems and it would be useful to explore the isotopic effects of this fertilizer, as well as any others that may have been utilized.

Additional fertilizer studies should also seek to quantify and isotopically analyze different N species in the soil to better understand the processes that influence the nitrogen isotopic composition of the plant from a more holistic perspective. Similarly, it would be useful to quantify and isotopically analyze specific plant compounds (individual amino acids for example) to better understand how various plant molecules are synthesized, moved, and stored within plants, and how these processes are influenced by fertilizer-derived N.

6.2 Human-Animal Interactions

6.2.1 Coastal Camelid Husbandry

Overall, the carbon and nitrogen isotopic compositions of the camelids from the two coastal settlements in the Virú Valley were higher than what is observed in modern highland animals. Additionally, the isotopic data presented for these archaeological camelids were extremely variable. These data may be explained by diversified management strategies, or the incorporation of camelids from a wide range of environments, or both. The restricted age range of the sacrificed camelids from Huaca Santa Clara, combined with their high isotopic variability, suggests that the isotopic variation was caused by variable management strategies at a local level, specifically small-scale animal management. The strength of this interpretation could be increased by the addition of oxygen isotope data from these same individuals.

6.2.2 Isotopic Zooarchaeology and Human-Animal Studies

Isotopic analysis has considerable potential with respect to zooarchaeological studies aimed at better understanding human-animal interactions. While this is certainly among the widely understood goals of zooarchaeology (Reitz and Wing, 2008), most zooarchaeological research focuses on understanding animal deaths, rather than animal lives. Isotopic analysis is one of a series of techniques that allows us to move beyond the death of the animal, and better understand how it lived, something that is particularly important for domestic animals. Certainly traditional zooarchaeological research that focuses on identification and quantification is of primary importance since it allows other techniques (such as isotopic analysis) to proceed – the bone must be identified before it can be subjected to isotopic analysis. Nevertheless, an approach that seeks to incorporate non-economic and non-symbolic aspects of human-animal relationships will be productive in creating better understandings of human-environment interactions. This approach has considerable potential with respect to isotopic analyses of domestic animals from a variety of contexts, both within the Peruvian Andes and throughout the world.

6.2.3 Future Directions in Peruvian Isotopic Zooarchaeology

The isotopic data presented in Chapter 5 provide an excellent case study for the analysis of human-animal interactions in a well-constrained context, but to make sense of camelid management practices in a more general sense, similar analyses must be undertaken at other sites in the region of variable size, sites in other coastal river valleys, sites associated with different political regimes, and sites located in markedly different environments (the highlands specifically). Oxygen isotopic analysis of bones and/or teeth would be useful for confirming the local nature of these camelids. Incremental $\delta^{13}C$ and $\delta^{18}O$ analyses of camelid teeth have recently been conducted by Goepfert et al. (Goepfert et al., 2013) in the Moche River Valley with promising results consistent with coastal camelid husbandry. Many sites on the north coast of Peru also contain preserved wool textiles and yarn fragments, which can be subjected to isotopic analysis. These data will provide insight into the production of wool and textiles in the region through the lens of animal management.

6.3 Interpreting Isotopic Data

6.3.1 New Approaches

A large portion of Chapter 5 was dedicated to exploring some novel ways of handling isotopic data derived from archaeological contexts. Specifically, this included an emphasis on quantifying and comparing isotopic variation, rather than focusing on diet compositions. Given the uncertainty associated with mixing model input data in archaeological contexts, combined with the dearth of appropriate baseline data, these techniques require serious consideration. They are not replacements for more traditional approaches, but at the very least provide alternatives or complements to them and perhaps better illustrate natural system variability.

Archaeologists and anthropologists should seriously consider the special nature of datasets derived from archaeological materials. Major issues such as source uncertainty, turnover rates, and limited sample size (both for sources and consumers) need to be addressed *as they specifically relate to archaeological contexts*. Ecologists have generally paid more attention to such issues (Bond and Diamond, 2010; Caut et al., 2008; Layman et al., 2012; Phillips, 2012; Robbins et al., 2010; Syväranta et al., 2013; Tarroux et al., 2010). These matters, and how they articulate with archaeological data in particular, deserve our full attention in future work.

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Appendices

The following appendices provide detailed data for analytical accuracy and precision for all runs associated with data presented in this dissertation (Bond and Hobson, 2012). Mean isotopic and elemental compositions are not reported where standards were used to generate the calibration curve.

Appendix A: Accepted δ values and elemental compositions for standards used. Accepted δ values for international standards are reported as per data presented on the IAEA website as of June 14, 2013.

Standard	**Material**	**$\delta^{13}C$**	**% C**	**$\delta^{15}N$**	**% N**
IAEA-CH-6	Sucrose	−10.449±0.033	42.08	–	–
NBS 22	Oil	−30.031±0.043	86.31	–	–
IAEA-N-1	Ammonium sulfate	–	–	0.4±0.2	21.54
IAEA-N-2	Ammonium sulfate	–	–	20.3±0.2	21.54
USGS40	Glutamic acid	−26.389±0.042	40.7	−4.5±0.1	9.52
USGS41	Glutamic acid	37.626±0.049	40.7	47.6±0.2	9.52
Keratin	*Internal	−24.04		6.36	

Appendix B: Analytical accuracy and precision for all standards associated with data presented in Chapter 3. Mean isotopic and elemental compositions are not reported where standards were used to generate the calibration curve.

			$\delta^{13}C$		$\delta^{15}N$		% C		% N	
Standard	**Run ID**	***n***	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**
IAEA-CH-6	C11-04	7	−11.74	0.22			43.84	1.05		
	CN12-01	4	−10.50	0.06			42.08	0.24		
	CN12-02	4	−10.63	0.13			40.32	0.53		
	CN12-03	5	−10.44	0.05			38.16	0.48		
	CN12-04	5	−10.43	0.06			40.71	0.66		
	CN12-05	5	−10.42	0.06			40.69	0.18		
	CN12-06	5	−10.43	0.06			40.84	0.31		
	CN12-07	5	−10.46	0.04			41.01	0.33		
	CN12-08	5	−10.45	0.11			41.33	0.26		
	CN12-09	4	−10.45	0.05			40.45	0.23		
	CN12-10	4	−10.45	0.05			40.53	0.43		
Keratin	C11-04	13	−24.37	0.10			50.53	1.05		
Internal	CN12-01	8			6.31	0.08			15.02	0.66
	CN12-02	9	−24.03	0.15	6.30	0.14	47.09	0.25	15.21	0.27
	CN12-03	8	−24.07	0.06	6.36	0.08	43.39	0.78	15.29	0.32
	CN12-04	8	−24.03	0.09	6.40	0.04	46.76	0.17	14.96	0.09
	CN12-05	8	−24.03	0.13	6.36	0.03	45.46	1.22	14.70	0.42
	CN12-06	8	−24.00	0.08	6.44	0.06	46.55	0.36	15.01	0.21
	CN12-07	8	−24.02	0.08	6.34	0.18	46.81	0.39	15.04	0.18
	CN12-08	7	−23.97	0.25	6.39	0.14	46.98	0.39	14.81	0.15
	CN12-09	8	−24.01	0.29	6.46	0.11	46.05	0.28	14.84	0.12
	CN12-10	8	−24.02	0.09	6.33	0.10	46.05	0.32	14.83	0.25
	N11-07	7			6.22	0.15			14.93	0.33
	N12-01	17			6.30	0.12			15.02	0.37
	N12-02	10			6.30	0.05			15.26	0.13
IAEA N2	CN12-01	3			20.30	0.24			21.16	0.25

			$\delta^{13}C$		$\delta^{15}N$		% C		% N	
Standard	**Run ID**	***n***	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**
IAEA N2	CN12-02	4			20.53	0.10			20.66	0.44
	CN12-03	4			20.50	0.15			21.77	0.27
	CN12-04	4			20.30	0.38			21.12	0.54
	CN12-05	4			20.30	0.25			21.04	0.34
	CN12-06	4			20.68	0.06			21.11	0.16
	CN12-07	4			20.43	0.11			21.03	0.24
	CN12-08	4			20.30	0.45			20.73	0.19
	CN12-09	4			20.30	0.38			20.76	0.11
	CN12-10	4			20.37	0.26			21.17	0.20
	N11-07	2			20.25	0.37			20.74	0.11
	N12-01	4			20.30	0.30			20.37	0.26
	N12-02	5			20.26	0.28			21.16	0.16
NBS 22	C11-04	4		0.02				3.40		
USGS40	CN12-01	5		0.06		0.06		0.09		0.09
	CN12-02	5		0.15		0.07		0.10		0.04
	CN12-03	5		0.04		0.06		0.95		0.26
	CN12-04	5		0.05		0.04		0.22		0.05
	CN12-05	5		0.05		0.04		0.22		0.05
	CN12-06	5		0.06		0.07		0.25		0.08
	CN12-07	6		0.04		0.08		0.31		0.08
	CN12-08	6		0.17		0.07		0.21		0.06
	CN12-09	5		0.25		0.07		0.17		0.05
	CN12-10	5		0.06		0.04		0.15		0.06
	N11-07	9				0.09				0.10
	N12-01	6				0.05				0.17
	N12-02	11				0.09				0.13
USGS41	CN12-01	4		0.07		0.08		0.15		0.15
	CN12-02	4		0.06		0.06		0.18		0.05
	CN12-03	5		0.07		0.40		0.23		0.04
	CN12-04	5		0.08		0.34		0.16		0.05

			$\delta^{13}C$		$\delta^{15}N$		% C		% N	
Standard	**Run ID**	***n***	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**
USGS41	CN12-05	5		0.10		0.06		0.28		0.06
	CN12-06	5		0.15		0.38		0.11		0.03
	CN12-07	4		0.07		0.28		0.28		0.09
	CN12-08	5		0.06		0.26		0.73		0.19
	CN12-09	5		0.24		0.45		0.50		0.14
	CN12-10	5		0.01		0.07		0.19		0.06
	N11-07	6				0.30				0.10
	N12-01	4				0.07				0.12
	N12-02	6				0.10				0.04

Appendix C: Analytical accuracy and precision for all standards associated with data presented in Chapter 3. Mean isotopic and elemental compositions are not reported where standards were used to generate the calibration curve.

			δ^{13}C		δ^{15}N		% C		% N	
Standard	**Run ID**	***n***	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**
IAEA-CH-6	C11-02	3		0.21				0.09		
	C11-03	3	−10.50	0.13			42.06	0.64		
	CN11-03	3	−10.27	0.05			41.98	0.18		
Keratin	C11-02	8	−24.20	0.16			49.33	1.04		
Internal	C11-03	7	−24.32	0.24			48.63	1.44		
	N10-01	10			6.22	0.09			15.23	0.31
	N10-02	12			6.47	0.10			15.49	0.87
	N11-01	9			6.37	0.09			15.62	0.22
	N11-02	9			6.33	0.12			15.56	0.32
	N11-03	7			6.34	0.13			14.47	0.51
	N11-04	7			6.42	0.05			14.46	0.17
	N11-06	7			6.29	0.06			15.05	0.13
	N11-08	7			6.27	0.27			15.36	0.48
	CN11-03	4	−24.01	0.06	6.54	0.21	47.44	0.52	14.89	0.12
NBS 22	C11-02	6		0.14				1.81		
USGS40	C11-02	3	−26.39	0.14			40.78	1.51		
	C11-03	3		0.65				1.42		
	CN11-03	2		0.02		0.28		0.21		0.17
	N11-01	7			−4.50	0.10			9.64	0.14
	N11-02	5			−4.63	0.04			9.76	0.13
	N11-03	9				0.08				0.32
	N11-04	9				0.06				0.28
	N11-06	9				0.07				0.16
	N11-08	4				0.23				0.29
USGS41	CN11-03	3		0.56		0.28		0.34		0.10
	N11-01	7			47.14	0.30			9.98	0.20

			$\delta^{13}C$		$\delta^{15}N$		% C		% N	
Standard	**Run ID**	***n***	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**
USGS41	N11-02	5			47.34	0.33			9.93	0.18
	N11-03	6				0.12				0.13
	N11-04	6				0.32				0.07
	N11-06	6				0.38				0.08
	N11-08	3				0.53				0.34
IAEA N1	10-01	6				0.10				0.36
	10-02	6				0.09				0.22
IAEA N2	10-01	8				0.18				0.42
	10-02	6				0.28				0.86
	11-01	6				0.08				0.61
	11-02	7				0.10				0.35
	11-03	2			20.31	0.08			20.31	0.03
	11-04	2			20.52	0.13			20.23	0.27
	11-06				20.30	0.05			20.83	0.08
	11-08				20.30	0.34			21.53	0.88

Appendix D: Analytical accuracy and precision for all standards associated with data presented in Chapter 4. Mean isotopic and elemental compositions are not reported where standards were used to generate the calibration curve.

			$\delta^{13}C$		$\delta^{15}N$		% C		% N	
Standard	**Run ID**	***n***	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**
Keratin	N11-02	9			6.33	0.12			15.56	0.32
Internal	N11-03	7			6.34	0.13			14.47	0.51
	N11-04	7			6.42	0.05			14.46	0.17
	N11-05	7			6.30	0.10			14.95	0.22
	N11-06	7			6.29	0.06			15.05	0.13
	N11-07	7			6.22	0.15			14.93	0.33
	N11-08	7			6.27	0.27			15.36	0.48
	N12-01	17			6.30	0.12			15.02	0.37
USGS40	N11-02	5			−4.63	0.04			9.76	0.13
	N11-03	9				0.08				0.32
	N11-04	9				0.06				0.28
	N11-05	8				0.06				0.33
	N11-06	9				0.07				0.16
	N11-07	9				0.09				0.12
	N11-08	4				0.23				0.29
	N12-01	6				0.05				0.11
USGS41	N11-02	5			47.34	0.33			9.93	0.18
	N11-03	6				0.12				0.13
	N11-04	6				0.32				0.07
	N11-05	6				0.23				0.07
	N11-06	6				0.38				0.08
	N11-07	6				0.30				0.10
	N11-08	3				0.53				0.34
	N12-01	4				0.37				0.12
IAEA N2	11-02	7				0.10				0.35
	11-03	2			20.31	0.08			20.31	0.03

			δ^{13}C		δ^{15}N		% C		% N	
Standard	**Run ID**	***n***	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**
	11-04	2			20.52	0.13			20.23	0.27
	11-05	2			20.30	0.05			21.36	0.10
	11-06	2			20.30	0.05			20.83	0.08
	11-07	2			20.25	0.27			20.74	0.11
	12-01	4			20.30	0.30			20.87	0.27

Appendix E: Analytical accuracy and precision for all standards associated with data presented in Chapter 5. Mean isotopic and elemental compositions are not reported where standards were used to generate the calibration curve.

			δ^{13}C		δ^{15}N		% C		% N	
Standard	**Run ID**	***n***	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**
IAEA-CH-6	09−01	5		0.04				0.37		
	09−02	7		0.08				0.70		
	09−03	6		0.08				0.75		
	09−04	10		0.09				0.75		
	09−05	12		0.06				0.44		
	09−06	10		0.04				0.36		
	09−07	7		0.11				0.29		
	10−01	5		0.05				1.96		
	11−03	3	−10.27	0.05			41.98	0.18		
	12−11	4	−10.45	0.06			40.84	1.42		
	12−12	3	−10.41	0.06			41.54	0.14		
	12−13	5	−10.45	0.01			40.50	0.35		
	13−01	4	−10.42	0.10			41.44	0.58		
NBS 22	09-01	6		0.03				2.01		
	09-02	7		0.06				2.18		
	09-03	7		0.05				1.98		
	09-04	6		0.05				1.73		
	09-05	6		0.03				1.25		
	09-06	5		0.07				1.99		
	09-07	6		0.07				3.36		
	10-01	5		0.08				2.54		
USGS40	09-04	2	-26.25	0.08	−4.52	0.13	40.19	0.47	9.44	0.01
	11-03	2		0.02		0.28		0.21		0.17
	12-11	5		0.03		0.07		0.43		0.09
	12-12	4		0.05		0.03		3.05		0.83
	12-13	6		0.04		0.02		1.28		0.35

			δ^{13}C		**δ^{15}N**		**% C**		**% N**	
Standard	**Run ID**	***n***	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**
USGS40	13-01	5		0.09		0.06		1.35		0.32
USGS41	11-03	2	37.95	0.09	47.44	0.04	42.02	0.45	9.93	0.14
	12-11	4		0.14		0.40		1.06		0.30
	12-12	3		0.07		0.07		0.93		0.21
	12-13	6		0.13		0.31		1.88		0.47
	13-01	5		0.24		0.08		0.65	9.67	0.17
Keratin	09-01	10	−24.05	0.05	6.49	0.24	49.16	2.89	15.45	0.93
(Internal)	09-02	9	−24.06	0.04	6.25	0.14	48.22	0.56	15.35	0.25
	09-04	8	−23.93	0.04	6.24	0.09	47.41	0.93	15.12	0.18
	09-03	9	−24.07	0.04	6.23	0.18	48.53	0.93	15.28	0.38
	09-05	11	−24.03	0.06	6.35	0.19	47.70	0.33	15.34	0.18
	09-06	7	−24.10	0.04	6.21	0.11	47.21	0.54	15.13	0.28
	09-07	8	−24.05	0.07	6.25	0.08	47.21	0.51	15.23	0.15
	10-01	7	−24.05	0.08	6.60	0.08	46.39	0.57	15.80	0.21
	11-03	4	−24.01	0.06	6.54	0.21	47.44	0.52	14.89	0.12
	12-11	8	−23.91	0.14	6.43	0.17	46.02	0.64	14.00	1.24
	12-12	6	−24.09	0.11	6.32	0.17	47.75	0.31	15.56	0.23
	12-13	10	−24.09	0.04	6.40	0.10	46.95	0.28	15.52	0.11
IAEA N1	09-01	5				0.13				0.20
	09-02	7				0.13				0.19
	09-03	7				0.10				0.28
	09-04	8				0.09				0.60
	09-05	12				0.14				1.44
IAEA N1	09-06	10				0.11				0.81
	09-07	7				0.11				0.23
	10-01	3				0.08				0.17
IAEA N2	09-01	6				0.46				0.31
	09-02	7				0.30				0.22
	09-03	7				0.39				0.35
	09-04	8				0.28				0.33

			$\delta^{13}C$		$\delta^{15}N$		% C		% N	
Standard	**Run ID**	***n***	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**	**Mean**	**σ**
IAEA N2	09-05	7				0.47				0.28
	09-06	6				0.26				0.23
	09-07	6				0.18				0.16
	10-01	5			20.69	0.55			22.24	0.26
	12-11	4			20.35	0.28			20.88	0.30
	12-12	3			20.48	0.19			21.92	0.12
	12-13	3			20.64	0.01			21.64	0.10
	13-01	3			20.51	0.07			21.08	0.05

Curriculum Vitae

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2013	**Szpak, P.**, T.J. Orchard, A.K. Salomon, D.R. Gröcke. Regional Ecological Variability and Impact of the Maritime Fur Trade on Nearshore Ecosystems in southern Haida Gwaii (British Columbia, Canada): Evidence from Stable Isotope Analysis of Rockfish (*Sebastes* spp.) Bone Collagen. *Archaeological and Anthropological Sciences* 5:159-182.
2013	**Szpak, P.**, C.D. White, F.J. Longstaffe, J.-F. Millaire, V.F. Vásquez Sánchez. Carbon and Nitrogen Isotopic Survey of Northern Peruvian Plants: Baselines for Paleodietary and Paleoecological Studies. *PLoS One* 8(1):e53763.
2012	**Szpak, P.**, J.-F. Millaire, C.D. White, F.J. Longstaffe. Influence of seabird guano and camelid dung fertilization on the isotopic composition of field-grown maize (*Zea mays*). *Journal of Archaeological Science* 39:3721-3740.
2012	**Szpak, P.,** F.J. Longstaffe, J.-F. Millaire, C.D. White. Stable Isotope Biogeochemistry of Seabird Guano Fertilization: Results from Growth Chamber Studies with Maize (*Zea mays*). *PLoS One* 7:e33741.
2012	**Szpak, P.**, T.J. Orchard, I. McKechnie, D.R. Gröcke. Historical Ecology of Late Holocene Sea Otters (*Enhydra lutris*) from Northern British Columbia: Isotopic and Zooarchaeological Perspectives. *Journal of Archaeological Science* 39:1553-1571.
2011	**Szpak, P.** Fish Bone Chemistry and Ultrastructure: Implications for Taphonomy and Stable Isotope Analysis. *Journal of Archaeological Science* 38:3358-3372.
2010	**Szpak, P**., D.R. Gröcke, R. Debruyne, R.D.E. MacPhee, R.D. Guthrie, D. Froese, G.D. Zazula, W.P. Patterson, H.N. Poinar. Regional Differences in bone collagen δ^{13}C and δ^{15}N of Pleistocene mammoths: Implications for palaeoecology of the mammoth steppe. *Palaeogeography Palaeoclimatology Palaeoecology* 286:88-96.
2009	**Szpak, P.**, T.J. Orchard, D.R. Gröcke. A Late Holocene vertebrate food web from southern Haida Gwaii (Queen Charlotte Islands, British Columbia). *Journal of Archaeological Science* 36:2734-2741.
2008	Debruyne, R., G. Chu, C.E. King, K. Bos, M. Kuch, C. Schwarz, **P. Szpak**, D. Gröcke, P. Matheus, G. Zazula, D. Guthrie, D. Froese, B. Buigues, C. de Marliave, C. Flemming, D. Poinar, D. Fisher, J. Southon, A. Tikhonov, R.D.E. MacPhee, H.N. Poinar. Out of America: Ancient DNA evidence for a

New World origin of Late Quaternary woolly mammoths. *Current Biology* 18:1320-1326.

Publications (Chapters in Edited Volumes)

2011 Orchard, T.J., **P. Szpak**. Identification of salmon species from archaeological remains on the Northwest Coast. *In* M. Moss and A. Cannon, eds. *The Archaeology of North Pacific Fisheries*. University of Alaska Press, Fairbanks, pp. 17-29.

Presentations at Professional Meetings

2013 **Szpak, P.** Significant Others: Understanding Animal Lives in the Archaeological Record. 36th Annual Meeting of the Society of Ethnobiology, Denton, TX.

2013 **Szpak, P.** Isotopic evidence for diversified camelid husbandry practices on the north coast of Peru. 41st Midwest Conference on Andean and Amazonian Archaeology and Ethnohistory, DeKalb, IL.

2012 **Szpak, P.**, C.D. White, J.F. Millaire, F.J. Longstaffe. Camelid Management Practices On the Prehispanic North Coast of Peru. 111th Meeting of the American Anthropological Association, San Francisco, CA.

2012 **Szpak**, **P.**, J.F. Millaire, F.J. Longstaffe, C.D. White. Impact of seabird guano and camelid dung on nitrogen isotopic composition of field- and growth chamber-grown maize. Archaeological Sciences of the Americas Symposium, Nashville, TN.

2012 **Szpak**, **P.** Molecular Perspectives on the Taphonomy of Fish Bone. 45th Annual Meeting of the Canadian Archaeological Association, Montreal, QC.

2012 **Szpak**, **P.**, J.F. Millaire, F.J. Longstaffe, C.D. White. Llama dung and seabird guano: Isotopic perspectives on Andean fertilizers from field and growth chamber studies. 45th Annual Meeting of the Canadian Archaeological Association, Montreal, QC.

2012 **Szpak**, **P.**, T. Orchard, I. McKechnie. Historical Ecology of Late Holocene Sea Otters (*Enhydra lutris*) from Northern British Columbia: Isotopic and Zooarchaeological Perspectives. 77th Annual Meeting of the Society for American Archaeology, Memphis, TN.

2012 **Szpak, P.,** F.J. Longstaffe, J.F. Millaire, C.D. White. Want Not the Waste? Seabird Guano Use in the Prehispanic Andes. 40th Midwest Conference on Andean and Amazonian Archaeology and Ethnohistory, Chicago, IL.

2011 **Szpak**, **P.**, F.J. Longstaffe, J.F. Millaire, C.D. White. Llama Dung and Seabird Guano: Isotopic Perspectives on Andean Fertilizers from Field and Growth Chamber Studies. 30th Northeast Conference on Andean Archaeology and Ethnohistory, Andover, MA.

2011 **Szpak**, **P.**, J.F. Millaire, F.J. Longstaffe, C.D. White. Isotopic effects of fertilization in the Andes: Implications for dietary reconstruction. 39th Annual Meeting of the Canadian Association for Physical Anthropology, Montréal.

2011 **Szpak, P.,** T. Orchard, R. Markel, I. McKechnie. Interactions between Humans and Sea Otters in Holocene British Columbia: Evidence from Stable

Isotope Analysis. 34th Annual Meeting of the Society of Ethnobiology, Columbus, OH.

2011 **Szpak**, **P.**, J.F. Millaire, F.J. Longstaffe, C.D. White. Effects of Seabird Guano on the Stable Isotope Composition and Growth of Maize (*Zea mays*): Results from a Controlled Study. 76th Annual Meeting of the Society for American Archaeology, Sacramento, CA.

2011 **Szpak**, **P.**, J.F. Millaire, F.J. Longstaffe, C.D. White. Effects of seabird guano fertilization on the stable isotope composition of plants: Results from a controlled study. 39th Midwest Conference on Andean and Amazonian Archaeology and Ethnohistory, Columbia, MO.

2011 **Szpak**, **P.**, J.F. Millaire, F.J. Longstaffe, C.D. White. Guano Fertilization on the coast of Peru: An Isotopic Perspective. 51st Annual Meeting of Institute for Andean Studies, Berkeley, CA.

2010 **Szpak**, **P.**, J.F. Millaire, F. Longstaffe, C. White. Guano Fertilization in the Prehispanic Americas: Experimental Evidence from a Controlled Study. 29th Northeast Conference on Andean Archaeology & Ethnohistory, Madison, NJ.

2010 **Szpak, P.,** T. Orchard. Foraging ecology of Late Holocene sea otters: Implications for past populations status and future impacts on nearshore ecosystems. 11th International Council for Archaeozoology International Conference, Paris, France.

2010 **Szpak, P.,** C.D. White, J.F. Millaire, F.J. Longstaffe. Isotopic Perspectives on Camelid Management Practices and Textiles Production in the Virú Valley, Northern Peru. 11th International Council for Archaeozoology International Conference, Paris, France.

2010 **Szpak, P.,** C.D. White, J.F. Millaire, F.J. Longstaffe. Isotopic Evidence for Traded Fabrics and Camelid Management Practices in the Virú Valley, Northern Peru (Early Intermediate Period). 38th Midwest Conference on Andean and Amazonian Archaeology and Ethnohistory, Fort Wayne, IN.

2010 Debruyne, R., A. Devault, J. Enk, **P. Szpak**, H. Poinar. Where hypotheses collapse, collide, or converge: structure and timing of the divergence of the mammoth lineages. 11th International Council for Archaeozoology International Conference, Paris, France.

2010 Debruyne, R., J. Enk, A. Devault, **P. Szpak**, H. Poinar. Phylogeography of the woolly mammoth: molecular divergence in space and time. 5th International Conference on Mammoths and their Relatives, Puy-en-Velay, France.

2010 Gröcke, D.R., **P. Szpak**, H.N. Poinar. Regional differences in bone collagen carbon- and nitrogen-isotope ratios of Pleistocene mammoths: Implications for paleoecology of the mammoth steppe. European Geosciences Union General Assembly, Vienna, Austria.

2010 Surette, F., **P. Szpak**, J.F. Millaire, C.D. White, F.J. Longstaffe. Stable Isotope, Contextual and Functional Analysis of Early Intermediate Period Textiles from the Virú Valley (Northern Peru). 75th Annual Meeting of the Society for American Archaeology, St. Louis, MO.

2009 **Szpak, P.,** C. White, J.F. Millaire, F. Longstaffe. Isotopic Evidence for Camelid Diet and Management Practices in the Virú Valley, Peru. 28th

	Northeast Conference on Andean Archaeology & Ethnohistory, New Paltz, NY.
2008	**Szpak, P.**, T.J. Orchard. Ecological Change Association with the Maritime Fur Trade in Southern Haida Gwaii (Queen Charlotte Islands, British Columbia). 41st Annual Meeting of the Canadian Archaeological Association, Peterborough, ON.
2008	**Szpak, P.**, D.R. Gröcke, T.J. Orchard. Isotopic and Archaeological Evidence of Regional Ecological Differences in Pre-Contact and Early Contact Haida Gwaii (British Columbia). 73rd Annual Meeting of the Society for American Archaeology, Vancouver, BC.

Invited Lectures

2013	A Biographical Approach to Zooarchaeology. Integrative Approaches in Zooarchaeology Workshop, Université Laval, Québec, QC.
2012	Animal Management Practices and Fertilization Practices in the Prehispanic Andes. Department of Archaeology Seminar Series, Simon Fraser University, Burnaby, BC.

Research Grants

2013	Dissertation Fieldwork Grant, Wenner Gren Foundation for Anthropological Research
2009	Anthropology Department Research Scholarship

Fellowships and Scholarships (since 2008)

2008-13	Western Graduate Research Scholarship
2010-13	Bombardier Canadian Graduate Scholarship (Doctoral), SSHRC
2010-11	Ontario Graduate Scholarship (Declined)
2009-10	Ontario Graduate Scholarship (Declined)
2008	Faculty of Social Science Dean’s Scholarship
2008-09	Ontario Textbook and Technology Grant

Teaching Assistantships

2013	Many Ways of Being Human (UWO)
2012	Introduction to Biological Anthropology and Archaeology (UWO)
2009	Introduction to World Archaeology (UWO)
2008	Introduction to World Archaeology (UWO)
2007	Introduction to World Prehistory (McMaster University)

Manuscripts Reviewed For

2013-	Chemical Geology
2013-	International Journal of Food Sciences and Nutrition
2012-	International Journal of Osteoarchaeology
2011-	Journal of Analytical and Atomic Spectrometry
2011-	Journal of Archaeology Sciences
2012-	Journal of the North Atlantic
2013-	Rapid Communications in Mass Spectrometry

2012-	Recent Patents on Food, Nutrition & Agriculture
2012-	Quaternary Science Reviews

Memberships in Professional Organizations

2012-	American Anthropological Association
2010-	American Association of Physical Anthropologists
2007-	Canadian Archaeological Association
2007-	Canadian Association for Physical Anthropologists
2009-	International Council for Archaeozoology
2006-	Society for American Archaeology
2006-	Society for Archaeological Sciences
2011-	Society of Ethnobiology