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INTERACTIONS BETWEEN HUMANS AND ENDEMIC CANIDS IN HOLOCENE SOUTH AMERICA

Peter W. Stahl

Humans inhabiting South America during early portions of the Holocene variably interacted with native foxes (Family Canidae) in different parts of the continent at a time when there is little firm evidence for the presence of domesticated dogs (Canis familiaris). Preserved specimens of native fox tend to be ubiquitous in early archaeological contexts for which we have associated archaeofaunal samples. In a few cases these include association with human interments. The foxes endemic to these regions are predisposed to broad-spectrum diets, opportunistic behaviors and a tolerance of a wide range of habitats, particularly in open settings with increased resource supply. This can underlie a tendency for fox species to habituate themselves to anthropogenic conditions and humans. Indigenous South Americans may have formed early, and at times intimate, connections with endemic canids which endure into the present.

Key words: Zooarchaeology, Early Holocene, South America, human-fox interactions

Los antiguos habitantes del continente sudamericano durante el Holoceno pueden haber variablemente afectado reciprocamente con las especies nativas de zorros (Familia Canidae) en diferentes partes del continente, a la vez que hay poca evidencia firme sobre la presencia del perros domesticados (Canis familiaris). Sin embargo, los especímenes preservados de zorro nativo tienden a ser ubicuos en contextos arqueológicos tempranos donde tenemos muestras arqueofaunísticas asociadas. En pocos casos incluyen asociaciones con entierros humanos. Los zorros endémicos son predispuestos a dietas de amplio espectro, tienen comportamientos decididamente oportunistas, y una gran tolerancia a variados hábitats, especialmente en zonas abiertas que cuentan con un creciente suministro de recursos. Esta puede ser la base de la tendencia que tienen las especies de zorro a habituarse a las condiciones antropogénicas y a los seres humanos. Los indígenas sudamericanos podrían haber formado una estrecha y temprana conexión con cánidos endémicos, la cual se ha mantenido hasta el presente.

Relatively few native animals were domesticated in the western hemisphere. These include the llama (*Lama glama*), alpaca (*Vicugna pacos*), cuy or Guinea pig (*Cavia porcellus*), turkey (*Meleagris gallopavo*), and Muscovy duck (*Cairina moschata*). It is curious that only the Muscovy duck may have been domesticated in the extensive lowland tropics of South America since many native cultivated plants likely originated in this biologically rich area (Clement 1999; Piperno and Pearsall 1998). Even the oldest domesticated animal, the dog (*Canis familiaris*), may have been absent throughout the Amazon basin and in some cases was not acquired until the 20th century (Koster 2009). Although some believe it accompanied early human populations into North America from Asia (Fiedel 2005), it is entirely possible that the domesticated dog was introduced into South America much later during the Holocene (Prates et al. 2009, 2010; Prevosti et al. 2009; Schwartz 1997). I explore the possibility that, in the absence of the domesticated dog, early South Americans may have interacted with native foxes at different times and places in various ways which might have assumed a range of symbiotic associations (*sensu lato*) encompassing commensalism, neutralism, and mutualism (Paracer and Ahmadjian 2000:6).

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Figure 1. Early South American Archaeological Sites Mentioned in Text.

My interest in the relationship between autochthonous canids and early human inhabitants of South America was first prompted by the association of a large sample of animal bones with the early Las Vegas culture of Ecuador's coastal lowlands. These bones were recovered from a number of related archaeological sites including the eponymous Las Vegas site (Figure 1), which was occupied during the Terminal Pleistocene/Early Holocene to Middle Holocene between 10,800 and 6600 years ago (Stohtert 1988). Although analysis of this large assemblage is still underway, preliminary data suggest that specimens of the small Sechuran desert fox (*Lycalopex sechurae*) dominate the sample, and some were recovered in direct association with human interments. Based upon previous analyses of small samples from Las Vegas (Byrd 1976; Chase 1988), Wing (1988, 1989) suggested the possibility that early humans had exercised control over endemic Sechuran fox, which may have been amenable to taming and could have fulfilled a similar role to that accorded to domestic dogs. The local abundance and context of fox bones is highly unusual in Ecuadorian archaeology, but perhaps less so when understood in the broader context of contemporaneous occupation sites throughout the continent.

Table 1. Endemic Native Canids of South America.

Scientific name	Common name	Geographical distribution
<i>Atelocynus microtis</i>	Short-eared dog	Western lowland South America
<i>Cerdocyon thous</i>	Crab-eating fox	Northern South America to Argentina
<i>Chrysocyon brachyurus</i>	Maned wolf	Central Brazil to northeast Argentina
† <i>Dusicyon australis</i>	Falkland Islands wolf	Falkland Islands
<i>Lycalopex culpaeus</i>	Culpeo	Colombia to Tierra del Fuego
<i>Lycalopex fulvipes</i>	Darwin's fox	Chiloe Island
<i>Lycalopex griseus</i>	S.A. gray fox	Chile to northern Tierra del Fuego
<i>Lycalopex gymnocercus</i>	Pampas fox	Grasslands of Southern Cone
<i>Lycalopex sechurae</i>	Sechuran fox	Southwest Ecuador, northwest Peru
<i>Lycalopex vetulus</i>	Hoary fox	Brazilian Highlands
<i>Speothos venaticus</i>	Bush dog	Forested lowlands to southern Brazil
† <i>Canis avus</i>	Extinct canid	Southern South America

†extinct

At least since Junius Bird's 1935 excavations at Cañadón Leona in southern Chile, where he recovered fox jaws in every level of Shelter 5 (Bird 1988:60), specimens of native fox have regularly appeared in the earliest South American archaeological contexts for which we have associated archaeofaunal material. Archaeologists have long speculated about the interactions between ancient humans and native foxes, and the formation of relationships that may have ranged along a continuum from predation to competition, commensalism, control, and possible taming (e.g., Clutton-Brock 1977; Mengoni Goñalons 1987:64; Miotti and Salemme 1999:60; Mondini 2000, 2002, 2004).

Although the supporting archaeological evidence is often equivocal, I suggest that lacking an allochthonous domesticated dog, early humans may have interacted with native foxes, possibly entering into a range of symbiotic relationships at different times and in different parts of the continent. My presentation begins with a brief review of the South American Canidae. I next examine the literature on canid specimens recovered from the earliest archaeological contexts in South America. I argue that based upon current data there is little firm evidence for the presence of domesticated dogs on the continent during the Early Holocene. The identification of domesticated dog specimens from earlier contexts has either already been revised or should be re-examined. However, native fox specimens are ubiquitous in most of the ancient contexts for which we have associated archaeofaunal materials and, in a few cases, are associated with human interments. This is followed by a discussion of how at least some of the native foxes commonly identified in association with early archaeological deposits are regularly inclined to habituate to humans. I raise the possibility that early human populations may have entered into enduring relationships with native foxes and that in some cases these types of relationships are present today. I conclude by offering some thoughts on why domesticated animals in general may have been missing from large portions of lowland South America.

Native South American Canids

Members of the family Canidae (Table 1) have been present in South America at least since the Plio-Pleistocene, and contemporary canids on the

continent include two genera of wolf-like species (*Chrysocyon* and *Speothos*) and three genera of foxes (*Atelocynus*, *Cerdocyon*, *Lycalopex*) (Berta 1988; Langguth 1975; Slater et al. 2009; Wang et al. 2004). The relatively large maned wolf (*Chrysocyon brachyurus*) is a solitary opportunist that forages nocturnally in permanent territories throughout the interior grasslands and scrub forests of central Brazil and ranged formerly into northern Argentina (Dietz 1985). The small bush dog (*Speothos venaticus*) is a highly carnivorous denizen of forests and lowland habitats ranging from Panama to southern Brazil where it is known to hunt cooperatively (Beisiegel and Zuercher 2005).

Depending upon which classification is used, upwards of nine species of native fox are assigned to as many as four genera, if we count the now extinct Falkland (Malvinas) Islands wolf (*Dusicyon australis*) (Clutton-Brock et al. 1976; Macdonald and Sillero-Zubiri 2004; Nowak 2005; Wang et al. 2004; Wozencraft 2003). The literature applies different taxonomic synonyms to the most species-rich genus (*Dusicyon*, *Lycalopex*, *Pseudalopex*); phylogenetic resolution is hindered by a shared primitive morphology. I follow Wozencraft's (2003) classification but refer throughout this paper to the designations used by different authors.

The medium-sized short-eared dog (*Atelocynus microtus*) is a solitary generalist scattered around western lowland Amazonia where it has been reported in a wide range of habitats (Leite Pitman and Williams 2004). The crab-eating fox (*Cerdocyon thous*) is a relatively common medium-sized solitary and omnivorous fox which feeds opportunistically in different habitats throughout northern South America and south of Amazonia to northern Argentina (Courtenay and Maffei 2004). The culpeo (*Lycalopex culpaeus*) is a large fox found in a wide range of habitats from sea level to high elevations, from southern Colombia to Tierra del Fuego. An opportunistic predator, the culpeo incorporates more vertebrates into its diet than most native canids, and although solitary, can be abundant in disturbed habitats where rodent prey is plentiful (Novaro 1997). Darwin's fox (*Lycalopex fulvipes*) is a tiny, stout canid endemic to the forests of Chiloe Island and the adjacent mainland where it forages opportunistically and in solitude on a wide variety of foods (Jiménez and McMahon 2004). The *chilla*, or gray fox, (*Lycalopex griseus*) is a small and locally common omnivorous generalist widespread on both sides of the Andes, especially in shrubby and open areas, from northern Chile to Tierra del Fuego where it was introduced in 1951 (González and Rau 2004). The pampas, or Azara's fox, (*Lycalopex gymnocercus*) is a relatively common medium-sized omnivore of the Southern Cone grasslands where it is a solitary and opportunistic generalist (Lucherini et al. 2004). The Sechuran fox (*Lycalopex sechurae*) is a tiny omnivore endemic to southwestern Ecuador and northwestern Peru where it forages opportunistically at night in open and disturbed habitats (Asa and Cossíos 2004). The hoary fox (*Lycalopex vetulus*) is confined to the dry and open habitats of central Brazil and adapts readily to agricultural lands where it forages nocturnally for insects and small vertebrates (Dalponte and Courtenay 2004). Important characteristics shared by endemic foxes, including an inclination toward broad-spectrum diets, opportunistic behavior, and tolerance of wide-ranging habitats, especially open settings with increased resource supply, underlie a tendency to habituate to anthropogenic conditions and humans. I return to this issue after I present the archaeological record of early canids in South America.

The Archaeological Record of Early Canids in South America

Preserved canid skeletal specimens have been recovered and identified in most of South America's earliest archaeological sites for which we have associated archaeofaunal samples (Table 2). The restricted geographical distribution of these contexts is potentially skewed by differential preservation and our limited archaeological knowledge of the continent. The relative frequency of canid skeletal specimens is typically low, and in some assemblages their presence cannot be unequivocally attributed to past human involvement. In this regard, Mondini (1995, 2002) has suggested that although local carnivores may not have played an important role in early faunal accumulation, their contribution to archaeological assemblage formation cannot be entirely ruled out, particularly at sites of early deposition that were alternatively occupied by humans and carnivores.

For example, two early fox (*Dusicyon*) bones are reported from Zone H at Pikimachay Cave in highland Peru, which is believed to date between 16,000 and 14,000 BP (MacNeish 1979:7). However, the integrity of these Ayacucho phase associations and their archaeological significance remain uncertain (e.g., Dillehay 2000:175–176). In some contexts, archaeological fox specimens yield no definite signatures implicating human involvement, whereas others display multiple signs of cultural and non-cultural modification (e.g., Borrero 2003, 2009; Mazzanti and Quintana 1997; Miotti and Salemme 1999). A further problem is the reliability of identifications, which is often a complex matter involving differential preservation and fragmentation, the diagnostic acuity of a preserved specimen, and the strong similarities shared amongst biologically related living and extinct animals. This problem is perhaps most acute when dealing with the early appearance of domesticated dogs on the continent and is treated separately below.

One point clearly emerges from the identifications listed in Table 2: canid bone specimens are regularly associated with buried contexts from the earliest Holocene archaeological sites. In some cases zoological resolution is ambiguous; specimens are identified as indeterminate Canidae, or simply as dog or fox. Nevertheless, beginning as early as the mid-twelfth millennium BP at Cueva Lago Sofía in southern Chile and continuing into subsequent millennia during early portions of the Holocene in Chile, Argentina, Peru, Ecuador and Colombia, specimens of native fox appear to be regularly associated with the earliest archaeological contexts for which we have associated archaeofaunal specimens. It is also interesting to consider that with a few exceptions, most specimens identified as domesticated dog tend to be associated with later contexts, possibly no earlier than around 7000 BP (Table 2).

Earliest Appearance of the Domestic Dog in South America

Dog domestication is likely very ancient in Eurasia, and later introduction of the dog into North America establishes a context for evaluating its pre-Columbian appearance in South America. Recent morphometric and molecular genetic evidence suggests the likelihood that domesticated dogs in North

Table 2. Early Post-Pleistocene Canid Identifications with Dated Associations in South America.

Site	Reported canid taxon	Earliest date (BP)	References
Pikimachay (Zone H)	<i>Dusicyon</i>	16,000-14,000?	MacNeish 1979
Cueva Lago Sofía 1	<i>Dusicyon avus</i>	11,575 ± 60	Borrero 2009; Casamiquela 1996–1997
Quereo	<i>Dusicyon, Dusicyon avus</i>	>11,000	Casamiquela 1996–1997; Jackson 2003
Tagua Tagua	<i>Dusicyon culpaeus, Canis</i>	11,380 ± 320	Casamiquela 1996–1997; Montané 1968; Palma 1969
Casa del Minero 1	Canidae, <i>Dusicyon avus</i>	10,999 ± 55	Borrero 2009; Paunero 2003
Myloodon Cave	Fox, Dog, <i>Dusicyon avus</i>	10,832 ± 400	Bird 1988; Casamiquela 1996–1997; Caviglia 1985
Chobshi Cave	<i>Canis cf. familiaris</i>	10,615 ± 90	Lynch and Pollock 1981
Tres Arroyos (TA1)	<i>Dusicyon avus</i>	10,575 ± 65	Arroyo-Kalin 1998; Borrero 2003, 2009; Caviglia 1985; Mengoni-Goñalons 1987
Paso Otero 5	<i>Dusicyon gymnocercus</i>	10,450	Gutiérrez and Martínez 2008; Miotti 1999
Cueva Tixi	<i>Dusicyon avus, Lycalopex gymnocercus</i>	10,375 ± 90	Borrero 2009; Gutiérrez and Martínez 2008; Martínez and Gutiérrez 2004; Mazzanti and Quintana 1997; Miotti 1999
Cueva del Puma	<i>Dusicyon avus</i>	10,345 ± 75	Borrero 2009
Fell's Cave	Canidae, <i>Dusicyon culpaeus, Dusicyon griseus, Canis familiaris</i>	10,180 ± 160	Bird 1988; Clutton-Brock 1988; Caviglia 1985; Caviglia et al. 1986; Mengoni-Goñalons 1986
Las Vegas	Canidae, <i>Dusicyon</i>	9800 ± 100	Stohtert et al. 2003
Cueva Arroyo Feo	<i>Dusicyon griseus</i>	9330 ± 80	Mengoni-Goñalons 1986
Cueva de Las Manos	<i>Dusicyon griseus</i>	9320 ± 90	Mengoni-Goñalons 1986
Las Buitreras	Canidae, <i>Dusicyon avus</i>	9100	Borrero 2009; Caviglia 1985; Caviglia et al. 1986
Uhcumachay	<i>Dusicyon culpaeus</i>	9000?	Wheeler Pires-Ferreira et al. 1976
Baño Nuevo	<i>Dusicyon avus, Pseudalopex culpaeus</i>	8880 ± 50	Mena et al. 2003; Trejo and Jackson 1998
Los Toldos (Toldense)	Canidae, <i>Dusicyon</i>	8750 ± 480	Cardich et al. 1977; Mengoni-Goñalons 1986
Palli Aike	Canidae	8639 ± 450	Bird 1988
Arroyo Seco (2)	<i>Pseudalopex gymnocercus, Chrysocyon brachyurus, Canis</i>	8558 ± 316	Fidalgo et al. 1986; Gutiérrez and Martínez 2008; Politis 1986
Cañadón Leona (5)	Canidae	8500	Bird 1988
Campo Laborde	<i>Dusicyon</i>	8080	Politis and Messineo 2008
Nemocón	Fox	7530 ± 100	Correal Urrego 1986
Panaulauca	<i>Canis familiaris</i>	7500?	Wheeler Pires-Ferreira et al. 1976
Uhcumachay	<i>Canis familiaris</i>	7500?	Wheeler Pires-Ferreira et al. 1976
Pachamachay	<i>Canis familiaris</i>	7500?	Wheeler Pires-Ferreira et al. 1976
Lauricocha	<i>Canis familiaris</i>	7500?	Wheeler Pires-Ferreira et al. 1976
Los Toldos (Casapedrense)	<i>Canis familiaris</i>	7260 ± 350	Cardich et al. 1977; Caviglia 1985, Tonni and Politis 1981
El Abra	<i>Canis</i>	7000?	Ijzereef 1978
Puente	<i>Dusicyon, Dog?</i>	6900	MacNeish and Vierra 1983
Telarmachay	<i>Canis familiaris</i>	6800	Wheeler 1985
La Moderna	<i>Canis familiaris</i>	6550 ± 160?	Politis 1986

America are descended from Middle Eastern grey wolves (*Canis lupus*) that had been subjected to multiple ancient domestication or breeding events both in the Middle East and in different parts of Europe (Germonpré et al. 2009; Gray et al.

2010; von Holdt et al. 2010). Competing genetic claims suggest colonization by at least five founding dog lineages related to a common ancestral Pleistocene grey wolf (*C. lupus*) from East Asia (Leonard et al. 2002; Savolainen et al. 2002). Regardless, the earliest currently accepted domestic dog specimens in North America were recovered from contexts at Danger Cave in Utah dating between 9000 and 10,000 BP (Grayson 1988; Morey 2010:105), and at the Koster site in Illinois dating to around 8500 BP (Morey and Wiant 1992). Recent evidence from coprolite contents directly dates the domestic dog to 9260 ± 170 BP at Hinds Cave in southwestern Texas (Tito et al. 2011). Although the domestic dog has been identified in some coeval early South American deposits, its antiquity is controversial.

Domestic dogs were clearly present in pre-Columbian South America; however, their earliest appearance may have been relatively late (Prates et al. 2009, 2010; Prevosti et al. 2009; Schwartz 1997), and in large portions of the continent they were apparently absent until quite recently. In parts of Amazonia the domestic dog was not acquired until the 20th century (Koster 2009). An ancient appearance of domesticated dogs in South America is difficult to substantiate because valid identification from bone specimens preserved in very old contexts can be problematic. Overall, canid skeletal morphology tends to be relatively conservative, domestication has introduced an enormous size variation, and many canids are capable of interbreeding. The specific osteological criteria that we use to distinguish domestication are found in the head and teeth, and regularly require examination of multiple characteristics on relatively intact specimens. In the absence of ancient biomolecular evidence, a relatively indeterminate identification is the only credible interpretation that can be made from a single, isolated and often fragmentary specimen, particularly when it originates from a less diagnostic portion of the skeleton (Lawrence 1968; Lawrence and Bossert 1967, 1975; Meadow 2000; Morey 1985, 1992; Nowak 1979; Olsen 1985).

Another problem in identifying early domestic dogs is possible confusion with morphologically similar, but extinct taxa. This issue may have arisen in at least some of the purportedly earliest archaeological sites from southern South America. The earliest positive identification of domesticated dog in South America was made from the deepest cultural units at Fell's Cave. Based upon examination of preserved skulls and teeth, Clutton-Brock (1988) identified two endemic fox species and the domestic dog. Most of the material was attributed to *D. culpaeus*, with one specimen identified as *D. griseus*; 18 specimens bore a much closer resemblance to *Canis* than to *Dusicyon*, and under the assumption that no species of *Canis* was indigenous to Patagonia, domestic dog was inferred. However, Clutton-Brock (1988:194) acknowledged earlier unpublished identifications by Alfredo Langguth, which include both endemic fox species and an extinct *Canis avus* (see also Amorosi and Prevosti 2008; Bird 1988:184–186; Caviglia et al. 1986:304). She suggested the need for further research as well as the possibility that the domestic dog specimens may be post-Columbian intrusions.

Canis (Dusicyon) avus is a large and robust canid described on the basis of a Pleistocene cranium from Buenos Aires province, Argentina (Berman and Tonni 1987). Salient contrasts with domestic *Canis* are found primarily in dental

morphology. *C. (Dusicyon) avus* is commonly identified in early archaeological deposits (Table 2). It is also identified in various Late Holocene contexts (Prates et al. 2009; Prevosti et al. 2011), such as Zanjón Seco (Politis 1986; Tonni and Politis 1981) and Lobería 1 (Tonni 1985), which are both in the same area from which it was originally described. Little can be said about the habits of extinct *Canis avus* other than that its larger size, relatively robust morphology and dental characteristics suggest the possibility of a heightened orientation toward carnivory (Berman and Tonni 1987). Researchers speculate that hybridization with introduced domestic dogs, environmental change, or perhaps human population increase led to its extinction (Berman and Tonni 1987; Borrero 2003, 2009; Miotti and Salemme 1999; Prevosti et al. 2011).

Reexamination of diagnostic material from a variety of the earliest southern South American archaeological contexts, including Fell's Cave, suggests that *C. (Dusicyon) avus* coexisted with recent endemic foxes. Moreover, the identification of this extinct canid in archaeological context requires a broader revision of early domestic dog discoveries, including the later Casapedrense identification at Los Toldos (Caviglia 1985; Caviglia et al. 1986; but see Tonni and Politis 1981). Outside of the Southern Cone, it is informative to note that most of the specimens identified as domesticated dog were recovered in later contexts mainly in the Andes to the north. For the most part, these are poorly described and isolated specimens that should remain only tentative identifications of domesticated dog pending further study. The Chobshi Cave specimen is an unspecified tooth recovered from deposits variably dated between 10,000 and 7500 BP. Although its identification as *Canis* is unconfirmed, it was compared to domestic dog (Lynch and Pollock 1981). The early Peruvian specimens are also problematic. An isolated specimen at Telarmachay remains unspecified (Wheeler 1985:67) and identification of domestic dog at Uchcumachay is based upon an axis vertebra and canine tooth associated with deposits indirectly dated through typological similarities with dated contexts at other sites. The unspecified elements from Panaulauca, Pachamachay and Lauricocha derive from similarly dated deposits (Wheeler Pires-Ferreira et al. 1976). Domesticated dog was very tentatively identified at El Abra on the basis of two unspecified specimens from vaguely described contexts which appear to represent over four millennia of occupation beginning some 7,000 years ago (Ijzereef 1978). Whether future study confirms these identifications or not, it remains interesting to consider that the available archaeological evidence appears to suggest a later appearance of domesticated dog following a long, ubiquitous, and in at least a few cases, possibly intimate association of humans and endemic fox in South America.

Humans and Native Canids in Early South American Burial Contexts

The Early to Middle Holocene Las Vegas culture of western Ecuador, which originally prompted my interest in the possibility of an ancient relationship between humans and native fox, provides the largest sample of human interments from an early context in the Americas. At the Las Vegas type site (OGSE-80), skeletons of at least 192 individuals were recovered as primary single burials and both small and massive secondary burials. Soil conditions often made it difficult to distinguish grave inclusions from fill, however, a variety of scarce

and unique grave offerings were encountered, including secondary single human bundle interments, tools and adornments fashioned from marine shells, heaps of stones and shells, ochre pigment, stone tools, and mammalian teeth. In particular, teeth and dentary and maxillary bones of the small Sechuran fox (*L. sechurae*) were associated with at least three burial features (Stoother 1988). Over 2700 fox bones and teeth, or more than 10% of the identifiable mammal bone were recovered from OGSE-80, an unusually high number of specimens for this taxon in any context. Moreover, fox specimens are also very common at a number of associated Las Vegas sites in the immediate area.

The ancient association of human interments with fox bone specimens at OGSE-80 is not an isolated occurrence. At Cueva Baño-Nuevo-1 in the Aisen region of Chile, *Pseudalopex (Lycalopex) culpaeus* specimens were identified in cave deposits which also included at least three human burials directly dated to 8850 ± 50 BP and 8880 ± 50 BP. Fox post-cranial specimens were found with all the burials, and a cut-marked dentary identified as *P. culpaeus* was clearly associated with human burials (Mena et al. 2003; Trejo and Jackson 1998). Site 2 of Arroyo Seco, near Buenos Aires, also yielded many single and individual burials, with one skeleton from the site's lower component yielding a direct date of 8558 ± 316 BP. Three skeletons included grave offerings of perforated canine teeth, and one infant was buried with a possible necklace of over 150 perforated teeth. Although canine teeth are not highly diagnostic for zoological identification, their size and morphology most probably implicate *P. gymnocercus* and perhaps *Chrysocyon brachyurus* (Fidalgo et al. 1986; Politis 1989).

To summarize the limited archaeofaunal evidence we have to date for early canids in the South American archaeological record, canid bone specimens tend to be ubiquitous associations in Early Holocene contexts. Nevertheless, there are no convincing data to support the identification of domestic dog on the continent certainly prior to 7000 BP. In their absence, the association of endemic canids, particularly foxes, is provocative. Although they were likely never domesticated, particularly in similar ways to that of dogs, the endemic South American foxes display behaviors that readily habituate to humans and anthropogenic settings.

Fox Behavior and Habituation to Humans

The endemic South American foxes comprise a highly variable canid assemblage sharing a number of important behavioral characteristics, particularly among those species frequently associated with early archaeological contexts. The extant South American fox species associated with ancient deposits, culpeo (*L. culpaeus*), chilla (*L. griseus*), Pampas fox (*L. gymnocercus*), and Sechuran fox (*L. sechurae*), are carnivores inclined toward increased omnivory. All are to some extent generalists who incorporate variable and often significant amounts of plant food into their diet. The culpeo is the most carnivorous but opportunistically adjusts to local conditions. Indeed, opportunism is a strongly shared characteristic amongst these species as they adjust their dietary preferences and timing of activity to local and seasonal conditions. They are comfortable in a range of habitats but prefer open settings, and tolerate anthropogenic disturbance, particularly where it increases local resource supply (Asa and Cossío

2004; Asa and Wallace 1990; González del Solar and Rau 2004; Huey 1969; Jiménez and Novaro 2004; Langguth 1975; Lucherini et al. 2004; Novaro 1997; Novaro et al. 2004). These flexible dietary and behavioral characteristics underlie a tendency for fox species to habituate to anthropogenic conditions and humans.

Records of docile wild South American foxes, captive maintenance, and even taming as pets are relatively common (e.g., Birdseye 1956; Cossíos 2004; Lucherini et al. 2004). Similar observations have been made for island species, such as Darwin's fox (*L. fulvipes*), which habituates to park visitors through uncontrolled feeding (Jiménez and McMahon 2004). California's endemic island fox (*Urocyon littoralis*) is credited with a docile nature. An opportunistic generalist like its South American counterparts, the island fox demonstrates little fear of humans, displays submissive behavior when grasped, and is easily tamed. Island foxes were important for indigenous groups who may have kept them as semi-domesticated pets. Preserved specimens are identified at many archaeological sites and have been recovered from intentional interments (Moore and Collins 1995; Rick et al. 2009; Roemer 2004; Vellanoweth et al. 2008:3120–3122).

The extinct Falkland Island wolf (*Dusicyon australis*), originally described by Darwin as the only indigenous mammal on islands located some 500 km from mainland Argentina, is today known only through museum specimens. While certain features suggested that it was either a relic domesticated native *Dusicyon* or a feral *Dusicyon/Canis* cross, DNA recovered from museum skins indicated genetic distance from *Dusicyon* and closer affinity with *Canis* (Clutton-Brock 1977; 1995), suggesting in either case that humans transported domesticated canids to the islands. However, recent nuclear and mtDNA analyses suggest its closest living relative was the South American maned wolf (*Chrysocyon brachyurus*) although it may prove to be even more closely related to the morphologically similar extinct *Canis (Dusicyon) avus* (Slater et al. 2009). On the mainland, Lt. Col. Charles Hamilton-Smith (1839), who travelled extensively in the western hemisphere during the early nineteenth century, described the local *aguara* dogs. These were entirely habituated hunting dogs used by indigenous people, and were either domesticated from endemic canids or were hybrid crosses between endemic foxes and the preferred European domesticate which gradually replaced them (Hamilton-Smith 1839:246–248). Numerous accounts from northern South America also refer to tamed wild canids that were crossed with domesticated dogs to produce hybrid hunting dogs (e.g., Cabrera and Yepes 1960:130; Civrieux 1980; Gilmore 1950; Im Thurn 1883; Latcham 1922; Linares 1987; Roth 1922).

The most celebrated example of habituation between foxes and humans did not take place in South America, but involved the controlled breeding of silver fox (*Vulpes vulpes*) undertaken by Belyaev and his co-workers beginning in 1959. Selection for individuals solely on the basis of behavior has led to characteristics associated with domesticated animals in only 10 generations, and after 40 years, or 30 to 35 generations, has created "unmistakably domesticated" animals (Trut 1999:163). The controlled breeding of tamable foxes that readily accepted hand-offered food, permitted petting and handling, and exhibited tail wagging and whining, rapidly produced developmental and physical changes in subsequent generations. These included juvenile delayed fear response and earlier eye

opening, loss of pigment, facial star patterns, floppy ears, rolled tails, shorter tail and legs, and malocclusion – all classic characteristics of domesticated canids (Trut 1999).

It is possible that early dog domestication took such a route. Coppinger and Coppinger (2001) outline the plausible development of a commensal relationship between humans and certain dogs which responded opportunistically to anthropogenic conditions rather than through avoidance. Individuals that are tamer and bolder would gain a selective advantage by exploiting a new and potentially attractive niche that provided increased feeding opportunities, reproductive success and injury avoidance. Self-domestication could have conceivably taken place as tamer canids began to separate into populations exhibiting less “flight distance” than their naturally wary counterparts. Increasingly isolated populations of tamer individuals began to change in shape as they accommodated a new scavenging niche. This could involve heterochrony or simple changes in the timing of growth processes. Belyaev’s experiments clearly demonstrate that this can be achieved through selection for behavioral traits. Coppinger and Coppinger (2001) suggest that Belyaev’s experiments demonstrate a process of canid domestication they call “Heterochronic Retarded Neotonic Development” in which juvenile shapes and care-soliciting behaviors are retained in the adult animal. This form of paedomorphosis in which juvenile traits are retained by adults has appeared in many kinds of domesticated animals, including domestic dogs (Morey 1994).

Discussion and Conclusions

The earliest archaeological record from South America clearly indicates a widespread association between human habitation and endemic canids. Most contexts do not yield sufficient evidence to infer why fox specimens had accumulated in association with ancient human refuse. However, some had obviously been fashioned into adornments, and in at least three geographically distant locations of southwestern Ecuador, eastern Argentina, and southern Chile were intentionally included with human interments. Moreover, although the data remain unclear at this point, it seems that the domesticated dog appeared on the scene later in the Middle Holocene. Although endemic foxes may never have been fully domesticated at any time in antiquity, it is entirely conceivable that in the absence of an allochthonous domesticated *Canis familiaris*, humans may have developed some sort of symbiotic relationship with foxes.

Such a relationship might be characterized as a form of unconscious selection with no intention of altering the animal (Rindos 1984:86). Some tamer foxes may have increased their survival chances through an enhanced ability to exploit anthropogenic niches; in some cases certain individuals may have been tolerated and preserved by humans. Less tame individuals with decreased ability to exploit new niches may have been dispatched as prey or undesirable pests. It is questionable as to whether this would constitute a true form of coevolution which would modify each partner species (Coppinger and Coppinger 2001:159), as only one (or neither) of the participants may have actually changed. Nonetheless, the human burials associated with intentionally interred endemic

fox specimens suggest that in some instances the relationship was more than simple one-sided commensalism, and possibly one of mutualism in which both parties derived benefit.

The intimate connection between endemic canids and early indigenous South Americans is but one example of a temporally deep and global relationship between humans and foxes (e.g., Maher et al. 2011; Uther 2006). Archaeological evidence attests to an enduring relationship throughout the subsequent millennia, particularly along the continent's Pacific coast where foxes are prominently featured in pre-Columbian ceramic art (e.g., Donnan 1976:106) and *L. sechurae* appears in human interments (Bourget 2006:26; Strong and Evans 1952:154). Today shamans still use foxes to heal, divine and attract good spirits (Asa and Cossío 2004:71; Cossío 2004:136). Throughout wide portions of South America, the fox persists as a lasting symbolic element in contemporary indigenous thought, particularly as it relates to curing, divining, seasons, crop success, and mythic origins (e.g., Benfer et al. 2011; La Barre 1951; Lévi-Strauss 1973; Urton 1985; Zuidema 1985).

Unlike the gregarious wolves and other canids that are inclined to live in hierarchically organized packs, foxes tend to be relatively solitary animals. When manifested, their minimal sociality most often coincides with procreation. This characteristic alone would be a major stumbling block in the way of full domestication on a continent where relatively few animals were domesticated. However, cultural attitudes like those shared by contemporaneous indigenous cosmologies in the Amazon that govern the relationships between humans and animals are more probable grounds for why humans did not enter into fully domesticated associations. Pálsson (1996) presents a paradigm of communalism which rejects any radical separation of society and nature and thereby stands in contrast to those which advocate human mastery over the wild. An emphasis on contingency, dialogue and entrance into personal relationships with animals as social beings, is strongly characteristic of Amazonian intellectual systems that include forms of animism and perspectivism that see non-humans as entities possessing human qualities (Descola 1992, 1996, 2001; Santos-Granero 2009; Viveiros de Castro 1992, 1998).

Hunting can be very problematic for cultures that consider potential prey to be similarly endowed with human and social qualities. Resolving this dilemma and compensating for loss of life between humans and non-humans can be realized within different relational modes: reciprocal predation in which non-humans as persons can enact revenge; reciprocal exchange of souls or services between equivalent life forms; and, protection of non-humans through dependency on humans, an option which is seldom associated with animic systems (Descola 1996). Nevertheless, various wild animals are regularly tamed by Amazonian peoples. This might be considered a process in which humans familiarize the other, thereby diminishing spatial and cognitive distance between similarly endowed beings through negotiation, coercion, seduction, etc. (Descola 2001; Fausto 1999; Lagrou 2009). Although familiarized animals are often the orphaned young of game animals acquired through human predation, once familiarized, they are no longer considered the same category of "being" (Erikson 2000). A familiarized animal is no longer a game animal, and it becomes

inedible as part of a contractual relationship between a human who see animals as animals and animals who see animals as humans (Viveiros de Castro 1998). At times human kinship terms are extended to familiarized animals (e.g., Cormier 2002, 2003), and in this sense they could be seen as “humanized.” This form of familiarization is not an incipient step toward domestication but an expression of predation in a symbolic universe where fundamental relations between humans and non-human others preclude attempts at domestication (Descola 2001:111; Erickson 2000:22). According to Hugh-Jones (2001:246), the absence of domestication has less to do with opportunity than with a prevailing concept of appropriate relations between animals and humans in which “true domestication is probably something more inconceivable than impossible.” Although species of endemic fox may never have been domesticated in the sense that domestic dog were in other places and times, the archaeological record suggests an intimate and enduring relationship with humans.

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