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Long-Term Human/Animal Interactions and their Implications for Hunter-Gatherer Archaeology in South America

A. Sebastián Muñoz and Mariana Mondini

Abstract
This chapter deals with the relationships of human hunter-gatherers to other animals in their communities from a long-term perspective, by focusing on the patterns and processes occurring at this scale in South America. A number of instances are analysed concerning both prey and predators, especially in the Andean-Patagonian sub-region, which can eventually be used in the construction of historical narratives concerning South American hunter-gatherers.

These analyses are grounded on the notion that anthropological and ethnographical short-term studies are appropriate for accounting for the mechanisms and proximate causes of human/animal interactions under particular circumstances, but if we are to understand the ultimate causes that have led to such situations, we need to study those long-term processes that have conditioned them. Although an ‘ethnographic’ or short-term approach to the hunter-gatherer archaeological record has had a strong influence in South America, a long-term perspective has recently been applied, particularly in the Southern Cone, with novel, productive outcomes. Here we aim at providing a new contribution to this perspective.

THE LONG TERM
The long term can be conceived of as a property of the empirical phenomena we study, as a property of the theoretical explanations we invoke to account for them, or both. These distinctions are very important in archaeology and anthropology, as they help understand a range of research traditions, and have very different implications.

By focusing on the long-term nature of the archaeological record, its temporal dimension is acknowledged. It should be noted, though, that assessing the age or temporal depth of the remains and deposits we study does not necessarily account for their temporal resolution (i.e., they can still be regarded as a juxtaposition of successive short-term events). The fossil record generated by hominids, as any other fossil record, is often the averaged result of multiple, more or less continuous events. The temporal resolution (i.e., the amount of time represented in the fossil record), resulting from taphonomic averaging and the completeness of the fossil
record, should be empirically determined for each particular case (Behrensmeyer et al. 1992). This is a methodological perspective of the long term in archaeology.

There is also a theoretical perspective, although it is not always paired with the acknowledgement of the long-term scale of empirical phenomena – which is, however, a prerequisite to the former. While the empirical conception of the long term relates to description, the theoretical one relates to explanation, in that it addresses ultimate-causation processes to account for the archaeological record.

If we are to understand past life relationships from the archaeological record, such as those between hunter-gatherers and their prey and other predators, causation in biological systems – broadly conceived – is a relevant issue (Gifford-Gonzalez 1991; see also Bailey 1983). Because these are complex systems, regularities in the results of the interaction of multiple variables are usually best described in probabilistic terms (Mayr 1982). As Mayr puts it, biological systems are hierarchical, each level being more than just the sum of its parts. Hence, any given level cannot be accounted for by the organisationally lower levels. In the terms we have been discussing here, we cannot account for long-term patterns in the archaeological record by resorting to a sum of ‘ethnographic’ states. While this could help infer proximate or functional causation (i.e., what and how questions), only ultimate or evolutionary causation (i.e., why questions), can fully account for a given problem (Mayr 1982, 1997).

There are several aspects of this we would like to draw attention to. One has to do with history. While no universal laws can be applied to account for complex systems, historical narratives can be used instead (Mayr 1982, 1997). These narratives have explanatory power, since earlier events in a sequence have a causal contribution to successive ones. The relevance of this approach in archaeology has been highlighted by Flannery (1986), Thomas (1986), and Gifford-Gonzalez (1991), among others.

This also relates to the fact that some ecological relationships between species can only be perceived at broad scales of comparison, since we are dealing with the rates at which tactics, actions, and decisions are repeated (Stiner 1993). Modern short-term observations, hence, may not wholly describe the consequences of the same processes in the long run.

Another dimension of the theoretical conception of the long term is that some processes only occur over long periods of time (Bailey 1983; Delcourt and Delcourt 1991; Dincauze 2000, among others, not to mention the literature on evolutionary theory). Their consequences, then, can only be perceived in the fossil record. Hence, the coarse grain of most archaeological records does not necessarily represent a drawback inherent to historical disciplines like archaeology, but, as it conforms to human ecology and evolution, is the appropriate scale for fully understanding long-term processes. Generally, these are precisely the processes we need to invoke if we are to infer ultimate causal relationships.

To sum up, the long term can be admitted to relate to the empirical phenomena we study, or to both these and the processes called upon to ultimately account for them. It is the last viewpoint that we are most interested in.

The long term is not the aggregate of a number of short-term events, then, although it does impinge on them. Therefore, to understand the significance of short-term events we need to deem them in the light of what we know about long-term causation. This way, it becomes apparent that short-term observations are instances of a range of variability of which we do not know a priori the whole reach. That is why modern short-term studies can be very productive when undertaken under a variety of conditions, which allows the understanding of the range
of factors affecting the patterns we observe (O’Connell 1995; also see Stiner 1993). Short-term studies, then, are not incompatible with a long-term approach.

Another implication of this is that a long time scale relates to a broad spatial scale, not only in the sense that we need to investigate the patterns we are interested in under multiple conditions, but also that the same processes conditioning taphonomic time averaging also affect the spatial resolution of the fossil record (Behrensmeyer et al. 1992). A more fundamental reason is that long-term causal processes also have frequently – although not necessarily – a broad spatial expression, and in spite of the fact that they affect locally operating processes, they cannot be generalised from small-scale studies (Delcourt and Delcourt 1991; Brown 1995; Dincauze 2000).

Taking all this into account, South America’s geography and biotic history are considered below, namely regarding the main prey and predators with which humans have had to interact.

THE SOUTH AMERICAN CONTINENT

Many ecological generalisations come from the Northern hemisphere, but they often do not apply to South America (Jaksic 1987). This partly derives from the fact that the ‘Sherwin-Williams effect’ has prevailed in historical biogeography (Crisci and Morrone 1990). The model so called, in reference to the logotype of a paint trademark in which a can is shown spilling paint over the globe from the Northern hemisphere to the Southern one, refers to the belief shared by some biologists at the end of the XIX century that the Northern hemisphere was the original place of all extant life forms; from there, and through different mechanisms, these organisms would have dispersed into the South (Crisci and Morrone 1990). It has now become clear that the Southern continents should not be interpreted in terms of exceptions, but that ecology and related disciplines need to incorporate this variability in their corpora (see Politis 1999 for related arguments regarding the human peopling of the Americas). As Jaksic (1987) puts it, the history and composition of South American habitats and communities is not background noise, but they should be regarded as an opportunity to prove the value of those generalisations.

The physical setting

The main physical properties of South America at the continental scale – although strictly speaking it is a subcontinent – have impinged on its particular biotic configuration. Much of the physical information on South America has been compiled by Morello (1984), and has recently been analysed relative to human dispersal by Pineau et al. (2003). Here we focus mainly on the South-Western, arid portion of the continent.

The South American continental landmass has the approximate shape of an upside-down isosceles triangle, narrowing southwards. This geometry prompts gradients such as those of increasing oceanity and increasing ecosystemic and morphostructural simplicity as latitude increases, and available physical space becomes more limiting a factor at higher latitudes (Morello 1984). The subcontinent is linked to North America by the Panama isthmus, which acts like a filter or membrane (sensu Rapoport 1982) to the flow of organisms. South America is in fact an island-continent, surrounded by open oceans and, unlike the large Northern continents, it is a peninsula within the oceanic hemisphere (Morello 1984). As a consequence, oceanity – instead of continentality, as in Northern continents – increases with latitude, and
this is in fact one of the most relevant characteristics of the continent.

The Andes Cordillera, running along the Western flank of the continent, is the most prominent orographic feature. It stops the westerly winds and, more generally, its influence is so profound and even throughout its range that it is considered to be the most important morphological element not only in the continent but also in the whole globe (Morello 1984). There are no large orographic barriers other than the Andes to generate consistent climatic frontiers, and large air masses flow from the Atlantic Ocean to the Andes, and from the Southern Pole to the North of South America (Morello 1984; Neiff 1999). South American lowlands are morphostructurally monotonous; and the Southern portion of the continent is more even than the Northern one (Morello 1984).

Another distinct feature of South America is the wetlands, which are the largest on Earth (Morello 1984; Neiff 1999). They are located in the main river drainage basins, namely the Orinoco and the Amazon, mostly in warm climate areas.

South American ecosystems share an equipotential property (i.e., their arrangement into latitudinal bands is dimmed), due to the effects of oceanity in conjunction with the Andes and marine currents (Morello 1984). Such a combination attenuates the gradient in biotic communities that should be expected from latitude exclusively, namely one that anticipates fewer species and larger ranges as latitude increases. It should also be noted that in spite of being the southernmost ice-free landmass in the Southern hemisphere, South America does not reach as high latitudes as Northern continents. Besides, it bears less rigorous, more homogeneous environments than we should expect from latitude only.

The fact that the Southern Cone is morphostructurally more even than the Northern part of the continent results in a fairly even stretch of land extending through several latitudinal bands (Morello 1984). This also relates to the fact that the Andes Cordillera runs perpendicular to the latitudinal gradient, which allows for migrations between environmentally different areas (Brown 1995). Also, the absence of important hydrological barriers allows a relatively continuous flow of organisms in the lowlands (Morello 1984). All of these factors, along with the intense oceanic influence that causes latitude-derived effects to be quite lessened here, result in the relative homogeneity of much of the South American continent.

**Historical background**

Southern continents share a history in which the main faunal connections are with the respective continents to the North, but such relationships have been intermittent and incomplete (Simpson 1965). The composition of the current South American biota is in fact the result of old continental connections, followed by long isolation, and the influence of recent migrations from Northern areas.

An important water barrier lay between South America and North America until the Pliocene, when the Panama isthmus was formed. South American mammalian fauna was definitely modelled in the Upper Pliocene, a time of interchange with North America, when a number of invasions and extinctions took place. Endemism reaches some of the highest levels in South America, and the continent is considered to be a case study in catastrophic extinctions, although various explanations have been proposed for these patterns (Simpson 1965; Delany 1982; Marshall et al. 1984; Morello 1984; Webb 1985; Marshall and Cifelli 1990; Crisci and Morrone 1990; Camacho 1990; Redford and Eisenberg 1992; Vrba 1992; Lessa et al. 1997; Politis et al. 1995; Borrero 1997, among others).
In sum, South America can be considered to be particular in many respects, both regarding its spatial geography and its faunal history. Its short human history relative to the Old World continents is also a relevant factor.

SOUTH AMERICAN FAUNAS

South America, along with Central America, has been defined from a biogeographical viewpoint as the Neotropics (Sclater 1858 and Wallace 1876, in Cox 2001) (Fig. 4.1) – although Cox (2001) suggests that South American would be more appropriate a biogeographical designation for the region. Significant habitat richness characterises the continent, with grasslands and tropical forests covering an important part. The tropical Andes are one of the most diverse physical and biotic mosaics in the world (Cabrera and Willink 1980; Delany 1982; Morello 1984; Ceballos and Simonetti 2002). Similar ecological conditions, though, can be found across quite distant ecosystems, particularly the high tropical mountains and the strongly oceanic subantarctic areas (Morello 1984).

Within the Neotropics, two sub-regions have often been identified, divided by the so-called sub-tropical line, which runs southwards from Ecuador, close to the Andes, through the South-East in Bolivia/North-Western Argentina, and down to the Atlantic coast in Brazil/Uruguay (Sclater 1858 and Wallace 1876, in Rapoport 1968). The area to the North-East has been called the Guyano-Brazilian sub-region, and the one to the South-West, is the Andean-Patagonian sub-region (see Rapoport 1968; Ruggiero et al. 1998, and bibliography therein). Ringuelet (1961, in Ruggiero et al. 1998) and Ruggiero et al. (1998) suggest that the area in-between is in fact not just a line but a region itself, limited by Wallace’s line to the North and by Sclater’s line to the South. Here we focus mainly on the Andean-Patagonian sub-region, with an emphasis on mammalian faunas.
The Pliocene faunal interchange between North and South America and the climatic changes during the Plio-Pleistocene had negative effects on both the immigrant and endemic faunas. As a result of these and other processes, temperate South America has currently many ecological niches only partially occupied by mammals as compared to North America, and even when mammal body sizes are similar in temperate North and South America, there are generally fewer species per feeding niche in the latter (Redford and Eisenberg 1992). South America is a case of unsaturated fauna, given the low numbers of large mammals in the continent (Keast 1972; Franklin 1982; Berta 1988; also see Cornell 1999).

While in Northern South America 50% of mammalian species are bats, bat species richness declines markedly South of 23° 30' S, where, as marsupials decrease, rodents become dominant. The Southern Cone is dominated by rodents and carnivores, and in the Southern end, marine mammals prevail over terrestrial ones (Redford and Eisenberg 1992).

Southern South America is associated to one of the areas with the highest oceanic productivity in the globe. The Atlantic sub-antarctic zone can support a large bird biomass, and some of the world’s largest marine biomass is found on the Pacific coast. Biomass and productivity are higher but rather unstable on the Pacific Coast, and lower but more stable on the Atlantic one (Redford and Eisenberg 1992; Ingmanson and Wallace 1995; Acha et al. 2004, among others; also see Boersma 1998, in Cruz 2001).

**Potential prey**

During the Pleistocene many taxa lived in South America, including megaherbivores, that later became extinct. These extinctions affected all large endemic herbivores and about half the immigrant herbivore genera. Among the last lineages to vanish are Glyptodontidae, Megatheriidae, Mylodontidae, Macraucheniiidae, Toxodontidae, Gomphotheriidae, Equidae, and Ursidae (Simpson 1965; Patterson and Pascual 1972; Webb 1985; Marshall and Cifelli 1990; Vrba 1992; Politis et al. 1995; Borrero 1997; Lessa et al. 1997, among others).

At present, rodents prevail in many herbivore niches in Southern South America, and have also adapted to insectivore and omnivore ones, which are usually occupied by different taxa in other continents (Redford and Eisenberg 1992). Ungulates, instead, are not well represented. One of the best examples of unsaturated faunas nowadays is in fact that of large herbivores in the Neotropics (Keast 1972). For instance, in spite of Africa and South America sharing some common features, there are 95 artiodactyl and perissodactyl species in the former and only 20 in the latter (Franklin 1982; Berta 1988).

Camelids have been the most important large herbivores since the end of the Pleistocene, given their ecological dominance. South American camelids differ from most North American ungulates in that the latter are rarely territorial, with the exception of endemic antelopes. On the other hand, unlike most territorial ungulates, whose territories are often based upon mating, South American camelids have a territorial system based upon feeding, which is quite exceptional (Franklin 1982, 1983).

**Mammalian predators**

The evolutionary history of the whole Order Carnivora is, as is that of herbivores, closely related to the emergence of the land bridge that linked South America to North America, with Pleistocene extinctions also playing a key role (Berta 1987, 1988; Marshall and Cifelli 1990). Berta (1988) has defined and compared the adaptive zones (after Van Valen 1971) of South
American carnivores on the basis of their body size and feeding specialisation, and subdivided them into guilds according to hunting strategies (after Keast 1977). These are:

- **Large to intermediate-sized carnivores, or ‘specialists.’** This adaptive zone is characterised by a decrease in diversity, especially as a result of the major Pleistocene extinctions of herbivore megafauna. In the Pleistocene, it included canids that were pursuit hunters and partially occupied the scavenging guild, and felids that were crouch-and-spring hunters. Nowadays only some of the latter are represented. It is noteworthy that at present South America lacks any counterparts for the large scavenging and hunting, bone-crushing hyaenids. Keast (1972) suggests that South America is today ecologically less sophisticated than Africa as regards its large carnivore fauna.

- **Large to intermediate-sized omnivores, or ‘generalists’** were not as severely affected by Pleistocene extinctions, largely due to the fact that the members of this adaptive zone did not depend on herbivore megafauna for feeding. Pleistocene representatives are a canid and some bears and procyonids, and today it is only represented by a canid and a bear.

- **Small-sized omnivores-carnivores** have been consistently diverse throughout the Pleistocene and Holocene, unlike other adaptive zones. They consist of small canids, as well as some felids, procyonids, and mustelids. Selection would have favoured those carnivores with omnivore, generalised teeth and, hence, more flexible feeding habits. This plasticity would have allowed them to adapt to significant changes such as those at the late Pleistocene.

At present, most carnivores in the Andean-Patagonian sub-region in particular belong to this last adaptive zone (Olrog and Lucero 1981; Berta 1988; Redford and Eisenberg 1992). They have been basically the same since the end of the Pleistocene, with few exceptions, notably the extinction of the fox *Dusycion avus* in Pampa-Patagonia, possibly in the Holocene (see Borrero 1997 and bibliography therein), and the introduction of the dog (*Canis familiaris*) at least by the Middle Holocene (Wing 1989).

One implication of unsaturated environments such as this is that competition among predators is not as intense (Pianka 1994), and this seems to have been the case in the Andean-Patagonian sub-region since the end of the Pleistocene. Solitary carnivores are another distinct feature in the area, unlike many regions in the globe where social carnivores are more common. All of these characteristics of the local predator community impinge on the particular way South American faunal communities are structured, and thereby, on human/animal interactions.

**HUMAN/ANIMAL INTERACTIONS**

*Interacting with prey*

Predator-prey relationships and their effects can be best understood in the long run. Humans evolved within the predator community in the Old World, and developed specific modes of interaction with the faunas. Under the physical, historical, and ecological conditions in South America described above, though, the interactions between human hunter-gatherers and their prey, and their co-evolution, would have assumed some particular characteristics.

Among such characteristics, the fact should be considered that while human hunter-gatherers would have been under *K*-selection in Eurasia before dispersing into the Americas (see Stiner 2002), as they entered these continents, the conditions would have been more favourable for
r-strategies (see Steele et al. 1998). K-selection, more common in stable or predictable environments, favors competitive efficiency, while r-selection, which predominates in unstable or unpredictable environments, favors reproductive efficiency (see Pianka 1994). K-selected organisms invest in the care of few offspring as the ability to compete successfully for limited resources is crucial, and they tend to live close to the environmental carrying capacity. Instead, r-selected organisms or r-strategists tend to reproduce more quickly, although each offspring is unlikely to survive to adulthood. The suggested dominance of r-strategies in entering the Americas relates to the obvious fact that the continent was devoid of humans, but also to other ecological properties, such as the increasing desaturation of the large herbivore and carnivore faunas in South America. We do not imply that a human demographic outburst should be expected, though, as factors other than intrinsic increase rates would have affected demographic parameters, namely those associated with very unstable environments. In this context, local extinctions of human groups would not have been uncommon (Borrero 1994–95).

Like other unsaturated communities, in which species tend to expand their niches (Pianka 1994), South America offered the conditions for a wider human diet breadth relative to available species richness, especially during the Holocene, as compared to other, more saturated contexts. That is, the conditions are given for amplified omnivory – yet it should be stressed that this is meant only in relative terms. Although still debated, some analyses suggest a rather generalised early subsistence in South America, which would provide some support to this expectation (Ardila Calderón and Politis 1989; Gnecco 1990; Dillehay 1997; Miotti and Salemme 1999; Borrero 1999; García 1999, among others).

Such a food niche breadth relative to local availability would have included both terrestrial and non-terrestrial animal items, such as small mammals, flying and non-flying birds, and aquatic resources such as fish, molluscs, and marine mammals, apart from other invertebrates and plant resources. Many of these resources, then, would not have been as subject to human predatory depletion, as part of their life cycles takes place out of the reach of human ranges. Furthermore, their feeding ecology partly relates to non-local primary production, implying an import or subsidy of energy that would otherwise not be available (see Yesner 1980; Schiavini 1993). Such is the case of migratory birds – which feed in different seasonal ranges –, and marine mammals – which not only feed upon coastal areas but also in extra-littoral ones. These observations are germane to South America since, as ungulates are not migratory here, their procurement by human hunter-gatherer populations can be more efficient (Binford 2001), and hence, they are more susceptible to hunting pressures.

Besides, if we consider the shape of the South American landmass, it becomes apparent that the ratio of coastal ecotones per terrestrial areas is very high in the Southern portion, which helps account for the importance of aquatic resources for some hunter-gatherer populations. As we mentioned, marine mammals are dominant over terrestrial ones in the Southern end of the continent, and long stretches of the coastal ecotones are very productive. The coastal perimeter of Southern South America thus implies the potential for an expansion of the human food niche so as to include marine resources in several areas. In such a scenario, the use of aquatic resources is not necessarily related to high human population densities, as is generally the case in ethnographic populations (Kelly 1995). Sites like those in Quebrada de los Burros (Lavallée et al. 1999) and Quebrada Tacahuay (deFrance et al. 2001) in coastal Peru, regarded as some of the oldest instances of maritime adaptations in the Western hemisphere, could be examples of this.
A relatively wide diet breadth relates to other aspects of hunter-gatherer populations, such as their mobility and other organisational dimensions. For instance, in Ancón-Chillón, Peru, sedentism seems to be associated to the exploitation of marine resources much earlier that the incorporation of cultigens (Göebel 1994). More generally, unlike trophic specialists, omnivores and generalists tend to reduce system stability (Binford 2001). This seems to have been the case in South America during the Holocene, where the archaeological record denotes a history of environmental transformations at different scales, not only environmentally but also anthropogenically induced (Stahl 1996).

Apart from food niche breadth and related organisational and ecological aspects, other dimensions of human/prey interactions call for some analysis. One of the most relevant aspects of the dispersal of Homo sapiens into South America relates to the fact that humans here reached the southernmost latitudes ever – until recent times, when sailing and energy-retention technologies allowed some settlements in the Antarctica. However, due to the effects of oceanity and the fact that there are no strongly marked latitudinal bands in South America, terrestrial faunal resources in the Andean-Patagonian sub-region share a distribution and broad ecological patterning that is not as tied to latitude as in Northern continents. For instance, in most of the area in the latitudinal range below the Tropic of Capricorn – for some 30 degrees of latitude –, the guanaco dominates the ungulate fauna in South America, while the same latitudinal range in North America – from the Tropic of Cancer to 55º N – exhibits a shift from the hot, dry Mexican deserts to the cold Canadian lands and its Hudsonian fauna. As a consequence, the conditions in Southern South America allow for a more generalised pattern of hunter-gatherer faunal exploitation throughout much of its latitudinal stretch, than under circumstances where structural properties of the continents favour ecosystems arranged into more distinct latitudinal bands and a higher incidence of continentality.

A higher degree of similarities in faunal exploitation can be expected not only across space, but also throughout the year, in comparison to settings at analogous latitudes with more seasonal regimes. One indication of this is the lower incidence of food storage in Southern South American ethnographic hunter-gatherer populations, compared to what would be expected on the basis of latitude alone (see Binford 2001 for a synthesis).

Conditions in much of the Andean-Patagonian sub-region are, therefore, favourable for more evenly forager strategies (sensu Binford 1980), in relative terms, as compared to North America and other landmasses. The factors conditioning the gradient from more forager to more collector adaptations with latitude are ameliorated here, and so can be human adaptations themselves: strategies in which consumers map onto resources can be more common. This seems to be the case of late Holocene pedestrian hunter-gatherers as far South as the Isla Grande de Tierra del Fuego. These groups would have had high residential mobility allowing them to exploit the sparse coastal and terrestrial mammals according to their abundance. These inferred forager strategies are consistent with other lines of faunal and non-faunal evidence (Muñoz 2004, 2005).

One exception to these conditions would be the Andean highlands, as altitude has effects analogous to those of latitude, prompting more collector strategies (see Aldenderfer 1998). This is further reinforced by the fact that for most of the history of human occupations much of these highlands have been desertic, with a patchy distribution of resources (Markgraf 1987). It should be noted that the Andean region includes not only the broken topography of mountains, where subsistence is usually costly (Gamble 1993), but also the high-altitude...
plateau to the East known as the Puna or Altiplano, which bears the effects of altitude without such a high habitat fragmentation as on the steeper slopes.

As species expand their activities and exploit many resources, as some human hunter-gatherers would have done in South America, the efficiency of exploitation may become relatively low (Pianka 1994). However, hunter-gatherers are able to exploit ungulates most effectively where they are territorial (Binford 2001), which is the case of camelids, generally the most common prey in arid South America. In fact, flexibility characterises the behaviour of both guanacos (Franklin 1983) and humans, and this combination may have been an advantage for the latter as they colonised hazardous environments, like the Southern tip of South America, at the end of the Pleistocene (also see Saxon 1979).

Camelids have been the staple animal resource throughout most of human history in an important part of the continent, and a co-evolutionary relationship developed, which eventually led to two domesticated species: the llama (Lama glama) and the alpaca (L. pacos), a process which appears to have occurred independently in different Andean areas (Browman 1989; Yacobaccio et al. 1994; Wheeler 1995). Different co-evolutionary trajectories have in fact taken place in South America between humans and camelids, both as wild prey (e.g., L’Heureux in press) – although under r-selection, human predators can be expected not to have been as selective on camelid prey as in those settings with stronger inter-specific competition –, and as domesticates (e.g., Reigadas 1992) – in which case stronger selection did take place.

As Pianka (1994) puts it, r-K selection is a continuum, and an organism’s position along it varies under different conditions in time and space. As the food niche widened, including more items of lower trophic levels, and demography increased, K-strategies would have become more common in human populations in South America. Among other consequences, K-selection leads to efficiency (Pianka 1994), which may have increased under these conditions.

**Interacting with other predators**

Humans have co-evolved not only with their prey, but also with other predators, and these interactions have also changed through time. Although according to Mayr (1997), humans occupy a whole adaptive zone by themselves, some overlap must be expected between it and those of other South American predators. If we follow the criteria used by Berta (1988), human hunter-gatherers would overlap to some extent with the large to intermediate-sized adaptive zones occupied by South American carnivores. Some observations seem to support this, such as those by Jorgenson and Redford (1993) on big cat populations in the Guayano-Brazilian sub-region which may decline as a result of competition with modern human hunter-gatherers. However, on the whole, inter-specific competition would not have been the rule in the history of human/carnivore interactions in South America. Human hunter-gatherers – being social predators, unlike most local carnivores – would not have had to customarily compete with carnivore packs, which is certainly a feature of the contexts in which Homo evolved. Also, it should be taken into account that as the continental fauna became unsaturated, especially in the Andean-Patagonian sub-region, competition can be expected not to have been as keen as in other continents. And just as carnivores seem to bear relatively low levels of inter-specific competition here, they also seem to compete little with humans, one of the most recent newcomers in the continental predator community. This has been observed, for instance, in modern and archaeological faunal assemblages in the Andean Puna (Mondini 2002). All of
this represents a particular arena in human evolution, with specific implications, of which we provide some examples here.

Competition has often been over-emphasised as a kind of interaction structuring communities. More recently, though, a critical light has been thrown over this kind of studies (e.g., Strong et al. 1984), aimed at showing that biologically-based patterns should not always be attributed to competition, but that other interactions between species can also help account for them. For instance, generalised symbiotic interactions such as commensalism can be as much or even more structuring than competition under some conditions.

There is a continuum between equilibrium and non-equilibrium communities (Wiens 1984), and non-equilibrium populations found in less diverse communities tend be below their maximum sizes, and to be less stable (Pianka 1994). Therefore, portions of such communities are often unsaturated with individuals, and inter- and intra-specific competition are commonly laxer. In these communities, it is the physical setting rather than the biotic interactions that demands adaptation; selection for rapid reproduction ($r$-selection) is strong, and relatively broad niches are common (Pianka 1994; also see Gamble 1993). Several characteristics of non-equilibrium communities, like density-independence and unsaturated habitats, in fact characterise South America, at least partially and/or temporarily. Models alternative to competition-centred ones, then, become germane for accounting for local faunal communities.

Even if classical community theory is still of much use, these alternative developments that have exposed the fact that several basic assumptions are not obligate should also be taken into account by archaeologists and anthropologists.

One instance in which this becomes particularly relevant is the fact that in the Andean-Patagonian sub-region the predator community is dominated by small-sized omnivores-carnivores. In the case of South American foxes in particular, for which scavenging is a rather important component of the diet – and human food refuse is an appreciated source –, commensalism is more relevant a concept than competition to describe the relationship of these animals to humans (Mondini 2002).

Interactions among human populations

Finally, it must be taken into account that human population densities would have increased with time. This would often have led to a shift from $r$- to $K$-selection in some hunting-gathering populations. This process would have been especially common in populations producing animal and plant foods: as they require smaller ranges and consume more resources at a lower trophic level, they can become denser. Even those communities that are not saturated with species can be saturated with individuals (Pianka 1994). Hence, regardless of the fact that inter-specific competition would generally not have been keen, intra-specific competition can be expected under some conditions as human demography increased. Other consequences of higher hunter-gatherer population densities are an intensification of commensalism between humans and scavengers, and the intensification of food procurement, eventually leading to the domestication of animal and plant species in several independent localities, which in turn may have favoured further population increases.

It should be stressed, however, that this was not an even trend throughout the continent, and while $K$-selection would have turned important in some areas during the Holocene, as seems to be the case in the Andes (e.g., Aldenderfer 1998), population densities would have
been kept low in many others, as in Fuego-Patagonia (e.g., Borrero 1994–95; see Scheinsohn 2003 for a synthesis at the continental scale).

Some taphonomic implications

These considerations on long-term human/animal interactions have some implications on the fossil record as well. One of the most outstanding ones is that the averaging of faunal assemblages accumulated by carnivores, which tend to be small in South America, with larger assemblages accumulated by humans would tend to result in the former ‘diluting’ into the latter, and hence becoming more analytically ‘invisible’ (Mondini 2005). This is in sharp contrast to the common situation in the Old World in which scanty hominid traces are intermingled in deposits largely formed by other predators.

Also, the fact that small carnivores with generalised teeth have been favoured in South America impinges on the chances of discriminating their traces from those of humans on fossil assemblages. Humans also produce tooth damage on bones and, given the characteristics of most local carnivores, the morphology of tooth marks by both agents would share some common features, which may turn these traces rather ambiguous regarding agency if not contextually analysed (Elkin and Mondini 2001).

CONCLUSIONS

In this chapter, a broad-scale analysis of the conditions under which long-term human/animal interactions would have taken place in South America has been presented, with a focus on the Andean-Patagonian sub-region. Very general expectations have been derived from such conditions, which are not intended to imply that such must have been the case in any particular instance. Rather, these expectations should be regarded as a model against which to compare the archaeological and ethnographic records. Moreover, divergences from this model can be read as interesting situations that call for further insight, usually from other sources, in order to account for them and, by placing limits to our generalisations, lead us to a deeper understanding of the long-term interactions of humans within the animal communities.

Human interactions with other members of the communities, including both prey and other predators, are potentially quite varied. Human/animal interactions have traditionally been studied with a focus on predation and, to some extent, competition, but other kinds of interactions, such as commensalism, can be as informative of past and present hunter-gatherers. Traditionally, an ethnographic or otherwise short-term perspective on human/animal interactions in South America has been common, which among other things has led to consider the ecology of human populations as static (see Bailey 1983). There are, however, very important exceptions to this approach, especially in the Southern Cone, which in fact have inspired some of the ideas in this paper (e.g., Borrero 1994–95; Stahl 1996). A long-term perspective involves actively taking into account the fact that human populations are part of larger communities that evolve in time (Behrensmeyer et al. 1992). Among other implications, this allows considering that the role of humans in communities mostly lacking other large social predators may entail important changes, and that the shifts from r- to K-selection as human populations became denser must have brought important consequences in their relationships to prey, to other predators, and among themselves. This approach allows
accounting for some variability in hunter-gatherers and their archaeological record that could otherwise remain unexplained.

The elements put together here comprise both some general principles embedded in concepts like unsaturation and the historic pathways that have shaped South American biotas generally and hunter-gatherer populations in particular, and can be used to construct historical narratives. This is one possible way of enriching a short-term perspective on human/animal interactions. It should be stressed that short-term studies are not inherently less powerful. Rather, short- and long-term perspectives can be fruitfully articulated (see Bailey 1983; Gifford-Gonzalez 1991; O’Connell 1995). In order to take full advantage of a long-term approach such as this, regionally relevant models should be advocated, which, by asking the questions at the appropriate time scale, deal with the particular ecological and historical properties of South America. This is not, however, a call for unique explanatory schemes. Instead, it is just an approach to long-term human/animal interactions in South America as an instance of the whole range of variability involved in the evolutionary history of hunter-gatherers, some of which is often not represented in other continents but is as relevant for understanding our history.

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