Mammalian Biology (2021) 101:387–406
https://doi.org/10.1007/s42991-021-00129-y

ORIGINAL ARTICLE

Human-canid relationship in the Americas: an examination of canid biological attributes and domestication

Valentina Segura[1] · **Marcelo R. Sánchez-Villagra**[2]

Received: 29 October 2020 / Accepted: 29 April 2021 / Published online: 19 May 2021

Abstract

Nineteen species of wild canids interact with humans in the Americas in different ways. The zooarchaeological record of burials, shifts in diet, abundance at sites, and ethnological information document the various kinds of interactions of canids and humans in the Americas. However, none of these native canid species has been domesticated. To understand past and present interactions of canids and humans, and explore the biological attributes of native canids (diet, gestation length, occurrence in captivity, temperament, social system, weight, activity pattern, and relative abundance) in view of their suggested potential for domestication, we selected 163 publications from the zooarchaeological record and ethnological sources from the Americas. The compilation ranged between the years 1823 and 2021. The two species with the highest domestication potential based on their life history, social system, and diet are *Canis latrans* and *Speothos venaticus*. For the domestication of a canid species to occur, it is necessary to have the biological attributes to facilitate the process, and for the (human) potential domesticator the worldview consistent with this practice. The latter likely explains the lack of domesticated canids in the Amazon region.

Keywords *Speothos* · *Canis* · *Cerdocyon* · *Chrysocyon* · *Lycalopex* · *Dusicyon avus* · Taming · Anthropology · Life history

Introduction

Only a few endemic vertebrate animals were (and still are) domesticated in the Americas: among birds the Muscovy duck *Cairina moschata* in the Amazon region, and the turkey *Meleagris gallopavo* in areas of what is today Mexico and the southwest US, and among mammals the llama *Lama glama*, alpaca *Vicugna pacos*, and the guinea pig or cui *Cavia porcellus*, all in the Andean region (Stahl 2008; Larson and Fuller 2014). The oldest mammal to be domesticated, the dog (*Canis familiaris*), has been on the continent from about at least 10,000 years before present (ybp), as the zooarchaeological record and ancient DNA studies confirm (Leathlobhair et al. 2018; Perri et al. 2019, 2021). Examples of these ancient dogs are Stilwell II (10,190–9,630 ybp, Illinois; Perri et al. 2019) and Koster (10,130–9,700 cal bp, Illinois; Perri et al. 2019) from North America. Dogs probably accompanied early human populations into North America from Asia before 15,000 ybp (Stahl 2012; Van Asch et al. 2013; Perri et al. 2021) and it is possible that dogs were introduced into South America later (Schwartz 1997; Prevosti et al. 2009; Prates et al. 2010a, b; Segura et al. 2021b). In South America, the most ancient record of dogs is from 5600 to 5000 ybp (Loma Alta, Ecuador; Rosamachay, Chile and Peru; Byrd 1976; Macneish and Vierra 1983; Stahl 1984). In some places of South America, such as the Amazon basin, dogs were not introduced until the twentieth century (Koster 2009).

Interactions among canid species are relevant to understand their biology and phylogenetic history. Dogs may have been subjected to genetic introgression of wild populations of *Canis latrans* and *C. lupus* (e.g., Frantz et al. 2020; Sinding et al. 2020). Ancient DNA analyses of Koster's dog, one of the oldest records in North America, revealed an affinity with coyotes, with which it may have been mixed (Perri et al. 2019). A dietary study based on isotopes (Monagle et al.

Handling editor: Frank E. Zachos.

✉ Valentina Segura
vseguragago@gmail.com

[1] Unidad Ejecutora Lillo, Consejo Nacional de Investigaciones Científicas y Técnicas–Fundación Miguel Lillo, 4000 San Miguel de Tucumán, Tucumán, Argentina

[2] Palaeontological Institute and Museum, University of Zurich, 8006 Zurich, Switzerland

2018) hypothesized that coyotes may have had a special role for Arroyo Hondoans people (New Mexico, US), and the Ute people (Utah, Colorado, US) in the Great Basin kept and tamed coyotes (Stewart 1942). Sinding et al. (2020) found no significant gene flow between ancient and modern American sled dogs and modern American–Arctic wolf populations, in contrast to the reports concerning the genetic exchanges of dogs with the Eurasian wolf (e.g., Leathlobhair et al. 2018; Perri et al. 2019).

There are 19 species of extant native wild canids on the American continent (Sillero-Zubiri 2009) (Fig. 1, Table 1) with a long evolutionary history partially documented in the fossil record (Wang and Tedford 2008; Prevosti and Forasiepi 2018). Since their arrival on the continent, human populations have interacted with native wild canids in direct (e.g., hunting, maintenance in captivity or as pets) and indirect (e.g., habitat change and habitat destruction) ways. However, none of these native wild canid species has been domesticated.

Here, to understand the interactions of canids and humans in the Americas in the past as well as the present, and explore the biological attributes of native canids in view of their suggested potential for domestication, we review 163 publications in the zooarchaeological record

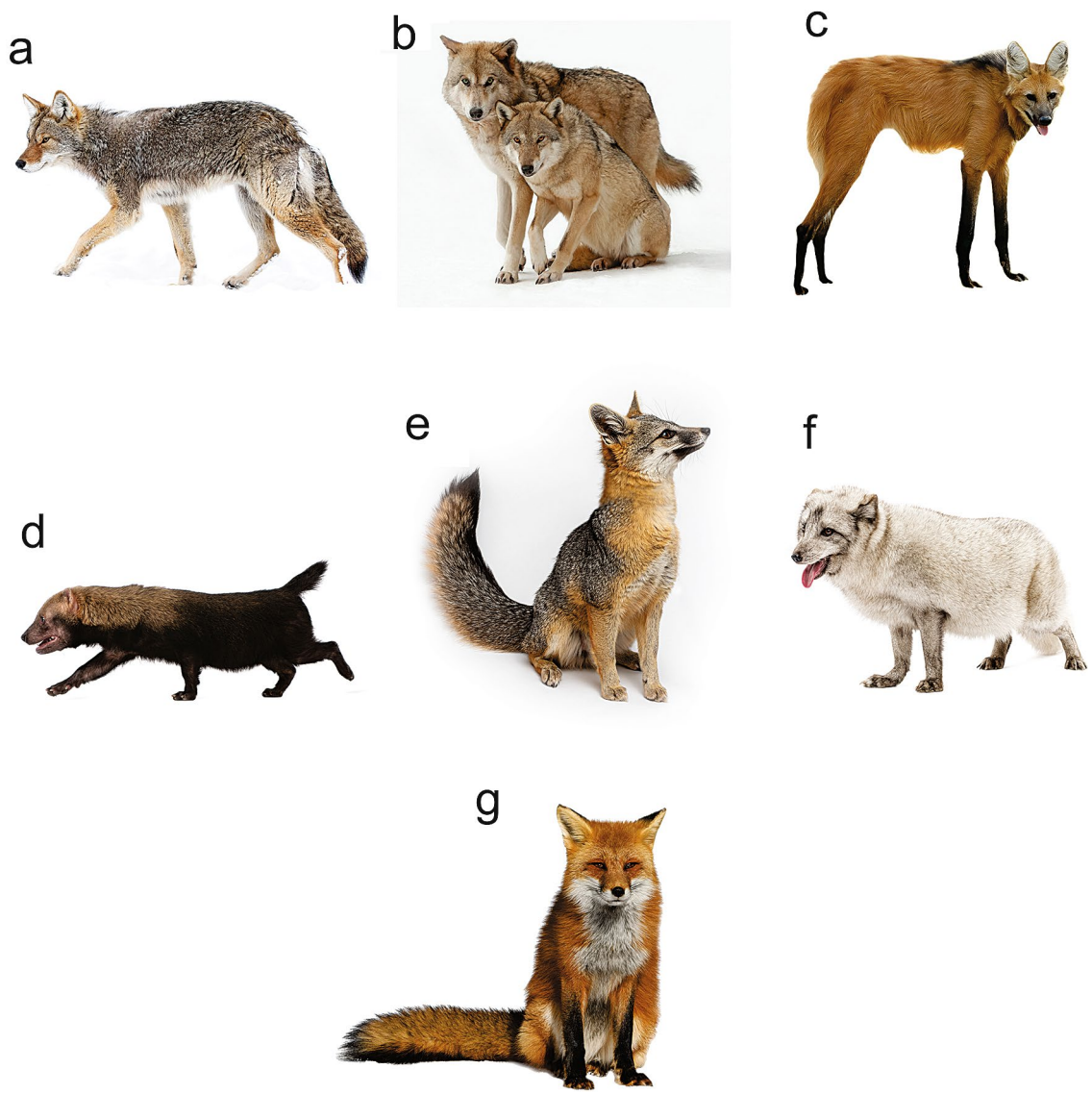

Fig. 1 Examples of wild canids from the Americas. Source of photographs: **a** Coyote *Canis latrans* (Jim Cumming), **b** Gray wolves *Canis lupus* (Sergei Brik), **c** Maned wolf *Chrysocyon brachyurus* (Anan Kaewkhammul), **d** Bush dog *Speothos venaticus* (Eric Isselee), **e** Gray fox *Urocyon cinereoargenteus* (Jay Pierstorff), **f** Artic fox *Vulpes lagopus* (Eric Isselee), and **g** Red fox *Vulpes vulpes* (FotoRequest)

Table 1 Geographic distribution of species of canids considered in this study

Species	Distribution
Atelocynus microtis (Short-eared dog) (1)	Bolivia, Brazil, Colombia, Ecuador, and Peru (2)
Canis latrans (Coyote) (1)	Belize, Canada, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, and USA *(3)*
Canis lupus (Gray wolf) (1)	Canada, Alaska and northern USA, Europe, and Asia from about 75° N–12° N (4)
Canis rufus (Red wolf) (1)	They exist as a reintroduced population in East of North Carolina, USA (1)
Cerdocyon thous (Crab-eating fox) (1)	Argentina, Colombia, Bolivia, Brazil, French Guiana(?), Guyana, Paraguay, Suriname, Uruguay, and Venezuela (5)
Chrysocyon brachyurus (Maned wolf) (1)	Argentina, Bolivia, Brazil, Paraguay, Peru, and Uruguay (6)
Lycalopex culpaeus (Culpeo) (1)	Argentina, Bolivia, Chile, Colombia, Ecuador, and Peru (7)
Lycalopex fulvipes (Darwin's fox) (1)	Endemic to Chile. (8)
Lycalopex griseus (Chilla) (1)	Argentina, Chile, and Peru (9)
Lycalopex gymnocercus (Pampas fox) (1)	Argentina, Bolivia, Brazil, Paraguay, and Uruguay (10)
Lycalopex sechurae (Sechuran fox) (1)	Ecuador and Peru (11)
Lycalopex vetulus (Hoary fox) (1)	Confined to Brazil (12)
Speothos venaticus (Bush dog) (1)	Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Guyana, Panama, Paraguay, Peru, Suriname, and Venezuela (13)
Urocyon cinereoargenteus (Gray fox) (1)	Belize, Canada, Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, USA, and Venezuela (14)
Urocyon littoralis (Island fox) *(1)*	USA (15)
Vulpes lagopus (Artic fox) (1)	Canada, Denmark (Greenland), Finland, Iceland, Norway, Russia, Sweden, and USA (Alaska) (16)
Vulpes macrotis (Kit fox) (1)	Mexico and USA (17)
Vulpes velox (Swift fox) (1)	Canada and USA (18)
Vulpes vulpes (Red fox) (1)	Across the entire northern hemisphere from the Arctic Circle to southern North America, Europe, North Africa, the Asiatic steppes, India, and Japan (19)

(1) Sillero-Zubiri (2009), (2) Leite Pitman and Williams (2004), (3) Kays (2018), (4) Mech and Boitani (2004), (5) Courtenay and Maffei (2004), (6) Rodden et al. (2004), (7) Jimenez and Novaro (2004), (8) Jiménez and McMahon (2004), (9) González Del Solar and Rau (2004), (10) Lucherini et al. (2004), (11) Asa and Cossíos (2004), (12) Dalponte and Courtenay (2004), (13) Zuercher et al. (2004), (14) Fuller and Cypher (2004), (15) Roemer et al. (2004), (16) Angerbjörn et al. (2004), (17) List and Cypher (2004), (18) Moehrenschlager and Sovada (2004), (19) Hoffmann and Sillero-Zubiri (2016)

and ethnological information from 13 different countries in the Americas.

Methods

Our work included comprehensive literature searches using online available information from databases (Pubmed, Scopus, Scielo, Google scholar, Latindex, Redalyc, DOAJ), and libraries (Biodiversity Heritage library, Library Genesis, Internet Archive), as well as opportunistic annotations from sources found based on consultation with experts and in our own work. We also scanned the reference lists of all publications that we collected looking for additional eligible articles. Our search strategy was carried out using the following terms: Canid domestication, wild canids, American canids (and combinations of canids with different countries), tamed canids, relationship between humans and canids, pet wild canids. Some of the references of works in Spanish were obtained through personal contact from sources not commonly available, contributing thus to circumvent the biases resulting from standard searches that are formally correct but which de facto potentially ignore relevant works (Nuñez and Amano 2021).

We considered relevant all types of publications (e.g., book chapters, dissertations) about ecology of wild canids (see below) and relationship between humans and canids. We included information from different countries, but restricted these to the Americas. We did not limit the search by language or date.

We included 163 publications (i.e., 72 papers, 38 book chapters, 38 complete books, 10 dissertations, and 5 web pages) ranging from the year 1823 (Latcham) to 2021 (Perri et al.). The extensive information was from 13 countries (Argentina, Belize, Brazil, Bolivia, Canada, Chile, Colombia, Ecuador, Guiana, Mexico, Peru, USA, and Venezuela) and from broader regions (e.g., South America). We also selected general information about wild canids of the America (see below for more details). The bibliography included only 15.3% of grey literature (that cannot be found easily through conventional publications

to materials published in traditional journals, and spanned from detailed chronicles and anecdotal experiences to specific information written exclusively about this topic).

We also selected general information about wild canids of the Americas. We used common names of canids exclusively from the "Family Canidae" chapter of the "Handbook of the Mammals of the World" Sillero-Zubiri (2009) (Table 1) throughout this manuscript.

Because historical geographic distribution and abundance data are not available for all species included in this work, and the population numbers (with the exception of *Canis latrans*) are stable or declining for wild canids, we only used current information on distribution and relative abundance of canids (Table 1). The main sources were the IUCN web page https://www.iucnredlist.org/ (accessed in March 2020), and different chapters and authors (for each species) extracted from the book "Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action" Sillero-Zubiri et al. (2009).

Table 2 includes requisites of The Anna Karenina principle (Diamond 1997) and three other attributes that may potentially affect the domestication potential (see below). Biological information about diet, activity pattern, gestation length, and weight of canids (Table 2) were mainly from Sillero-Zubiri (2009) and when such information was not available, we used the "Mammalian Species" series (https://academic.oup.com/mspecies), and "Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan" Sillero-Zubiri et al. (2009) for each species. Other biological information collected included social system, relative abundance, occurrence in captivity and temperament (Table 2) from different sources ranging from specific literature such as "Mammalian species" series (https://academic.oup.com/mspecies), and "Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan" Sillero-Zubiri et al. (2009), to papers where this information was anecdotal (e.g., Birdseye 1956). We also used current information from the IUCN web page https://www.iucnredlist.org/ (accessed March 2020) for each species, as well as classic sources including Mivart (1890), Cabrera and Yepes (1960), Ewer (1973), and Nowak (2005).

All the biological information presented in Table 2 was interpreted as categories that served to establish a quantification of the added potential of the species to be domesticated based on their biological attributes (Table 3). Each category has a value, which is maximum (1) if the domestication requisite is completely fulfilled, minimum (0) when the requisite is not fulfilled, and an intermediate value (0.5) when the requirement is moderately fulfilled. Then, we added the numbers and obtained a percentage, considering eight (all requirements fulfilled) equivalent to 100%, and expressed the potential for domestication with this percentage value.

When we considered the requisite diet flexibility, we categorized omnivorous canids (which eat both plant and animal matter) as '1', mesocarnivores (of which the diet consists of 50–70% meat) as '0.5', and hypercarnivorous canids (which have a diet that is more than 70% meat) as '0'. We categorized as '1' all canids because they have a short growth rate (i.e., gestation length around 2 months). When we considered the requisite captive breeding, we categorized the canids that live and breed well in captivity as '1', '0.5' when few specimens are kept in captivity or when the mortality rates of cubs are high, and '0' when individuals of the species are not held in captivity. Concerning temperament, we selected the category '1' for tamed species, and '0.5' for docile species or those not particularly cautious. Concerning social structure, we categorized as '1' social canids that live in packs, '0.5', when the basic social unit is a breeding pair, and '0' when canids are solitary. In relation to size, we considered as '1' large canids (weighing more than 10 kg), '0.5', medium-sized canids (weighing 5–10 kg), and '0', small canids (weighing 1–5 kg). When we considered activity pattern, we categorized as '1' canids with diurnal activity, '0.5' canids with crepuscular activity, and '0' canids mostly nocturnal. In relation to relative abundance, we categorized as '1' abundant canids (i.e., species that, because of habits and conspicuousness, occur in very large numbers), '0.5', common canids (i.e., species that occur in large numbers) or rarer canids (i.e., species recorded in low numbers), but less difficult to see because they travel in packs, and '0', canids scarce (i.e., species infrequently encountered). The latter three requisites are related to being more conspicuous or easy to find for humans and more probably domesticated. In this sense, the most conspicuous obtained the greatest value (1).

Data regarding cultural perception of domestication in different cultures were accessed from several publications, and the most frequently cited herein were Descola (1994, 1996, 2013), Erikson (2000), Stahl (2008, 2012, 2013, 2014), and Ferreira Vander Velden (2009).

To discuss the possibility of the domestication of *Dusicyon avus*, we collected information from several authors including Prevosti et al. (2009, 2011, 2015), Prates et al. (2010a; b, c), Prevosti and Soibelzon (2012), Prevosti and Martin (2013), Prates (2014), and Prevosti and Forasiepi (2018).

To explore the relationship between humans and canids in the present, we collected information from "Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan" (Sillero-Zubiri et al. 2009), IUCN web page https://www.iucnredlist.org/ (accessed August 2020) and other recent sources for each species. On the other hand, to explore the relationship between humans and canids in the past, we compiled information from

Table 2 Biological information of canids endemic to the Americas extracted from the literature

Species	Diet	Gestation length (days)	Occurrence in captivity	Temperament	Social system	Weight (kg)	Activity pattern	Relative abundance
Atelocynus microtis (Short-eared dog) (1)	Omnivorous (2)	Unknown	No short-eared dogs are currently held in captivity (2)	Docile (2)	Solitary. It has been reported hunting alone and in pairs (1)	9–10 (1)	Both diurnal and nocturnal activity (2)	Rare (1)
Canis latrans (Coyote) (1)	Mesocarnivores (1)	63 (1)	They readily reproduce in captivity and survival is high (3)	Tamed (4)	Social. It is considered less social than wolves. An alpha pair is the basic social unit (3)	7–16 (1)	Diurnal, with peaks of activity during the early morning and around the sunset (1)	Abundant (3)
Canis lupus (Gray wolf) (1)	Hypercarnivorous (1)	63 (1)	Lives and breeds well in captivity and is common in many zoological gardens (5)	Can be tamed (4)	Social. Live in packs (1)	62 (1)	Mostly nocturnal and crepuscular (1)	Wolf populations in various parts of the original range vary from extinct to relatively pristine (5)
Canis rufus (Red wolf) (1)	Mesocarnivores (1)	61–63 (1)	Breed in captivity (6)	Unknown	Social. Live in family units and packs (1)	22–34 (1)	Mostly nocturnal (1)	Common within the reintroduction area (6)
Cerdocyon thous (Crab-eating fox) (1)	Omnivorous (1)	56 (1)	Present in many zoos and private collections throughout South America where it generally breeds well (7)	Pretty tamable (8)	Live in social group (family). They travel in pairs but hunt individually (7)	4.5–8.5 (1)	Primarily nocturnal (1)	Common (1)
Chrysocyon brachyurus (Maned wolf) (1)	Omnivorous (1)	65 (1)	They have been kept in captivity in zoos and different institutions (1)	If captured as cubs they can be tamed (8)	Solitary. Facultatively monogamous (1)	20.5–30 (1)	Nocturnal and crepuscular (1)	Relatively common (1), although it is less visible to people because it is timid (9)
Lycalopex culpaeus (Culpeo) (1)	Mesocarnivores (1)	58 (1)	Common in zoos throughout Chile and Argentina (10)	Very docile (11) Probably tamed (12)	Solitary (1)	3.4–13.8 (1)	Almost completely nocturnal, although it has been reported diurnal (1)	When hunting pressure is reduced, culpeo populations usually can recover quickly (10)
Lycalopex fulvipes (Darwin's fox) (1)	Omnivorous (1)	Unknown	Few specimens kept in captivity (13)	Tame well (14)	Solitary (1)	1.9–3.95 (1)	Diurnal (1)	Scarce (13)

Table 2 (continued)

Species	Diet	Gestation length (days)	Occurrence in captivity	Temperament	Social system	Weight (kg)	Activity pattern	Relative abundance
Lycalopex griseus (Chilla) (1)	Omnivorous (1)	53–58 (1)	Occurs in many zoos of Argentina and Chile, but details of breeding in captivity are not known (15)	Unknown	Solitary. Monogamous (1). Combined litters (associated with polygyny) and the presence of female helpers may occur (15)	2.5–5 (1)	Crepuscular (1)	Common (1)
Lycalopex gymnocercus (Pampas fox) (1)	Omnivorous (1)	55–60 (1)	Successfully bred in captivity (16)	If captured as cubs they can be tamed (17)	Solitary. Monogamous (1)	4–8 (1)	Primarily diurnal (1)	Common (16)
Lycalopex sechurae (Sechuran fox) (1)	Omnivorous (1)	Unknown	Some specimens are kept in captivity (18)	Can be tamed (19)	Solitary (20)	2.6–4.2 (1)	Primarily nocturnal (1)	Common in Peru, not common in Ecuador (20)
Lycalopex vetulus (Hoary fox) (1)	Omnivorous (1)	50 (21)	Breed in Brazilian zoos. High mortality rates due to starvation amongst captive cubs (22)	Timid (23). Can be tamed (22)	Monogamous (1)	2.5–4 (1)	Nocturnal (1)	Abundant (22)
Speothos venaticus (Bush dog) (1)	Hypercarnivorous (1)	67 (1)	Bush dogs do occur in captivity and are breeding successfully (24)	Can be tamed (24)	Social (1). Monogamous with cooperative hunting (24)	5–8 (1)	Mostly diurnal (1)	Rare, although they are more visible when they travel in pack (1)
Urocyon cinereoargenteus (Gray fox) (1)	Omnivorous (1)	60 (1)	Fare well in captivity (25)	Tamed (23)	Monogamous with occasional polygyny (1)	3.4–5.5 (1)	Mostly nocturnal (1)	Common (1)
Urocyon littoralis (Island fox) (1)	Omnivorous (1)	50–53 (26)	Kept in captivity (26)	Tamed (23)	Monogamous pair (1)	1.4–2.5 (1)	Mostly nocturnal (1)	Variable (26)
Vulpes lagopus (Artic fox) (1)	Mesocarnivores (1)	51–54 (1)	Occur widely in captivity on fur farms (27)	Unknown	A breeding pair (1)	3.58–4.23 (1)	Primarily nocturnal (1)	Common (23)
Vulpes macrotis (Kit fox) (1)	Mesocarnivores (1)	49–55 (1)	Kept in captivity (28)	Not particularly cautious (23)	Primarily monogamous with occasional polygyny (1)	1.7–2.7 (1)	Mainly nocturnal (1)	Density fluctuates from common to rare (28)
Vulpes velox (Swift fox) (1)	Omnivorous (1)	51 (1)	Kept in captivity (29)	Not very cautious (23)	Primarily monogamous. The typical social group is a mated pair with pups (1)	1.6–2.5 (1)	Nocturnal (1)	Was considered abundant, but numbers were severely depleted (29)

Table 2 (continued)

Species	Diet	Gestation length (days)	Occurrence in captivity	Temperament	Social system	Weight (kg)	Activity pattern	Relative abundance
Vulpes vulpes (Red fox) (1)	Mesocarnivores (1)	49–55 (1)	Kept in captivity (30)	Tamed (31)	Basic social unit is a pair, but groups can share the territory (1)	3–14 (1)	Mainly nocturnal and crepuscular (1)	Variable (31)

(1) Sillero-Zubiri (2009), (2) Leite Pitman and Williams (2004), (3) Gese and Bekoff (2004), (4) Stewart (1942), (5) Mech and Boitani (2004), (6) Kelly et al. (2004), (7) Courtenay and Maffei (2004), (8) Cabrera and Yepes (1960), (9) Consorte-McCrea (2011), (10) Jimenez and Novaro (2004), (11) Massoia and Chebez (1993), (12) Petrigh and Fugassa (2014), (13) Jiménez and McMahon (2004), (14) Jiménez et al. (1991), (15). González Del Solar and Rau (2004), (16) Lucherini et al. (2004), (17) Mivart (1890), (18) Asa and Cossíos (2004), (19) Birdseye (1956), (20) Cossíos (2010), (21) Dalponte (2009), (22) Dalponte and Courtenay (2004), (23) Nowak (2005), (24) Zuercher et al. (2004), (25) Fuller and Cypher (2004), (26) Roemer et al. (2004), (27) Angerbjörn et al. (2004), (28) List and Cypher (2004), (29) Moehrenschlager and Sovada (2004), (30) Macdonald and Reynolds (2004), (31) Trut (1999), Trut et al. (2004)

archaeological, ethnological, and paleontological publications in an intensive bibliographic search for both reports of skeletal material and relevant cultural artefacts as well as discussions of the subject (see Table 4).

Biological perspective of canid domestication

Domestication has been defined as a process in which humans assume control over the movement, feeding, protection, distribution, and reproduction of a population of animals, at some point if not right from the start directed at achieving a specific purpose (Clutton-Brock 1994, 2012; Vigne 2011; Zeder 2012, 2014). Many alternative definitions exist in what are continuous interactions, stretching from selection for tameness, voluntary or not, to intensified selection for specific traits (Vigne 2011).

There is a large number of species from the Americas that were not domesticated while their close Eurasian relatives or counterparts were (Diamond 1997). These includes for example the American peccary, similar to the pig, the American bison, similar to the aurochs, water buffalo, yak, gaur and banteng, and the North American bighorn sheep, similar to the Eurasian wild sheep. One should note in this context thought that the European bison has not been domesticated either. Among canids, the large number of American native forms does not include a known, uncontested case of domestication (see below).

Diamond (1997) argued that the adoption of European domesticated animals by American indigenous peoples after 1500 is evidence of a lack of cultural barriers to domestication by those peoples. For example, European horses and dogs were adopted by several groups of indigenous peoples across the continent. Diamond also mentioned the widespread practice of keeping wild animals as pets among indigenous peoples, an old practice maintained through time, seen as an initial stage of domestication (Galton 1865). Diamond (1997) then argued how purely biological reasons must be considered to explain the few domesticated animals on the continent. In this context, he followed Galton (1865) in considering how the list of "requisites" for domestication shows the lack of suitable species on the continent: flexible diet, reasonable growth rate, captive breeding, pleasant disposition, steady temperament, and modifiable social hierarchy (The Anna Karenina principle, see below). Diamond (2002) hypothesized that the Americas were markedly deficient in large land mammals that could have been domesticated by humans. A small mammal such as the cavy or guinea pig was domesticated in South America though, so the relevance of body size for the likelihood of domestication remains speculative.

The Anna Karenina principle states that a deficiency in any one of a number of factors dooms an endeavor to failure. According to it (Diamond 1997), the best candidate

Table 3 Quantification of the domestication potential of each species of wild canids in the Americas

Species	Diet flexibility	Growth rate	Captive breeding	Temperament	Social structure	Size	Activity pattern	Relative abundance	Total (%)
Atelocynus microtis	1	?	0	0.5	0	0.5	0.5	0	31.25
Canis latrans	0.5	1	1	1	1	1	1	1	**93.75**
Canis rufus	0.5	1	1	?	1	1	0	0.5	62.5
Cerdocyon thous	1	1	1	1	0.5	0.5	0	0.5	68.75
Chrysocyon brachyurus	1	1	1	0.5	0	1	0	0	56.25
Lycalopex culpaeus	0.5	1	1	0.5	0	1	0	1	62.5
Lycalopex fulvipes	1	?	0.5	1	0	0	1	0	43.75
Lycalopex griseus	1	1	1	?	0.5	0	0.5	0.5	56.25
Lycalopex gymnocercus	1	1	1	0.5	0	0.5	1	0.5	68.75
Lycalopex sechurae	1	?	0.5	1	0	0	0	0.5	37.5
Lycalopex vetulus	1	1	0.5	0.5	0.5	0	0	1	56.25
Speothos venaticus	0	1	1	1	1	0.5	1	0.5	**75**
Urocyon cinereoargenteus	1	1	1	1	0.5	0	0	0.5	62.5
Urocyon littoralis	1	1	1	1	0.5	0	0	0.5	62.5
Vulpes lagopus	0.5	1	1	?	0.5	0	0	0.5	43.75
Vulpes macrotis	0.5	1	1	0.5	0.5	0	0	0.5	50
Vulpes velox	1	1	1	0.5	0.5	0	0	0.5	56.25
Vulpes vulpes	0.5	1	1	1	0.5	1	0	0.5	68.75

species for domestication must be easy to feed and have a flexible diet. Although there are many wild canids whose diet is omnivorous or generalist, they do not have the other requisites needed. In addition, fast growth is a requirement to be economically profitable. As all canids have a gestation period of between 49 and 67 days, they are considered good candidates in this regard (Tables 2, 3). The species must breed well in captivity and have a good temperament and many wild canids from the Americas are docile. This is important because all canids are carnivores and predators, although most of them are small or medium-sized and could not prey on humans. The social structure is an important factor because a species that has a strong, well-defined social hierarchy is more likely to be domesticated; species that can become imprinted by a human as the head of the hierarchy are better suited.

Although other related biological attributes of the species, such as weight, activity pattern (i.e., diurnal, nocturnal) and relative abundance are not enlisted in the Anna Karenina principle (Diamond 1997), they may potentially affect access and visibility to humans and domestication potential. For example, a diurnal canid with larger size, abundant occurrence, traveling in packs, is more visible for humans and thus more likely to become domesticated, than one with contrary features to those just listed. Size was not a hindrance in the domestication of the cavy or guinea pig, but it may have been one in the case of canids.

Cultural perspective of canid domestication

The notable lack of native domesticated animals by indigenous peoples in the Amazon contrasts with the presence of such species in the Andean region of South America and in areas of Central and North America. Stahl (2014) argued that in different Amazonian cultures the particular worldview of nature and surrounding environment precluded processes of animal domestication, as opposed to a high diversity of domesticated plants in the Amazonian region: "The reason that Amazonians 'fail to domesticate' animals is not based on the lack of raw material or opportunity; rather, it rests with their shared logic which guides how appropriate relations are conducted between sentient beings (Hugh-Jones 2001). Indigenous Amazonians don't domesticate animals because it doesn't make any sense to them." A rich body of ethnological literature concerning

Table 4 Burials of non-domesticated canids from the archaeological record of the Americas

Species	Place	Evidence	Date	References
Canis latrans	Moon Pyramid (Teotihuacan, Mexico)	1 individual	250–350 CE	1, 2, 3
	Cueva de las Varillas (Teotihuacan, Mexico)	2 individuals	1521–1800 CE	4
	Teopancazco (Teotihuacan, Mexico)	5 individuals (fragments of frontal, cranial, left maxilla, ribs, radius, phalanges, cervical vertebrae and molars)	401–600 CE	4
	Santa Cruz Atizapan (Toluca, Mexico)	2 individuals (metapodials, left mandible, left tibia)	501–800 CE	4, 5
	Zultepec-Tecoaque (Tlaxcala, Mexico)	Cooked left femur, 2 left metatarsals	1519–1520 CE	4
	Cañón de las Tinajas (Durango, Mexico)	Right mandible	Possibly pre-Hispanic	4
	Malpaís Prieto (Michoacan, Mexico)	Complete radius	1300–1425 CE	6
	Tipu (Belize)	2 individuals	1400–1520 CE	7
	Grasshopper Ruin (Arizona, USA)	3 individuals (1 complete skeleton, 1 left mandible, 1 left premaxila and maxilla)	1301–1400 CE	8
	Arroyo Hondo Pueblo (New Mexico, USA)	3 individuals	1300–1420 CE	9, 10
Canis lupus	Moon Pyramid (Teotihuacan, Mexico)	29 individuals: 3 complete skeletons in the burial 2, 1 in a cage, 14 heads in the burial 3, and 9 skulls	250–350 CE	1, 2, 3, 11
	Sun Pyramid (Teotihuacan, Mexico)	1 skull of juvenile specimen	200–250 CE	2
	Quetzalcoatl Pyramid (Teotihuacan, Mexico)	Cranium and mandible	200–250 CE	2
	Teopancazco (Teotihuacan, Mexico)	Right femur of a juvenile wolf, distal part of a femur, burned distal half of the fifth right metacarpal with cut marks and worked	401–600 CE	12, 13
	Santa Cruz Atizapan (Toluca, Mexico)	1 individual (left metatarsal converted in a punch)	501–800 CE	5
	Zultepec-Tecoaque (Tlaxcala, Mexico)	Fragment of mandible	1519–1520 CE	14
	Templo Mayor (Tenochtitlan, Mexico)	2 complete individuals (offerings 120 and 125)	1486–1502 CE	15, 16
	Hunchavin (Chiapas, Mexico)	A juvenile of 4 months (fragment of right maxilla, left mandible with deciduous and definitive teeth, fragment of pelvis and hind legs)	501–700 CE	14, 17, 18
Cerdocyon thous	Carúpano (Venezuela)	Mandible, maxilla, and teeth	Late Holocene 425–445 ybp	19
Chrysocyon brachyurus	Arroyo Seco 2 (Buenos Aires, Argentina)	Pierced canine teeth (25)	Middle Holocene 6495 ± 65 ybp	20
	Nutria Mansa 1 (Buenos Aires, Argentina)	Incomplete right metatarsal fifth	Late Holocene 2700–3100 ybp	21, 22
	La Bellaca 2 (Buenos Aires, Argentina)	Right mandible and teeth	Late Holocene 680 ± 80 ybp	23
Dusicyon avus	Baño Nuevo 1 (Aisén, Chile)	Remains	Early Holocene 7070 ± 25 ybp	24
	Loma de los Muertos (Río Negro, Argentina)	Remains	Late Holocene 2972 ± 50 ybp	25, 26, 27
	Nutria Mansa 1 (Buenos Aires, Argentina)	Remains	Late Holocene 2700–3100 ybp	21, 20

Table 4 (continued)

Species	Place	Evidence	Date	References
	Cueva Tixi (Buenos Aires, Argentina)	20 teeth, an articulated mandible with dentition, and an incomplete left mandibular ramus	Middle Holocene 4865 ± 65 ybp	28
	Río Luján I (Buenos Aires, Argentina)	Skull	Late Holocene 724 ± 52 ybp	29
	Tres Arroyos 1 (Tierra del Fuego, Chile)	Mandible	Late Pleistocene 10,575 ± 65 ybp	30
	Calera (Buenos Aires, Argentina)	Remains	Late Holocene 1750–3400 ybp	31, 32
Lycalopex culpaeus	Ecuador and Peru	Remains	1700 BCE	33
	Chuquiña site (Oruro, Bolivia)	Skull	2000 BCE-400 CE	34
	Putuni and Miraflores sites (La Paz, Bolivia)	Remains of two specimens	400–1100 CE	34
	Arroyo Seco 2 (Buenos Aires, Argentina)	Pierced canine teeth	Middle Holocene 6495 ± 65 ybp	20
	Baño Nuevo 1 (Aisén, Chile)	Mandibles with cuts	Early Holocene 7070 ± 25 ybp	24
	Cabo Vírgenes (Santa Cruz, Argentina)	Hemimandibles, scapulae	Late Holocene 733 ± 47 ybp	35
Lycalopex griseus	Colqapata (Bolivia)	3 metacarpals	Formative period No date	36
	Achocalla (La Paz, Bolivia)	1 radius	240 ± 30 CE	36
Lycalopex gymnocercus	Arroyo Seco 2 (Buenos Aires, Argentina)	Pierced canine teeth	Middle Holocene 6495 ± 65 ybp	20
	Cueva Tixi (Buenos Aires, Argentina)	Teeth	Middle Holocene 4865 ± 65 ybp	28
	Calera (Buenos Aires, Argentina)	Remains	Late Holocene 1750–3400 ybp	31, 32
	Nutria Mansa 1 (Buenos Aires, Argentina)	Remains	Late Holocene 2700–3100 ybp	21, 22
Lycalopex sechurae	Santa Elena (Peru)	Skeletal elements, teeth	7000–8500 ybp	37
	Las Balsas (Ecuador)	Remains and 2 left humerus transformed in flute	2030 ± 60 ybp	38
	Las Vegas (Ecuador)	Remains in dumps, teeth	6600–10,000 ybp	39, 40, 41
Speothos venaticus	Moraes (São Paulo, Brazil)	Remains	4000–6000 ybp	42
Urocyon cinereoargenteus	Santa Cruz Atizapan (Toluca, Mexico)	1 individual	501–800 CE	5
	Teopancazco (Teotihuacan, Mexico)	Remains	401–600 CE	12, 13
	Grasshopper Ruin (Arizona, USA)	3 mandibular fragments	1301–1400 CE	8
Urocyon littoralis	Santa Rosa, Santa Cruz, San Nicolas, San Clemente Islands (California, USA)	Remains of 39 intentional burials	550–7230 ybp	43, 44
Vulpes lagopus	Tayara (Canada)	Remains with cuts	1900–2500 ybp	45
Vulpes vulpes	Tayara (Canada)	Remains with cuts	1900–2500 ybp	45
	Marmes (Washington)	Remains with cuts	8525–10,830 ybp	46
	Uyak (Alaska)	Remains with cuts	2000 ybp	47

ybp years before present, BCE before current era, CE current era

(1) Schwartz (2011), (2) Sugiyama (2014), (3) Sugiyama et al. (2013), (4) Valadez et al. (2008a), (5) Valadez and Rodríguez (2009), (6) Manin et al. (2015), (7) Emery (1999), (8) Olsen (1968), (9) Lang and Harris (1984), (10) Monagle et al. (2018), (11) Sugiyama and López Luján(2007), (12) Rodriguez Galicia (2006), (13) Valadez (2017), (14) Valadez et al. (2008b), (15) Lopez Luján and Chavez Balderas (2010), (16) López Luján et al. (2012), (17) Valadez (2014), (18) Sosa Rodríguez (2017), (19) Linares (1987), (20) Politis et al. (2012), (21) Bonomo (2005), (22) Bonomo (2006), (23) García Esponda et al. (2001), (24) Trejo and Jackson (1998), (25) Prates (2014), (26) Prates et al. (2010b), (27) Prevosti et al. (2011), (28) Mazzanti and Quintana (1997), (29) Prevosti et al. (2015), (30) Borrero (2005), (31) Alvarez (2009), (32) Kaufmann and Alvarez (2007), (33) Wing (1989), (34) Mendoza (2019), (35) Belardi et al. (2011), (36) Popovic et al. (2020), (37) Marcos (1988), (38) Sánchez Mosquera 1996), (39) Gutierrez Usillos (1998), (40) Stother (2003), (41) Stother and Sánchez Mosquera (2011), (42) Plens (2010), (43) Collins (1991), (44) Roemer et al. (2004), (45) Monchot and Gendrom (2011), (46) Lyman (2012), (47) West and Yeshurun (2019)

peoples in the Amazon region shows that the keeping of pets should not be seen as a precursor to domestication, as the conception of human-animal interactions is different from that of Europeans (Descola 2013). Among Amazonian peoples (e.g., the Kalapalo [Xingu National Park, Mato Grosso state, Brazil], Maquiritare [Roraima state, Brazil; Bolivar and Amazonas state, Venezuela], Matis [Vale do Javari, Amazonas state, Brazil], Matsés [border in between Peru and Brazil, Amazonia], Matsiguenga [southeastern Peru], Panare [Cedeño, Bolivar state, Venezuela], Yagua [Mariscal Ramón Castilla and Putumayo provinces, Loreto, Peru; Santa Sofía and El Progreso, Colombia], Tucano [Vaupes and Amazonas state, border in between Brazil and Colombia], Txicão [Xingu National Park, Mato Grosso state, Brazil], Wayampi [southeastern border area of French Guiana and Amapá and Pará states in Brazil]), wild pets are obtained by the hunter who killed their mother. Supernatural entities offer animals as prey to hunters, and women raise their young as part of reestablishing a natural balance or compensating for the destructive effects of hunting (Erikson 2000).

The large biogeographic diversity of the Americas is associated with considerable cultural diversity including numerous worldviews and relationships with the surrounding animals. This diversity renders inapplicable any possibility of standardizing the environmental (and temporal) situations under which a process of domestication could have occurred. The cultural influences on the existence and mode of domestication across the continent are not universal.

Alternative perspectives of canid domestication

The presence of domestic dogs since at least 10,000 ybp in the Americas (e.g., Koster, Hinds Cave) and their relationship with humans may have prevented or hindered the intention or initiative to domesticate local wild canids beyond the taming of puppies commonly practiced even nowadays, which in general do not show the gregarious and social customs of the wolves (Segura et al 2021a). The process of domestication in non-dog canids would possibly have represented an unnecessary effort when the domestic dog was already in coexistence.

It has been argued that animal protein in the Amazon region is easily secured in aquatic environments, leading to no need to domesticate animals aside from the Muscovy duck (Sauer 1952). The secure diet available at the edges of rivers, shores, and savannas (Harris 1972) through hunting and fishing promoted increased sedentism, and opportunity for plant experimentation (Stahl 2014).

Another perspective considers dogs as expensive to humans, because of the need to care for them. Although they can eat the same diet as humans, their presence suggests that those humans have an excess of food or at least enough food to feed them. In this sense, it is not for all members of society and not for all societies (Wylde 2017). Perhaps the same notion of cost of investment of time and money is relevant when considering the potential domestication of wild canids.

Current and past human interactions with canids in the Americas

There are no definitive records of active domestication of wild canids by humans in the past or at present in the Americas, although these canids do show a disposition to humans. Currently, some wild canids (e.g., *Atelocynus microtis*, *Cerdocyon thous*, *Chrysocyon brachyurus*, *Lycalopex fulvipes*, *L. sechurae*, *L. vetulus*, *Urocyon cinereoargenteus*, *Vulpes macrotis*) are captured by local peoples as pets (Asa and Cossíos 2004 2004; Courtenay and Maffei 2004; Dalponte and Courtenay 2004; Fuller and Cypher 2004; Jiménez and McMahon 2004; List and Cypher 2004; Rodden et al. 2004; Leite-Pitman and Williams 2011) or to sell to zoos or private collections. The latter is the case for *A. microtis* and *C. brachyurus* (Leite-Pitman and Williams 2011; Paula and DeMatteo 2015). Some species such as *L. culpaeus*, *L. fulvipes*, *L. griseus*, *L. gymnocercus*, *Canis latrans*, *C. lupus*, *Vulpes lagopus*, and *V. vulpes* are hunted and trapped for fur (Angerbjörn et al. 2004; Gese and Bekoff 2004; González del Solar and Rau 2004; Jimenez and Novaro 2004; Lucherini et al. 2004; Macdonald and Reynolds 2004; Mech and Boitani 2004; Silva-Rodríguez et al. 2016).

Some wild canids are hunted for use in magic–religious rituals, fabrication of amulets, handicrafts, and local medicines. For example, in Brazil, farmers hang tails of *C. thous* in animal sheds to avoid bats with rabies (Courtenay and Maffei 2004) and some body parts of *C. brachyurus* are used to cure bronchitis and kidney disease, or as treatment for snakebites (Rodden et al. 2004). In Bolivia, farmers believe that sitting on *C. brachyurus* fur will protect them from bad luck (Rodden et al. 2004). In Peru, *L. sechurae* are dissected and parts of their bodies (e.g., paws, tails, heads, fat) are used to perform traditional magic-religious rituals or for the treatment of bronchial illness and stomach disorders. They are also used to attract good spirits or energies during premonition rituals or to manufacture amulets, called *seguros*. In the department of Piura, dried adult animals in a sitting position are offered to tourists for home protection (Asa and Cossíos 2004; Cossíos 2004).

Stahl (2012, 2013), based on zooarchaeological records, suggested that in the past there were intense interactions between humans and endemic foxes in the Americas. Many species of canids (coyotes, foxes, wolves) have been tamed (see Table 2), and presumably crossbred with American dogs by indigenous peoples, as relatively detailed chronicles

and anecdotal experiences show (Latcham 1823; Mivart 1890; Allen 1920; Fernández de Oviedo y Valdés 1944; Cabrera and Yepes 1960; Colton 1970; Valadez et al. 2001; Stahl 2013). Some chroniclers and ethnozoologists (Latcham 1823; Allen 1920; Gilmore 1950) have proposed some varieties of pre-Columbian domestic dogs as derived from endemic canids (e.g., from *Speothos venaticus* or *Cerdocyon thous,* as more frequently mentioned). Such ideas have been questioned based on genetic evidence and the impossibility of producing litters reproductively viable, although the presence of tamed wild canids that were mistaken with domestic dogs by the early chroniclers is possible (Stahl 2012, 2013). The possibility of interbreeding of dogs and American canids has been considered remote given the difference in chromosome number (Wayne et al. 1987; Vilà and Leonard 2012).

Although most canid burials excavated in the Americas correspond to *Canis familiaris* (Segura et al. 2021b), there are many burial sites containing wild canids (Table 4). Excavations at the Santa Elena site (8500–7000 ybp, Peru) showed remains of fishing and gathering peoples where dogs are absent, but burials show a remarkable amount of skeletal material of *Lycalopex sechurae*, the Sechuran fox (Marcos 1988). The offerings included stone objects, carved shell ornaments, and teeth from this species of fox, in some cases contained in little bags. Remains of this fox were also found in dumps, suggesting economic use (Gutierrez Usillos 1998; Stother 2003; Stothert and Sánchez Mosquera 2011), and some skeletal elements had been transformed, as in the case of the left humerus of this species found at the Las Balsas site (Ecuador), used as a flute (Sánchez Mosquera 1996). Inhabitants of the Andean region of Ecuador, Peru, and Bolivia practiced hunts and burials of *Lycalopex culpaeus* (culpeo foxes) for ceremonial purposes (Table 4; Wing 1989; Mendoza 2019), and it was suggested that they may have been tamed by indigenous people in Tierra del Fuego (Hamilton-Smith 1839; Petrigh and Fugassa 2014). In Arroyo Seco 2 (Argentina), pierced canines of this species and from *Chrysocyon brachyurus* (maned wolf) and *L. gymnocercus* (pampas fox) were deposited as grave goods (Politis 2012), while in Baño Nuevo 1 (Chile) and Cabo Vírgenes (Argentina), mandibles and scapulae of *L. culpaeus* showed cuts suggesting economical use for meat consumption or fur exploitation (Trejo and Jackson 1998; Belardi et al. 2011).

In addition, remains of *L. gymnocercus* were found at Argentinian sites such as the Calera, Nutria Mansa 1, and Cueva Tixi, without exposure to fire or processing cuts (Table 4). Specimens of *Dusicyon avus* (an extinct fox, see below) were also found at these sites (Mazzanti and Quintana 1997; Bonomo 2005, 2006; Kaufmann and Álvarez 2007; Álvarez 2009). Less frequent in archaeological sites, *C. brachyurus* was also reported by García Esponda et al. (2001) in La Bellaca 2 (Argentina) describing a mandibular fragment and a lower canine, and by Bonomo (2005, 2006) who found a metatarsal bone in Nutria Mansa 1 (Argentina). Linares (1987) reported fragments (mandible, maxillae and teeth) of *C. thous* from Carúpano, northeastern Venezuela dated from around 1500 of the current era. Popović et al. (2020) determined that three metacarpals from Colqapata Site (Bolivia), and one isolated radius from Achocalla (Bolivia) belonged to *L. griseus*, and Plens (2010) reported remains of *S. venaticus* (Bush dog) from Moraes (Brazil).

In North America, foxes have a long history of exploitation and analyses suggest they were used for a variety of purposes. In terms of noneconomic uses, people on Kodiak (Alaska) may have kept *Vulpes vulpes* (red fox) as pets (West and Yeshurun 2019). Foxes such as *V. vulpes* and *V. lagopus* (arctic fox) were hunted in the past for their fur and meat and possibly for the bone itself, as interpreted based on specimens with cut-marked bones from the Marmes archaeological site in southeastern Washington State (USA), Dorset site of Tayara in Nunavik (Canada), and Uyak Site (Alaska) (Monchot and Gendron 2011; Lyman 2012; West and Yeshurun 2019) (Table 4).

Indigenous peoples of the Channel Islands (California) kept *Urocyon littoralis* (island foxes) as pets and harvested them to make clothes from their fur. These foxes played a spiritual role, and in some cases were intentionally buried with humans, as burial remains have shown. Thirty-nine intentional burials of island foxes have been recovered from Santa Rosa, Santa Cruz, San Nicolas, and San Clemente Islands (Table 4). On the northern islands the burials have been directly associated with human remains, for example, in one of them two fox skulls were associated with a child burial, in other, a fox skull was placed between the pelvises of a man and woman, and in the third, a fox skull was wrapped in a mat with two bone tubes, coated with asphalt and wrapped with rope. In the southern islands, foxes were not directly associated with human remains or with artifacts, but were probably buried after having been skinned for their pelts (Collins 1991; Roemer et al. 2004). Some authors interpreted these relationships between humans and canids as evidence of domestication. Although not thoroughly tested, these findings strongly suggest close human contact with fox populations, furthermore; genetic evidence supports human-induced foxes translocation from the northern to southern Channel Islands (Hofman et al. 2015).

The symbolic importance of *Canis latrans* (coyote) and *C. lupus* (wolf) in many cultures across the northern hemisphere can be evidenced in ethnographic and ethnohistorical sources and archaeological remains. The coyote was seen as a trickster, fellow hunter, brave fighter, and a god among the Hopi (Arizona, US), while to Mescalero Apache (New Mexico, US), coyotes have supernatural powers, which make them dangerous (Titiev 1971; Basehart 1974; Schwartz 2011). For Miwok and Yokuts (California, US), coyotes

were totemic symbols for lineages, and in some past Mesoamerican civilizations they were presumably considered crafty, intelligent, revengeful, skillful as hunters, and related to the libido and the arts (Valadez et al. 2008a; Byrd et al. 2013; Sugiyama 2014). A study based on diet of several archaeological specimens in Arroyo Hondo Pueblo (New Mexico, US) through isotopes (Monagle et al. 2018) demonstrated that coyotes might have been treated as dogs for Arroyo Hondoans people, based on an overlap in the diet of domestic dogs and wild coyotes.

In Mexico, coyote remains were preserved in Moon Pyramid and caves (Teotihuacan), and in sites such as Santa Cruz Atizapan (Toluca), Zultepec-Tecoaque (Tlaxcala), Cañón de las Tinajas (Durango), and Malpaís Prieto (Michoacan). Coyote remains in other countries include those found in Tipu (Belize) and Grasshoper Ruin (Arizona, USA) (Table 4; Olsen 1968; Emery 1999; Valadez et al. 2008a; Valadez and Rodríguez 2009; Schwartz 2011; Sugiyama et al. 2013; Sugiyama 2014; Manin et al. 2015). Some of these remains were interpreted as natural accumulations, others as materials to manufacture clothes and offerings related to human burials (Valadez et al. 2008a; Schwartz 2011; Sugiyama et al. 2013; Sugiyama 2014; Manin and Evin 2020). In Santa Cruz Atizapan, Teopancazco, and Grasshopper Ruin sites, remains of *Urocyon cinereoargenteus* (gray fox) were also found (Olsen 1968; Rodríguez Galicia 2006; Valadez and Rodríguez 2009; Valadez 2017).

Wolves were important hunters and respected figures in some American cultures (Titiev 1971; Basehart 1974; Schwartz 2011). Among the Zuni (New Mexico, US), wolves played an important mythic role and likely evoked a fearful respect (Schwartz 2011). The Huichol people (Nayarit, Mexico) believed that wolves taught them how to hunt deer, with the peyote cactus considered the heart of the deer. Before going hunting, the Zuni made offerings and sang to wolves (Sugiyama 2014). For Teotihuacan peoples (Mexico), the wolf was a symbol of war and it was represented wearing a feather headdress. Wolves were related to religious ceremonies for the elite of the Teotihuacan society (Valadez et al. 2008b).

The wolf was more frequently found than other canids in the archaeozoological record and always associated with extraordinary deposits (Manin and Evin 2020). Wolves were found in Teotihuacan, (Table 4) in Teopancazco, and in the Sun, Quetzalcoatl, and Moon pyramids (Rodríguez Galicia 2006; Sugiyama and López Luján 2007; Schwartz 2011; Sugiyama et al. 2013; Sugiyama 2014; Valadez 2017). In the latter, the burials were considered an assertion of state power and militarism and contained human remains considered elite (Sugiyama and López Luján 2007; Schwartz 2011). In Burial 2, archaeologists found a complete and well-preserved skeleton of a wolf inside a wooden cage, probably buried alive (Sugiyama and López Luján 2007). The most surprising offerings in Burial 3 were 18 heads of decapitated pumas and wolves (Table 4) (Sugiyama and López Luján 2007). Another site in Mexico, Zultepec-Tecoaque, included a fragment of mandible (Valadez et al. 2008b), and in Santa Cruz Atizapan researchers found a left metatarsal worked by hand and converted into a punch, indicating an association with human activities (Valadez and Rodríguez 2009). Two complete individuals were included as offerings in the ancient city of Tenochtitlan, richly adorned with ornaments crafted from precious stones and metals, sacrificial flint knives, wooden ear muffs and nose rings, belts made of shells, necklaces of green stone beads, shell pendants and anklets, and gold and copper bells (López Luján and Chávez Balderas 2010; López Luján et al. 2012). In Hunchavin, Chiapas, a juvenile wolf of estimated four months of age was recovered based on a left mandible with deciduous and adult teeth, right maxilla, a fragment of pelvis and hind limbs (Valadez et al. 2008b; Valadez 2014; Sosa Rodríguez 2017).

The interaction with *Dusicyon avus*

Many authors considered the possibility that this now extinct canid had been domesticated. *Dusicyon avus* was a medium-sized canid with an estimated body mass of 10–14 kg. It lived in Uruguay, southern Brazil, and the Pampean and Patagonian regions of Argentina during the Late Pleistocene and Holocene, inhabiting open areas (e.g., grass steppe, shrub steppe) under a wide range of climatic conditions (Prevosti and Forasiepi 2018; Prevosti et al. 2015). It could have had a more carnivorous diet that the living *Lycalopex culpaeus* (culpeo fox) (Prevosti et al. 2009), hunted mainly medium-sized rodents, armadillos, and juveniles of larger ungulates (Prevosti and Martin 2013).

Several specimens of *D. avus* were recovered from archaeological sites (Table 4). In some places, such as Cueva Tixi (Argentina), remains of this fox were found without signs of human intervention (Mazzanti and Quintana 1997), while at other sites, such as Tres Arroyos 1 (Chile), there was evidence of consumption (Borrero 2005), though the latter does not seem to be common (Prevosti et al. 2011; Prates 2014). This fox was used for ritual purposes, usually deposited as grave goods in mortuary contexts or used as material for ornaments; for example, its teeth were utilized in confection of necklaces (Prates 2014; Prevosti et al. 2015). In two sites of Argentina, Loma de los Muertos, and Río Luján, *D. avus* was associated with mortuary contexts. Moreover, Prates (2014) inferred that a specimen from Loma de los Muertos, which showed no trauma marks in its skeleton, was intentionally buried, as a human would have been (Prevosti et al. 2011). The practice of burying animals was almost exclusively restricted to certain domestic species, especially dogs. For this reason, the special treatment

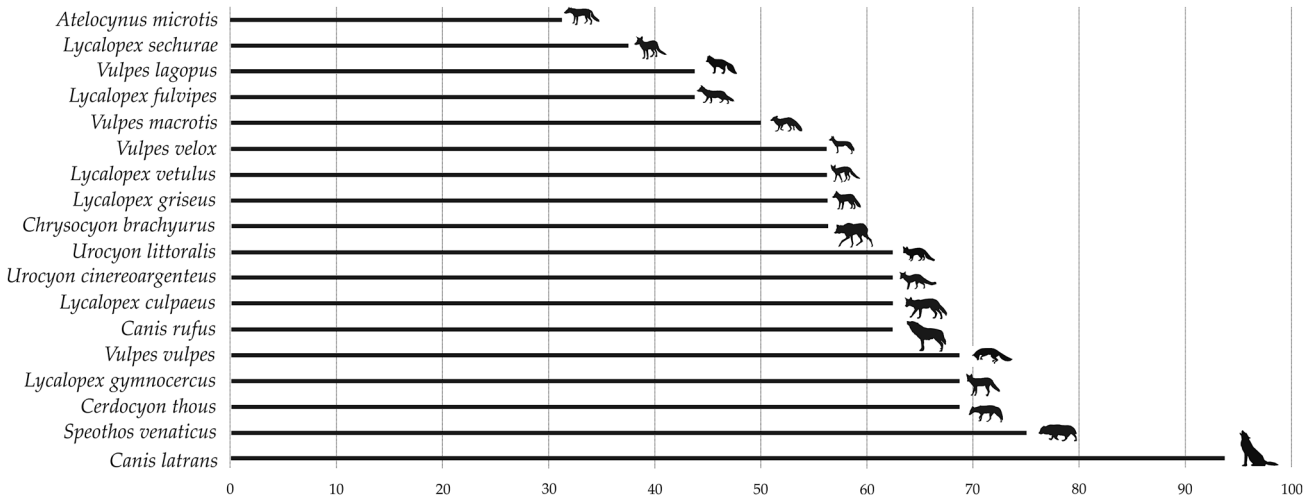

Fig. 2 Estimated percentage based on categories described in the text of domestication potential in wild canids from the Americas

of the fox suggests the possibility that it was part of the social structure, kept in captivity, and tamed as pets (Prates et al. 2010c). As this species is extinct, we cannot know if *D. avus* fulfilled all the biological "requisites" of the Anna Karenina Principle to be domesticated as enunciated by Diamond (1997). The archaeological record surely suggests that a close human-animal relationship did occur.

Species with potential to be domesticated

Most wild canids from the Americas are currently tamed or integrated into indigenous societies to different degrees, as some species would be behaviorally suitable for domestication, although they rarely adjust to the other "requisites" proposed by Diamond (1997). Those species, although docile or tamable, are difficult to reproduce in captivity, or the wild populations are at a low density and not easy to see (Tables 2, 3). However, taming wild canids in the Americas without an active domestication process is a highly common practice among indigenous populations and people in rural regions. Taking into account all the suggested requisites for domestication (Diamond 1997), the species with the most potential to be domesticated are *Canis latrans* and *Speothos venaticus* (93.75% and 75%, respectively, Table 3, Fig. 2).

Coyote (*Canis latrans*): biological characteristics and cultural aspects

The coyote (*Canis latrans*) is one of the species with a life history that fulfils most of the domestication "requisites" (Table 3, Fig. 2). It is a medium-sized canid of wide distribution that uses almost all available habitats, including urban areas (Kays 2018). They are mesocarnivores (i.e., with diets mostly composed of vertebrates but incorporating some consistent amount of insects, fruits or other non-vertebrate items) (Prevosti and Soibelzon 2012), but also generalists as they can eat a wide variety of food items (Sillero-Zubiri 2009). The basic social unit is an alpha pair, although they can form packs but are less social than wolves (Gese and Bekoff 2004). The coyote is easily tamed as a pup (Stewart 1942). However, young coyotes have more severe fights between 25 and 35 days of age than wolves or dogs at the same age (Bekoff 1974).

Coyotes were important elements in indigenous peoples mythology (e.g., Flathead [western Montana, US], Crow [southern Montana, US], and other Great Plains peoples [Canada, US]) (Gese and Bekoff 2004), and parts of their bodies were worn as ceremonial clothing (Valadez et al. 2008a). In folktales of some indigenous peoples in the United States southwestern and Plains regions, coyotes are seen as tricksters, probably due to their intelligence and adaptability. However, American coyote characters vary widely from group to group (Watts 2007).

The reasons why coyotes have not been domesticated are unknown. These could include the spiritual vision indigenous peoples had of them, the high level of pup aggression and breeding difficulty, their elusive nature (Bekoff 1977), and/or the fact that indigenous peoples had already raised dogs from wolves. Nevertheless, coyotes may have contributed genetic material to the ancient dog populations in the Americas (Adams et al. 2003; Dobney and Larson 2006; Vilà and Leonard 2012), such as an ancient DNA analysis of the oldest record in North America, the Koster's dog, revealed (Perri et al. 2019).

Bush dog (*Speothos venaticus*): biological characteristics and cultural aspects

Some aspects of the life history of the bush dog are similar to those of the wolf, such as their friendly behaviour in captivity as well as social and hypercarnivorous habits. These characteristics (Table 3, Fig. 2) make the bush dog a suitable candidate to have been domesticated by the Amazonian peoples based on Diamond's "requisites". Remarkably, the morphology and size of the bush dog suggest possible paedomorphic transformations in their evolutionary development within canids (Biben 1983; Wayne 1986a, b; Segura 2014; Segura et al. 2021a), which have been suggested for the differentiation of dogs and wolves (Wayne 1986a; Wayne and Ruff 1992; Sánchez-Villagra et al. 2017).

The benefits of the presence of domestic hunting dogs among the Amazonian peoples include the addition of food items only possible to reach with the help of the dog (Varner and Varner 1983; Schwartz 1997). However, apart from some occasionally tamed specimens, there are no reliable records showing that the bush dog has been actively domesticated. One hypothesis to explain this is the susceptibility of this species to diseases of the domestic dog (Uhl et al. 2019), but the Amazonian peoples spent thousands of years without domestic dogs and without taming (or domesticating) the bush dog. Alternatively, its low density and elusive natural behaviour in an environment such as the Amazon rainforest or subtropical forests may have prevented its domestication (Beisiegel and Zuercher 2005; Sillero-Zubiri 2009).

The lower carnassial teeth of *S. venaticus* differ from the canid common pattern; the inner cusp of the talonid is missing, resulting in this part of the tooth forming a subsidiary blade and not a basin, emphasizing the cutting surfaces over grinding surfaces. These dentition features suggest a highly predacious habit with diminished importance of vegetable foods in the diet, i.e., an exclusively carnivorous diet (Ewer 1973; Zuercher et al. 2004; Beisiegel and Zuercher 2005). Maybe the lack of feeding flexibility related to anatomical dental restriction present in this species could have precluded domestication, as better candidates are omnivorous and generalist animals that are easy to feed.

The coexistence and close relationship between the Amazonian peoples and the bush dog (*Speothos venaticus*) are important and well documented (Descola 1994; Schwartz 1997; Zuercher et al. 2004). The bush dog is a species with a social structure, small size, and cooperative hunting in the tropical forest and open savannas (Table 2, Beisiegel and Zuercher 2005), with documented good experiences in reproduction in captivity (Chebez 1999; Zuercher et al. 2004). Indigenous peoples have occasionally kept bush dogs as pets and hunting dogs, emphasizing their superior hunting abilities when pursuing burrowing prey, especially paca and armadillos (Zuercher et al. 2004). Early naturalists reported small "dogs" that hunted in groups and were easily tamed and integrated by indigenous Amazonians (Wallace 1889; Rivière 2006), which according to Stahl (2013) could refer to the bush dog. However, other informants reported that bush dogs were difficult or impossible to domesticate because of their fierceness. Quechua peoples from eastern Ecuador still maintain a deeply spiritual and mystical vision of bush dogs (they have spiritual 'owners') for which they are reluctant to capture or kill bush dogs because it would be equivalent to stealing or killing a neighbour's hunting dog (Zuercher et al. 2004). Many indigenous peoples consider the bush dog to be one of the best hunters in the forest, sometimes singing songs to their own dogs in hopes of passing on the bush dog's skills (Descola 1996; Schwartz 1997).

Cultural reasons may have contributed to the impossibility of an active domestication of the bush dog. They could be esoteric or mystical, part of the indigenous worldview of the bush dog, which is partially in agreement with the conception of Stahl (2014). The lack of flexibility in its diet could be a strong biological reason, in agreement with the conception of Diamond (1997). A variety of possible causes could have precluded the bush dog domestication, despite its apparent favorable characteristics.

Final considerations

The relationship that occurs during domestication can be conceptualized as resulting from the interactions between biological aspects and the human's intellectual construction and action about the environment. Both, intertwined, are essential to facilitate the domestication process of a canid species. The Anna Karenina Principle (Diamond 1997) provides a comparative guide for biological plausibility (Tables 2, 3). However, domestication also requires a human worldview consistent with this practice (Ingold 2000), apparently absent in human societies from the Amazon (Stahl 2014). Humans have the inclination to tame, nurture, and live with almost all species of vertebrate animals (Clutton-Brock 2012), perhaps as part of what has been called biophilia (Wilson 1990). If domestication involves the domain of culture (human, active, creative) over nature (animal, objectified), some human societies in the Americas cannot conceive this idea (Ferreira Vander Velden 2009; Stahl 2014). In these societies (e.g., Achuar, distributed around the border in between Ecuador and Peru, Amazonia), the systems of logic clearly preclude animal domestication (Stahl 2014) because they do not view animals as being subordinated to humans (Ferreira Vander Velden 2009). In this sense, domestication as a cultural and biological combination does not occur when one of two components fails.

However, there are other important processes and relationships between humans and animals to recognize and consider when investigating the relations of humans and canids, as shown on the American continent.

An area of potential interest when considering canid-human interactions in the Americas is comparative mythology as studied by cultural evolution approaches. This subject has great potential to reveal historical patterns that mirror biological phenomena or suggest hypotheses on the history of human-animal interactions (Thuillard et al. 2018).

Acknowledgements We thank David Flores and Francisco Prevosti for the critical revision of this manuscript, Tesla Monson and Madeleine Geiger for discussions on canids in the Americas, Philippe Erikson for sharing bibliography, and Judith Recht for corrections of English language and for useful editorial suggestions. We also thank two anonymous reviewers who provided precise comments that helped us much to considerably improve this article, and Frank Zachos for editorial work. This research was supported by SNF grant 31003A_169395 to M.R.S.–V.

Author contributions VS and MRSV designed the work, conducted the acquisition, analysis, and interpretation of data and prepared the manuscript.

Funding Financial support was provided by the Swiss National Science Foundation Grant No. 31003A_169395 to MRSV.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethics approval No ethical approval was required.

Consent to participate All authors and institutions have approved this participation.

Consent for publication All authors and institutions have approved this publication.

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