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CANIS SPP. IDENTIFICATION IN CENTRAL MEXICO AND ITS ARCHAEOLOGICAL IMPLICATIONS : TOWARD A BETTER UNDERSTANDING OF THE ECOLOGY AND THE CULTURAL ROLE OF CANIDS IN ANCIENT MESOAMERICA

INTRODUCTION

Animal domestication induces not only biological changes of the targeted populations but also cultural shifts in the way the domesticated populations are perceived¹. The grey wolf (*Canis lupus*) was certainly the first animal to be involved in this bio-cultural transformation, leading to the appearance of the dog (*Canis familiaris*)², although the precise timing of this change is still intensely debated³. Regardless, during the Late Upper Palaeolithic, alterations in the animal's morphology⁴ and modifications in the behaviour of humans and “proto-domesticated dogs” alike⁵ consensually characterise the early steps of dog domestication. Once domesticated, the dog accompanied human groups in their migrations across the world until regions where the wolf has never been present, such as Australia⁶ and South America⁷.

However, this strong relationship never became exclusive and human societies maintained strong economic and symbolic interactions with the dog's wild relatives. In Europe, the red fox (*Vulpes vulpes*) has been used, by turns, as a companion⁸ and a fur provider⁹. Archaeological evidence also points toward the symbolic consideration of the grey wolf in many cultures across the Northern hemisphere, as a participant in ritual paraphernalia¹⁰. Nonetheless, all the studies aiming at precisely reporting the distinct role of dogs and non-dog canids in the archaeological record have been hampered by the difficulty in identifying the different canid species from their osteological remains¹¹.

With 18 to 20¹² identified species¹³, the American continent hosts the largest diversity of canid species in the world. The multiplicity of biologically closely related species increases both the potential of interaction with human societies and the ambiguity in their skeletal identification. In Mesoamerica¹⁴, four different species are present since the

1 e.g. Russell 2002; Vigne 2011; Zeder *et al.* 2006.

2 In this chapter, we chose to use the nomenclature suggested by Gentry *et al.* (2004) and refer to the dog as *Canis familiaris*, and not *Canis lupus familiaris* as advised by the taxonomic authorities (e.g. the Integrative Taxonomic Information System, <http://www.itis.gov>), in order to highlight the difference of status between the dog and the wolf.

3 e.g. Boudadi-Maligne & Escarguel 2014; Germonpré *et al.* 2009; Larson & Bradley 2014; Morey 2014; Ovodov *et al.* 2011; Perri 2016.

4 Boudadi-Maligne *et al.* 2012; Napierala & Uerpman 2012; Pionnier-Capitan *et al.* 2011.

5 Boudadi-Maligne *et al.* 2018; Larson *et al.* 2012; Morey 2006; Morey & Jeger 2017.

6 Balme *et al.* 2018; Fillios & Taçon 2016.

7 Guedes Milheira *et al.* 2017; Prates *et al.* 2010.

8 Grandal-d'Anglade *et al.* 2019 (but see Janssens & Lawler 2019 for a more nuanced interpretation); Guthmann *et al.* 2016.

9 Baxter & Hamilton-Dyer 2003; Bond 1996.

10 e.g. Losey *et al.* 2011; Pluskowski 2006; Sugiyama *et al.* 2014.

11 e.g. Lawrence 1967; Olsen 1985; Pluskowski 2006; Walker & Frison 1982.

12 The status of two taxa, the Eastern wolf (*Canis lycaon*) and the red wolf (*Canis rufus*), is still debated as they arise from a fairly recent admixture between the wolf (*Canis lupus*) and the coyote (*Canis latrans*) while presenting increased fitness to their environment (vonHoldt *et al.* 2016a; 2016b).

13 Wilson & Reeder 2005.

14 Mesoamerica is a cultural area ranging from central Mexico to western Honduras arising among agricultural societies ca. 2500 a.C. Despite encompassing regions of contrasting environments, constant exchanges and trade allowed the

beginning of the Holocene: the grey fox (*Urocyon cinereoargenteus*), the coyote (*Canis latrans*), the Mexican wolf (*Canis lupus baileyi*) and the dog¹⁵. Because of its very small size (on average 3-7kg for a body length of 1m including the tail¹⁶), the grey fox can often be disentangled from the other species, even from fragmented bones. As a matter of fact, this species is often identified in the archaeozoological record, albeit never in large proportions¹⁷. It is particularly scarce in the iconography¹⁸ and, unlike the other canids, the fox does not stand as a particular symbol in the Mesoamerican cosmogony (see § Cultural background). Therefore, we focused our study on the identification of the three other species, namely the dog, the wolf and the coyote.

In this paper, we aim to deepen our understanding of the role of large canids (*Canis* spp.) in Mesoamerica by providing a more accurate identification of the canid remains to the species level. After introducing the ecological and cultural background of each animal, we first present a geometric morphometric (GMM) analysis of the first lower molar and test its efficiency to discriminate specimens of known species using a reference collection of 42 modern and archaeological specimens. This approach is then applied to 22 archaeological teeth, each from a unique individual, from four archaeological sites in central Mexico. The subsequent identification is used to contrast our perception of canid diversity and their interaction with human societies in the region.

emergence of a common tradition and its consolidation up to the beginning of the 16th century p.C. (López Austin & López Luján 2012; Matos Moctezuma 1994).

15 Arroyo Cabrales & Carranza Castañeda 2009; Ceballos & Arroyo Cabrales 2012.

16 Fritzell & Haroldson 1982.

17 e.g. Alvarez & Ocaña 1999; Götz 2008.

18 Seler 1996, 193.

Ecological background

It is now widely accepted that the dog has been introduced to America after its domestication from Eurasian wolves¹⁹ while no evidence for the local domestication of a population of American wolves has been identified so far. Genetic evidence indicate that, outside of the Arctic region, the American dogs evolved in a distinctive monophyletic clade²⁰. It is only after 1492, with the European colonisation and the introduction of large numbers of Eurasian dogs, that this lineage faded, until becoming virtually absent in modern populations, including in breeds of American origin²¹. In pre-Columbian Mesoamerica, carbon and nitrogen stable isotope analysis indicates that dogs often show similar diets to those of humans²². This trend has been interpreted as an evidence of their close relationship, whether dogs would have been fed purposely on household diet or were scavenging food waste and human faecal material²³. In contrast, some individuals with more distant diets also suggest the presence of likely feral dogs, or at least loosely managed ones, around the settlements²⁴.

The Mexican wolf is the smallest subspecies of grey wolf²⁵ and genomic analyses have shown a clear distinction from the other North American populations²⁶. Once inhabiting the dry pine-oak forests ranging from the Southern United States to the isthmus of Tehuantepec²⁷, the subspecies was extinct in the wild by 1980²⁸. Based on seven (captive) founder individuals, an intensive programme of captive breeding, management and release led to a new wild population of 21 Mexican wolves in

19 Leonard *et al.* 2002; Ní Leathlobhair *et al.* 2018.

20 Ameen *et al.* 2019; Ní Leathlobhair *et al.* 2018.

21 van Asch *et al.* 2013; Castroviejo-Fisher *et al.* 2011; Ní Leathlobhair *et al.* 2018.

22 Manin 2017a; White 2004.

23 Gerry 1997; White *et al.* 2001; White & Schwarcz 1989.

24 White 2004; White *et al.* 2004.

25 Bogan & Mehlhop 1983; Hall & Kelson 1959 vol.2, 847.

26 García Moreno *et al.* 1996; vonHoldt *et al.* 2011; Wayne *et al.* 1992.

27 Leopold 1959, 401.

28 Brown 2002; cited by Harding *et al.* 2016.

Northern Mexico and around 100 in Arizona and New Mexico, according to a 2015-2016 census²⁹. Reports from the beginning of the 20th century indicate that the Mexican wolves were hunted to extinction to protect livestock³⁰. Nevertheless, studies of scats from wild Mexican wolves in the Blue Range Wolf Recovery Area (spanning between Arizona and New Mexico) show that their natural diet is centred on large preys, more specifically elk (*Cervus elaphus*) and deer (*Odocoileus* spp.)³¹.

The coyote is a widespread Nearctic canid. Whereas Pleistocene deposits have yielded evidence of its presence as far south as Costa Rica³², climate change following the Late Pleistocene would have led to the contraction of its natural distribution to the north³³. The coyote is particularly well adapted to prairies and human-modified environment, and during the last centuries, land clearance and the extirpation of its major predator, the wolf, have allowed the species to colonise most of North America and to extend across Central America³⁴. In central Mexico, the coyotes feed mostly on small to medium preys (Lagomorpha, Rodentia), but also fruits during the wet season³⁵, which would have all been available in the vicinity of ancient Mesoamerican settlements.

Due to habitat restriction and population depletion, hybridisation between coyotes and dogs³⁶ as well as wolves and coyotes³⁷ appear to be quite frequent amongst modern North American populations. Besides, pre-contact American dogs share some alleles with modern coyotes and North American wolves, indicating that this admixture goes back to prior 1492³⁸. Whilst the spatiotemporal extent of this hybridisation is not well understood yet,

29 Harding *et al.* 2016.

30 Leopold 1959, 401.

31 Merkle *et al.* 2009; Reed *et al.* 2006.

32 Lucas *et al.* 1997.

33 Hody & Kays 2018.

34 Hidalgo-Mihart *et al.* 2004; Hody & Kays 2018.

35 Aranda & Lopez-de-Buen 1995; Hidalgo-Mihart *et al.* 2001.

36 Adams *et al.* 2003; Schmutz *et al.* 2007.

37 vonHoldt *et al.* 2011; 2016a.

38 Ní Leathlobhair *et al.* 2018.

it may have played a role in the characterisation of wild and domestic populations alike.

Cultural background

Dogs and humans are closely associated in the Mesoamerican cosmogony. A Mexica belief, reported by the Spanish, tells us that only a dog was able to guide the spirit of the deceased through the death realm and to help him cross the Chiconahuapan river³⁹. The presence of dog remains⁴⁰ and dog effigies⁴¹ in human burials, or dog graves associated with funerary structures⁴² have all been interpreted as an evidence of those beliefs. In the Mexica mythology, Xolotl, the sky demon responsible for the movements of the stars, was represented by a dog⁴³. But the presence of the dog in daily life is also illustrated by the rare architectural models characteristic of the Late Preclassic (300 a.C. - 300 p.C.) in Western Mexico. These complex ceramic objects represent domestic and village scenes where dogs are often depicted⁴⁴. Testimonies of the early Spanish conquerors relate the consumption of dogs amongst the populations of central Mexico⁴⁵, which is confirmed by recurrent presence of dog bones in Mesoamerican middens, sometimes presenting typical patterns of burning or cut marks⁴⁶.

The identification of other canid species is more heterogeneous. Whether looking at the iconography or the ethnohistoric records, there does not seem to be a straight discrimination between coyotes and wolves in Mesoamerica. In his *Historia General de las Cosas de Nueva España*, Fray Bernardino de Sahagun introduces the *coiotl*, an animal close to both the wolf and the fox but neither one of them⁴⁷.

39 de Sahagun 1829, 263.

40 Martínez de León Mármol & Reyes Carlo 2007.

41 Jarquin & Martinez Vargas 2004.

42 Rodríguez Galicia *et al.* 2001.

43 Seler 1996, 182.

44 Day *et al.* 1996.

45 Diaz del Castillo 1996, 334; de Sahagun 1829, 160.

46 e.g. Clutton-Brock & Hammond 1994; Emery 2004; Manin & Lefèvre 2018; Valadez Azúa *et al.* 2013.

47 de Sahagun 1830, 524.

He describes it as a fierce and resentful animal that does not hesitate to attack people and their domestic animals. Its Nahuatl name, *coiotl*, is at the origin of the modern term “coyote”. A similar animal, only depicted in the Nahuatl version of this ethnohistoric work is the *cuatlachtli* that could correspond to the wolf⁴⁸. Perhaps because of the transparency of the term *coiotl*, historians and archaeologists often identify the non-dog canids present in the Mesoamerican iconography and folklore as coyotes rather than wolves, even though no morphological or ethological reasons are given⁴⁹.

However, the coyote is particularly discrete in the archaeozoological record: our review of the literature found only six occurrences. Two individuals have been identified in the superficial layers of Cueva de las Varillas, in Teotihuacan, and interpreted as natural accumulation⁵⁰. Still in Teotihuacan, one coyote has been identified in burial 6 of the Moon Pyramid⁵¹. In Western Mexico, on the site of Malpaís Prieto, a complete radius found in the midden of an elite house is particularly slender, and it was identified as a possible coyote⁵². Finally, two potential individuals (cf. *Canis latrans*) are mentioned in the Late Postclassic and Colonial occupation of Tipu, Guatemala⁵³. Nonetheless, many authors maintained their identification to the level of the genus (*Canis* sp.), acknowledging the possible presence of coyotes⁵⁴.

Without being largely more common than the coyote yet, the wolf is more frequent in the archaeozoological record and always associated with extraordinary deposits. In Teotihuacan, in the dedicatory burials of the Moon Pyramid (burial 2, 4 and 6), the remains of at least 22 wolves were present⁵⁵, and others were found in the Quetzalcoatl Pyra-

mid, although there is no count⁵⁶. Several skeletons of wolves were also recovered in the ancient city of Mexico Tenochtitlan⁵⁷, including two complete individuals (offerings 120 and 125) richly adorned with green-stone beads, shell pendants and gold and copper bells⁵⁸. Other findings include various remains from tronco-conical pits in Cuanalan, Basin of Mexico⁵⁹, and a single isolated mandible in a ceremonial cache in Cantona, Puebla⁶⁰.

It appears from this brief overview that the dogs, the coyotes and the wolves present distinct behaviours and ecological characteristics ranging from domestic (dogs) to commensal (coyotes) and wild animals (wolves). This gradient might be reflected in their cultural perception in ancient Mesoamerica, denoting their relative proximity to the anthropized environment and hence human settlements. Therefore, a more systematic identification of the remains in the archaeozoological record would enhance our understanding of the relationships between human societies and canid populations.

TOOTH GEOMETRIC MORPHOMETRICS: TESTING A “NEW” TOOL FOR CANID SPECIES IDENTIFICATION

Geometric morphometrics (GMM) is an approach allowing the precise capture of phenotypic variations⁶¹. Because, in mammals, the shape of each tooth is strictly controlled by complex genetic signals⁶² and this tissue is hardly ever remodelled through the lifetime of an individual⁶³, tooth morphometry is believed to retain a strong taxonomic and phylogenetic signal. Indeed, recent GMM

application to archaeological teeth of rodents⁶⁴, pigs⁶⁵ or equids⁶⁶ have shown the potential of this approach to refine taxonomic identification of ancient remains and unravel population history. Yet, while canid complete skulls and mandibles have been the object of in-depth GMM analyses⁶⁷, single-tooth morphometrics have been studied less intensively⁶⁸.

Reference collection

In order to distinguish between the three species of Mesoamerican large canids, we developed a two dimensional GMM protocol on the first lower molar. Forty-two teeth (one per individual) of known species were first analysed (**tab. 1**). They consist in 16 modern coyotes, 10 modern wolves, 8 modern dogs and 8 archaeological Mesoamerican dogs genetically identified in previous studies⁶⁹. All specimens were adults with fully erupted first molars.

When selecting the wolves, priority was given to the Mexican subspecies, whether they were wild or captive (N=2). A very limited number of individuals was available within this category⁷⁰, which can be related to the scarcity of the population in the wild. Thus the sampling was extended to wild individuals of known provenience (N=8). Individuals which skull presented “dog” characteristics such as a steep angle between the forehead and the snout⁷¹ and a larger orbital angle⁷², were considered as questionable identification and not used for this study. Simi-

larly, Eastern and red wolves were not considered in this study as they may represent different degrees of hybridisation between wolves, coyotes, and dogs to a lesser extent⁷³.

Because they would match the expected size and robustness of ancient Mesoamerican dogs⁷⁴, seven modern dogs used as reference were chosen amongst dolicocephalic / mesocephalic and medium-sized breeds. One village dog from Northern Peru, affected with canine ectodermal dysplasia (CED), was also included. Although this congenital defect also impacts the teeth morphology⁷⁵, all the landmarks used in our protocol were visible on this individual. Because our archaeological collection included dogs potentially affected by CED⁷⁶, it appeared particularly useful to consider this variation in the tooth morphology. Finally, we used eight archaeological dog mandibles from Tizayuca, Basin of Mexico, that were previously identified as dogs based on their metrics and mitochondrial DNA⁷⁷.

Archaeological samples

A total of 22 teeth of unidentified canids from four archaeological sites of central Mexico (**fig. 1**) was analysed for species identification. All the teeth were fully mineralised and showed limited wear. All the landmarks used in our protocol were visible on each of these teeth.

The site of Nogales represents the western end of the collection analysed in this study. It was occupied by sedentary agriculturalists from ca. 500 p.C. until its abandonment around 1000 p.C.; a brief re-occupation by groups of hunters is noted ca. 1450-1500 p.C.⁷⁸. A fragmented mandible analysed in this study comes from the early occupation of the site, around 500 p.C., and was found in the filling

48 Blanco *et al.* 2007.

49 e.g. Carballo 2007; Kubler 1972; Seler 1996, 193.

50 Valadez Azúa & Rodríguez Galicia 2009, 622.

51 Sugiyama *et al.* 2014.

52 Manin 2015, 316.

53 Emery 1999.

54 e.g. Álvarez & Ocaña 1999; Valentín Maldonado 1997.

55 Sugiyama & López Luján 2006; Sugiyama *et al.* 2014.

56 Álvarez & Ocaña 1999, 82.

57 Álvarez & Ocaña 1999, 82.

58 López Luján & Chavez Balderas 2010; López Luján *et al.* 2012.

59 Álvarez & Ocaña 1999, 82.

60 Valentín Maldonado com. pers. 2014.

61 Adams *et al.* 2004, 2013.

62 Jernvall & Thesleff 2000; Thesleff 2006.

63 Hillson 2005, 152.

64 Cucchi *et al.* 2013; Hulme-Beaman *et al.* 2018; Valenzuela-Lamas *et al.* 2011.

65 Cucchi *et al.* 2011; Evin *et al.* 2013; 2015.

66 Cucchi *et al.* 2017; Seetah *et al.* 2014.

67 Ameen *et al.* 2019; Drake *et al.* 2017; Drake & Klingenberg 2010; Fisher 2019; de Moura Bubadué *et al.* 2016; Schmitt & Wallace 2014.

68 Amano 2011; Pionnier-Capitan 2010.

69 Manin *et al.* 2018; Ní Leathlobhair *et al.* 2018.

70 Our study was carried out mainly in the collections of Anatomie Comparée of the Muséum national d'Histoire naturelle, with a short complementary stay in the Laboratorio de Arqueozoología M. en C. Ticul Álvarez del Instituto Nacional de Antropología e Historia, Mexico.

71 Lawrence & Bossert 1967.

72 Iljin 1941.

73 vonHoldt *et al.* 2011.

74 Blanco Padilla *et al.* 2009.

75 Kupczik *et al.* 2017; Shirokova *et al.* 2013.

76 Manin *et al.* 2018.

77 Manin *et al.* 2018; Ní Leathlobhair *et al.* 2018.

78 Pereira 2008.

Individual	Species	Category	Origin	Logarithm of the centroid size	Det
MNHN-ZO-1928-1912	<i>Canis latrans</i>	Modern	Mexico city, Mexico*	1,725	Coyote
MNHN-ZO-1887-1253	<i>Canis latrans</i>	Modern	Mexico	1,544	Coyote
MNHN-ZO-2007-454	<i>Canis latrans</i>	Modern	USA	1,730	Coyote
MNHN-ZO-2007-456	<i>Canis latrans</i>	Modern	Kansas, USA	1,747	Coyote
MNHN-ZO-2007-457	<i>Canis latrans</i>	Modern	Unknown	1,819	Coyote
MNHN-ZO-2007-458	<i>Canis latrans</i>	Modern	Michigan, USA	1,862	Coyote
MNHN-ZO-1962-966	<i>Canis latrans</i>	Modern	Texas, USA	1,867	Coyote
MNHN-ZO-1962-967	<i>Canis latrans</i>	Modern	Pensylvania, USA	1,857	Coyote
MNHN-ZO-1880-839	<i>Canis latrans</i>	Modern	Unknown	1,689	Coyote
MNHN-ZO-1929-280	<i>Canis latrans</i>	Modern	Unknown	1,752	Coyote
MNHN-ZO-1931-691	<i>Canis latrans</i>	Modern	Unknown	1,795	Coyote
INAH-1539	<i>Canis latrans</i>	Modern	Mexico	1,780	Coyote
INAH-7270	<i>Canis latrans</i>	Modern	Mexico	1,775	Coyote
INAH-7753	<i>Canis latrans</i>	Modern	Mexico	1,804	Coyote
INAH-7754	<i>Canis latrans</i>	Modern	Mexico	1,652	Coyote
INAH-7755	<i>Canis latrans</i>	Modern	Mexico	1,744	Coyote
MNHN-ZO-1997-457	<i>Canis lupus</i>	Modern	Pyrenees, France	2,098	Wolf
INAH-7757	<i>Canis lupus bayleyi</i>	Modern	Mexico	1,918	Wolf
MNHN-ZO-1927-2353	<i>Canis lupus bayleyi</i>	Modern	Mexico city, Mexico*	1,977	Wolf
MNHN-ZO-1990-23	<i>Canis lupus</i>	Modern	Quebec, Canada	2,050	Wolf
MNHN-ZO-1911-754	<i>Canis lupus</i>	Modern	Xinjiang, China	2,068	Wolf
MNHN-ZO-1997-452	<i>Canis lupus</i>	Modern	Lubelskie, Poland	2,104	Wolf
MNHN-ZO-1974-339	<i>Canis lupus</i>	Modern	Kurdistan, Iran	1,958	Wolf
MNHN-ZO-1974-340	<i>Canis lupus</i>	Modern	Hamadan, Iran	2,002	Wolf
MNHN-ZO-1962-1525	<i>Canis lupus</i>	Modern	Unknown (Rusian wolf)	2,187	Wolf
MNHN-ZO-1934-72	<i>Canis lupus</i>	Modern	Unknown (Arctic wolf)	2,041	Wolf
MNHN-ZO-1985-1208	<i>Canis familiaris</i>	Modern	France (Brittany spaniel)	1,801	Dog
MNHN-ZO-1985-1216	<i>Canis familiaris</i>	Modern	France (Belgian Shepherd Dog)	1,811	Dog
MNHN-ZO-1985-1219	<i>Canis familiaris</i>	Modern	France (Cocker)	1,717	Dog
MNHN-ZO-1985-1232	<i>Canis familiaris</i>	Modern	France (Brittany spaniel)	1,819	Dog
MNHN-ZO-1985-1259	<i>Canis familiaris</i>	Modern	France (Brittany spaniel)	1,768	Dog
MNHN-ZO-1985-1289	<i>Canis familiaris</i>	Modern	France (Dachshund)	1,619	Dog
MNHN-ZO-1985-1297	<i>Canis familiaris</i>	Modern	France (German Shorthaired Pointer)	1,810	Dog
Peru_mand01	<i>Canis familiaris</i>	Modern	Peru	1,721	Dog
MT-01	<i>Canis familiaris</i>	Archaeological	Tizayuca, Hidalgo, Mexico	1,659	Dog
MT-02	<i>Canis familiaris</i>	Archaeological	Tizayuca, Hidalgo, Mexico	1,771	Dog
MT-04	<i>Canis familiaris</i>	Archaeological	Tizayuca, Hidalgo, Mexico	1,720	Dog
MT-05	<i>Canis familiaris</i>	Archaeological	Tizayuca, Hidalgo, Mexico	1,673	Dog
MT-08	<i>Canis familiaris</i>	Archaeological	Tizayuca, Hidalgo, Mexico	1,734	Dog
MT-15	<i>Canis familiaris</i>	Archaeological	Tizayuca, Hidalgo, Mexico	1,718	Dog
MT-17	<i>Canis familiaris</i>	Archaeological	Tizayuca, Hidalgo, Mexico	1,671	Dog
MT-20	<i>Canis familiaris</i>	Archaeological	Tizayuca, Hidalgo, Mexico	1,690	Dog

Tab. 1. List of the samples in the reference collection.

*: Captive individuals from the Zoologico de Chapultepec.

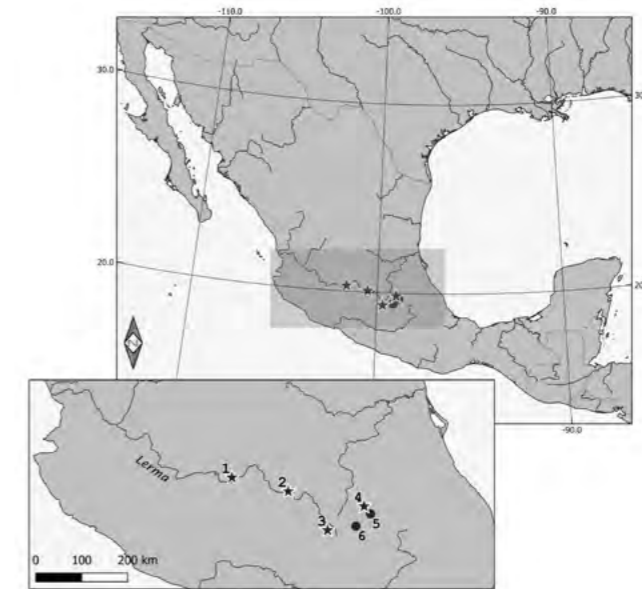


Fig. 1. Location of the sites analysed in this study (stars) and the main sites mentioned in the text (dots).

1 = Nogales; 2 = JR74; 3 = Calixtlahuaca;
4 = Tizayuca; 5 = Teotihuacan; 6 = México-Tenochtitlan.

of a platform. The other two remains were isolated teeth found in disturbed layers.

The site of El Mezquite – Los Azules (JR74) is located in the cradle of the Chupicuaro culture, in the Lerma basin⁷⁹ and was occupied from ca. 600 a.C. to 400 p.C.⁸⁰. The sample analysed in this study comes from an isolated mandible found in the filling of a Chupicuaro structure dated to the Classic period, between 250 p.C. and 400 p.C.⁸¹.

Calixtlahuaca is a large urban centre located in the Toluca valley and occupied between ca. 1100 and 1530 p.C. Historical documents indicate that the city was conquered by the Aztecs of the triple alliance between 1475 and 1478. In 1530, in order to establish their authority on the valley, the Spaniards evacuate the city and relocate its inhabitants in Toluca⁸². The zooarchaeological analysis shows that the canids were the taxonomic group the most represented in the site, both in terms of NISP (88;

55% of the total NISP) and MNI (5; 24% of the total MNI)⁸³. The two samples analysed here come from structure 307, the domestic midden of a high-status residence associated with the Ninupi phase (1380-1450 p.C.).

Tizayuca is a settlement located in the basin of Mexico. Architectural, lithic and ceramic remains from the Teotihuacan complex, Toltec and Aztec cultures, as well as sporadic Colonial elements indicate that the area was occupied persistently from 200 to 1520 p.C. However, the stratigraphic layers were particularly thin and prevented the clear chronological attribution of the bone remains⁸⁴. As in Calixtlahuaca, the canids outnumbered the other taxa (NISP = 877, or 25 % of the total NISP; MNI = 42). Three adults and one juvenile canids were found in burials, the adults being all identified as dogs on the basis of their mitochondrial DNA⁸⁵. Sixteen first lower molars of unidentified canids were analysed in this study.

79 Porter 1956.

80 Faugère in prep.

81 Manin in prep.

82 Huster & Smith 2015; Tomaszewski & Smith 2011.

83 Manin 2017b; 2015, 160.

84 Equihua *et al.* 2008.

85 Manin *et al.* 2018; Ní Leathlobhair *et al.* 2018.

Method

Each tooth was photographed on the occlusal view using a standardised protocol. The teeth were positioned with the talonid being on a horizontal plan and photographed using a Canon EOS 1000D digital camera equipped with a 70-300 mm macro lens. Tooth shape was assessed by digitising five landmark and 60 sliding semi-landmark coordinates on the images (**fig. 2**) using tpsDig2 v2.19⁸⁶. Superimposition and subsequent statistical analyses were performed using R 3.5.3⁸⁷. The coordinates of the different specimens were superimposed and scaled using the Morpho package⁸⁸. Size analyses were based on the log-transformed centroid size and shape analyses were based on the Procrustes residuals (coordinates after superimposition). Differences in size were tested using Kruskal-Wallis and Wilcoxon tests and visualised by boxplots. Analysis of shape variation was based on a principal component analysis (PCA), before testing the differences between groups using multivariate analysis of variance (MANOVA) and linear discriminant analysis (LDA) after reduction of the dimensionality of the data⁸⁹. The LDA was paired with a leave-one-out cross validation assessing the discriminant power of the analysis. The threshold to confidently identify an individual was set to 95%. Identifications made with a probability of 75% to 95% were only considered as plausible.

Statistical tests were performed using a reference threshold of $\alpha=0.05$ on R v3.5.3⁹⁰

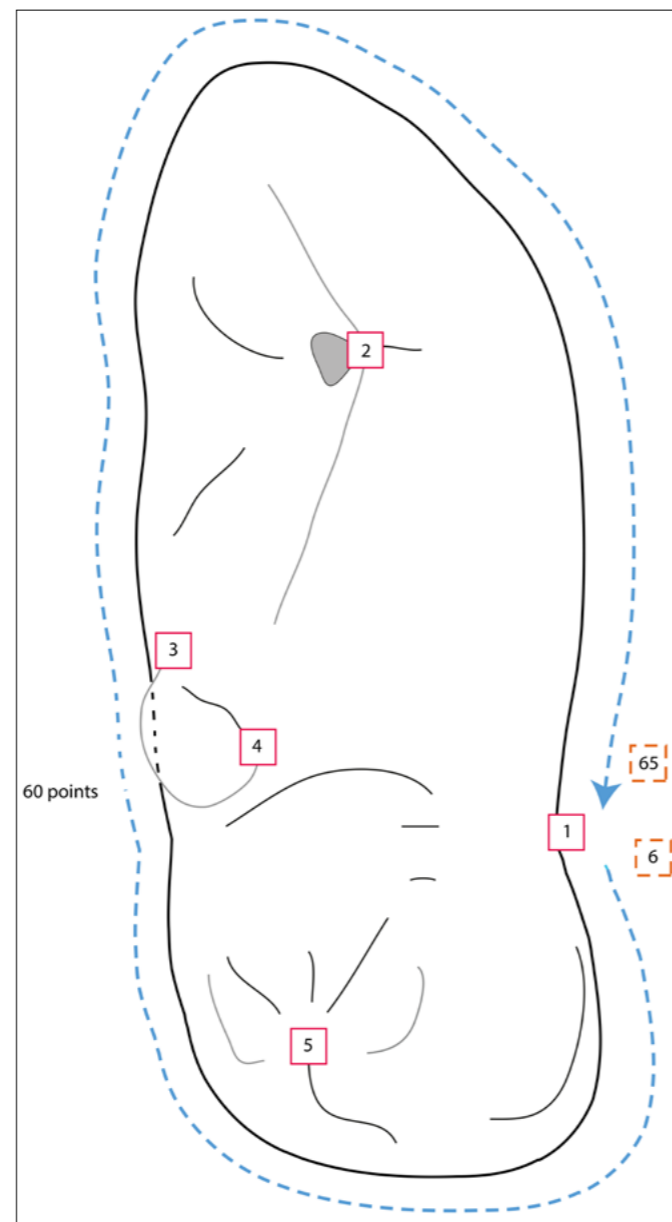


Fig. 2. Protocol of analysis. Red squares = landmarks; blue line = succession of semi-landmarks.

IDENTIFYING THE CANID SPECIES PRESENT IN CENTRAL MEXICO

Coyotes, dogs and wolves from the reference dataset differ in size (Kruskal-Wallis test, $H=23.5$, $df=2$, $p=8e-6$), although when they are compared two by two only the wolf differs from the others (Wilcoxon test, $p=3.8e-7$ for both comparisons), while the coyote does not differ in size from the dog ($p=0.17$) (**fig. 3**). The molar log-transformed centroid size of the wolf ranges from 1.918 to 2.187, that of the coyote from 1.554 to 1.867 and that of the dog from 1.619 to 1.819 (**fig. 3**). The molar size of the unknown archaeological samples ranges from 1.637 to 1.799 (**tab. 2**) overlapping the sizes of the dogs ($p=0.052$) while being slightly smaller than the coyote ($p=0.0016$) and considerably smaller than what we observed in wolves ($p=1.9e-7$) (**fig. 3**).

The first two axes of the shape PCA (21.55 % and 15.96 % of total variance respectively, **fig. 4**), tend to separate wolves from the other groups. While coyotes and archaeological unidentified specimens are clearly separated from the wolves, the reference group of dogs (including both modern and archaeological) overlap with wolves and coyotes along axis

one, and mostly with coyotes along axis 2. The unidentified archaeological specimens clearly overlap with the coyotes and the dogs, and not a single one overlap with the wolves.

The three reference taxa differ in their first lower molar shape ($F(10, 72)=16.369$, $p=6e-15$), and the discriminant analysis reach 88.3 % of correct cross validation. The dog and the coyote are differentiated along the first discriminant axis (67.1 % of the total variation, **fig. 5**) while the wolf differentiates along the second component (32.9 % of the total variation). Predicted position of most of the archaeological unknown specimens overlaps with the dog except one (**fig. 5**). Among the unknown archaeological specimens, 18 dogs were identified with a probability ranging from 96.7 % to 100 % (**tab. 2**). Lower probabilities of identification led to the identification of two 'possible dogs' with probabilities of identification of 75.1 % (MT18) and 80.1 % (MT25) and one 'possible coyote' (MT14) identified with a probability of 86.2 %. Finally, the last specimen (MT24) was identified with a probability of 69.7 % to dog, 22.7 % to coyote and 7.6 % to wolf and was left unidentified (**tab. 2**).

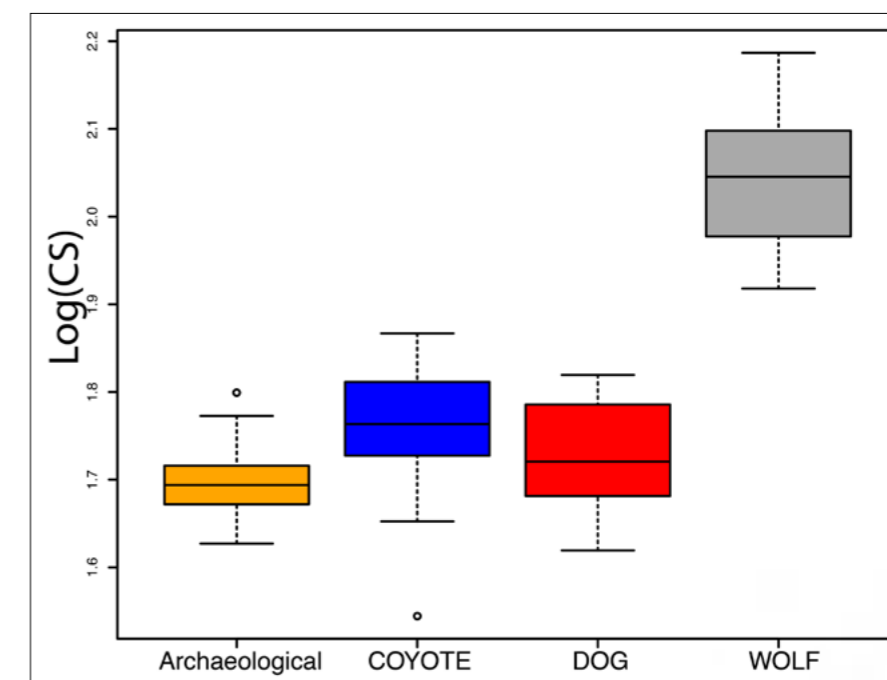


Fig. 3. Boxplot of the logarithm of the centroid size (LogCS) amongst the reference groups and the archaeological unidentified specimens.

86 Rohlf 2015.

87 R Core Team 2019.

88 Schlager 2017.

89 Baylac & Friess 2005.

90 R Core Team 2019.

Individual	Logarithm of the centroid size	Probability of identification ^a		
		Coyote	Dog	Wolf
Barajas (400-1100 AD)				
MBo1	1.723	0	100	0
MBo2	1.773	0	98.9	1.0
MBo3	1.716	0	99.9	0
Calixtlahuaca (1380-1450 AD)				
MCo1	1.637	0.1	99.8	0
MCo2	1.717	0.1	99.9	0
JR74 (250-400)				
MCh01	1.708	0	100	0
Tizayuca (350-1500 AD)				
MT03	1.672	0	100	0
MT06	1.672	0	100	0
MT07	1.647	0	99.7	0.3
MT09	1.799	0	100	0
MT12	1.663	0	99.7	0.2
MT13	1.696	0.1	99.9	0
MT14	1.653	86.2	12.1	1.7
MT16	1.769	0	99.9	0.1
MT18	1.707	0.2	75.1	24.7
MT19	1.704	2.5	96.7	0.8
MT21	1.692	0.1	99.6	0.4
MT22	1.692	2.1	97.8	0.1
MT23	1.678	0.8	98.6	0.6
MT24	1.627	22.7	69.7	7.6
MT25	1.682	0.1	80.1	19.8
MT26	1.696	0	100	0

Tab. 2. Probability of identification of the unknown samples based on predictive linear analysis.

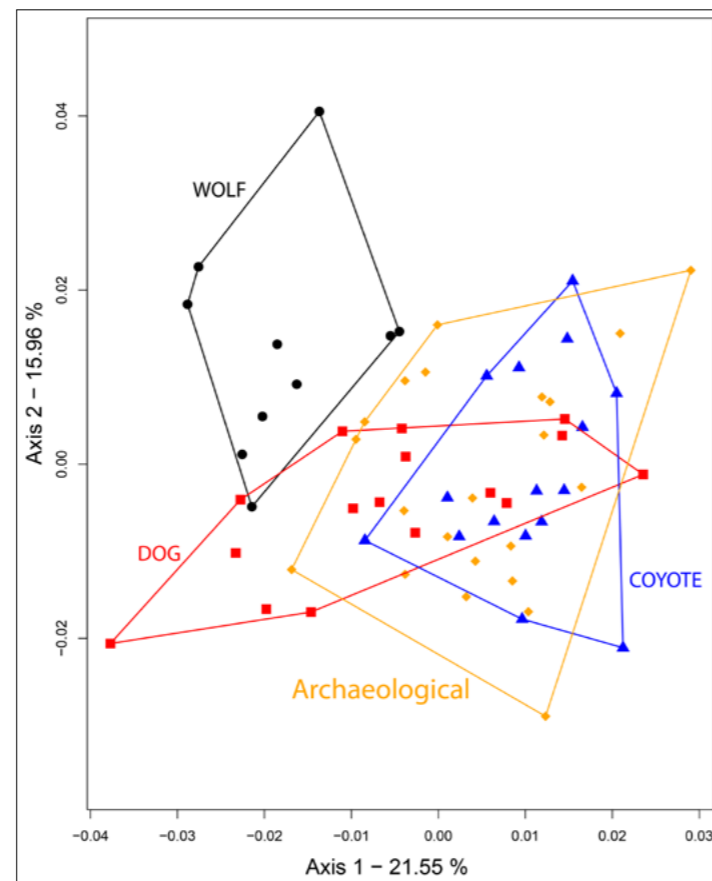


Fig. 4. Shape variation: two first axes of a Principal component analysis.

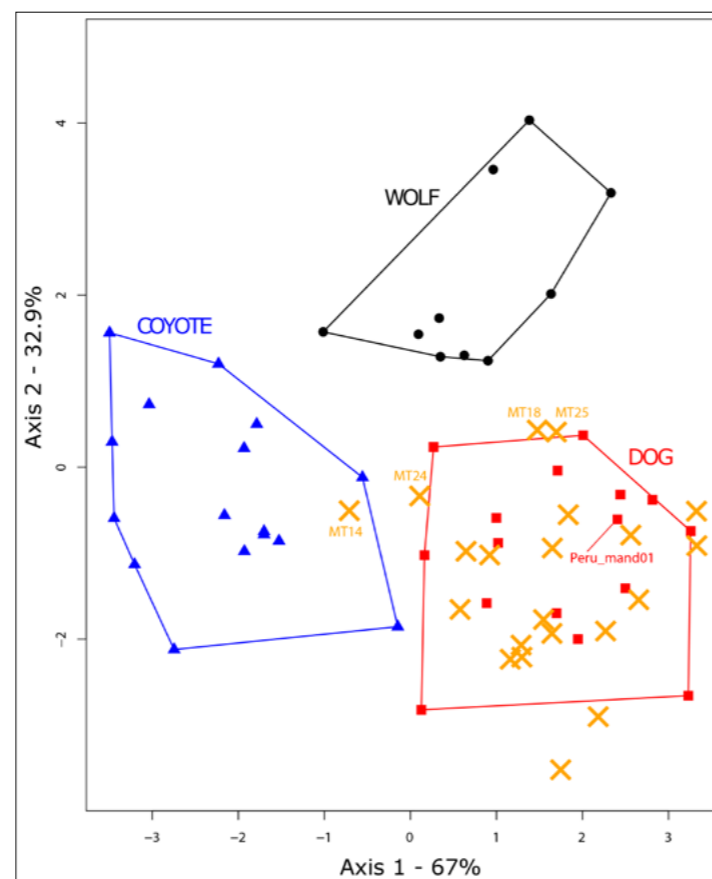


Fig. 5. Linear discriminant analysis on shape. The position of the archaeological specimens was calculated using a predictive linear discriminant analysis.

DISCUSSION

This preliminary study confirms that the GMM analysis of the first lower molar is a promising tool for the taxonomic identification of North American canids. From a set of reference individuals, we show that coyotes, dogs and wolves can be successfully discriminated through their size and shape using a 2D landmark-based approach. Applying this same approach to archaeological samples allows us to discuss more in depth the species distribution and its cultural and ecological implications.

Dogs

Most of the archaeological first lower molars analysed in this study securely come from dogs (18 (+2 possible dogs) out of 22). This result is consistent with previous zooarchaeological studies showing the constant presence of dogs in central Mexico⁹¹. In fact, all the individuals from Nogales, JR74 and Calixtlahuaca present a molar morphometry consistent with dogs. The identification in Tizayuca is, however, more problematic. Twelve individuals are confidently identified as dogs whereas two individuals could only be identified as possible dogs due to their lower probability of identification. This variation in the probability of identification may be related to a more diverse tooth shape spectrum in the dogs from Tizayuca. Yet, the dogs from this site show diverse morphotypes, including the presence of possible hairless dogs⁹². The hypothesis that some individuals might be the result of hybridisations between dogs and wolves or dogs and coyotes is also considered below (4.d).

Coyotes

Although coyotes are quite rare in the archaeological record of central Mexico, one individual from Tizayuca have been identified as a possible

coyote on the basis of its tooth shape, with a probability of 86 %. The presence of a coyote in this specific site could be related to the high number of faunal remains retrieved during the archaeological exploration (more than 3 000, including 877 canid remains), as a larger amount of bones would increase the probability of identifying scarce or new species⁹³. The large number of canid individuals identified in Tizayuca and their prevalence on the site also suggest a major interest for that taxonomic group, whether it was for economic or symbolic purposes. However, while dogs have been found in burials, associated with civic-ceremonial or domestic spaces, the possible coyote mandible was found as isolated and fragmented, in a pit, with very limited contextualisation.

Wolves

No wolves were confidently identified in our study, although they have been reported in other sites in the region, in particular Teotihuacan and Mexico-Tenochtitlan⁹⁴. In these two sites, their bodies were found in exceptional offerings where they took part in state-level rituals⁹⁵. As none of our samples come from such symbolic context, the absence of wolves is consistent with their peculiar cultural association.

Hybridization between dogs and wild canids?

Evidence of genetic admixture between dogs and wolves or coyotes has been found in the archaeological record⁹⁶ and amongst modern populations⁹⁷. Discovering the bones of hybrids of dogs and wolves, or coyotes, in the archaeological record

⁹³ Lyman 2008, 180.

⁹⁴ López Luján & Chávez Balderas 2010; Lopez Lujan *et al.* 2012; Sugiyama *et al.* 2014; Valadez Azúa & Rodríguez Galicia 2009.

⁹⁵ *ibid.*

⁹⁶ Ní Leathlobhair *et al.* 2018.

⁹⁷ Adams *et al.* 2003; Schmutz *et al.* 2007 vonHoldt *et al.* 2011; 2016b.

⁹¹ Manin & Lefèvre 2016; Valadez Azúa & Rodríguez Galicia 2014.

⁹² Manin *et al.* 2018.

is thus plausible. As a matter of fact, some authors have suggested the identification wolf-dog hybrids based on morphoscopic and metric analyses, assuming that first generation hybrids would inherit a mixture of characters from each parent⁹⁸. Nonetheless, the relationship between genotype and phenotype is not strictly cumulative, in particular due to epistatic phenomena where a combination of genes and alleles will interact to produce a specific phenotype. Experimentations have shown that if some hybrids tend to present an intermediate morphology⁹⁹, others display an original phenotype¹⁰⁰. Questionable specimens MT18 and MT25, and above all MT24, might be the evidence of a significant admixture between dogs and wild canids. However, addressing this question would require to expand the reference collection in three directions. First of all, the use of a larger reference collection for each species is required to ensure the diversity of tooth shape is adequately captured in the analysis. Secondly, the inclusion of known hybrid populations such as the Eastern and the red wolves, in large enough numbers, would provide an overview of the diversity in such groups. Finally, the degree of admixture in these hybrid individuals should be quantified using genetic tools, in order to identify the range of morphological variations in connection with relative dog, wolf and coyote ancestry.

Ecological and cultural impact of the distribution of canids in the archaeological sites of central Mexico

Through this study, we highlight the broad distribution and the prevalence of the dog amongst the canids present in the zooarchaeological record of central Mexico. By its absence in the corpus analysed here, the highly symbolic role of the wolf is comforted. Although it is hard to infer past distribution of a species from its modern distribution, the

wolf's ecology and behaviour implies that it would not have been found regularly near human settlements but rather in forested habitats. There are numerous testimonies of the importance of hunting in the Mesoamerican ritual life¹⁰¹. While the deer was a prey of choice in different societies, associated with elite rituals and ceremonial hunting¹⁰², the capture or hunting of wolves could have taken place in the same context.

On the contrary, as a species of open and disturbed environment, the coyote may have thrived in past agricultural landscapes and it can be considered as a commensal species. Its formal identification in the archaeological record has proven to be problematic and often requires the use of ancient DNA¹⁰³. Using a systematic GMM approach, we suggest that only a small minority of coyotes were present in the archaeological sites of central Mexico, which confirms previous zooarchaeological results. The scarcity of the coyote in the Mesoamerican archaeological record could be related to a cultural bias and a conscious choice of wolves against coyotes in ceremonial paraphernalia and state-level rituals, due to ecological and ethological distinctions. But whereas today coyotes proliferate in central Mexico they may have been only occasional in the past. The development of agropastoralism leading to land clearance and increasing hunting pressure on its natural predator, the wolf, has allowed the coyote to extend its natural distribution during the past 500 years¹⁰⁴. Its previous natural distribution is not well understood and the mountain range of central Mexico could have represented its southernmost limit. This hypothesis would strengthen previous suggestions that the wild canids represented in the iconography, in particular in the site of Teotihuacan, are wolves rather than coyotes¹⁰⁵.

CONCLUSION AND FUTURE DIRECTIONS

In this paper, we used a GMM approach to identify first molars of large canids from 4 archaeological sites in central Mexico. We demonstrate that the dog, the wolf and the coyote can be differentiated using the size and shape of their teeth. Using the same approach on unidentified archaeological samples, we succeeded in the confident identification of 18 dogs, as well as two possible dogs and one possible coyote. One sample from the archaeological site of Tizayuca remains unidentified.

Overall, we confirm the prominent place of dogs in ancient Mesoamerica and the typical association of wolf remains and state-level rituals. The scarcity of coyote remains suggest this species was not as highly valued as the two others, whether it was in economic or symbolic terms. The ambiguous identification of some individuals that present an intermediate phenotype also led us to raise the question of the presence of hybrids, although a larger study would be required to fully address this question.

This preliminary study demonstrates the potential of a GMM approach for the identification

of canid species in ancient Mesoamerica. However, it still relies on a very limited amount of reference individuals that will have to be expanded in the future. The confrontation of the GMM results to a genetic identification, through the analysis of ancient mitochondrial and nuclear DNA, would also be necessary to confirm the species identification and identify the degree of admixture between taxa.

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101 e.g. Olivier 2015.

102 Dehouve 2010; Faugère 2008; Olivier 2015.

103 Byrd *et al.* 2013; Kemp *et al.* 2017; Monagale *et al.* 2018.

104 Hidalgo-Mihart *et al.* 2004; Hody & Kays 2018.

105 Sugiyama 2014.

98 Valadez Azúa *et al.*, 2006; Walker & Frison 1982.

99 e.g. Evin *et al.* 2015.

100 e.g. Renaud *et al.* 2009.

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