Extinctions in near time: new radiocarbon dates point to a very recent disappearance of the South American fox *Dusicyon avus* (Carnivora: Canidae)

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Almost all large carnivorans (Carnivora; > 20 kg) that inhabited South America became extinct around the Late Pleistocene–Early Holocene transition. Two exceptions were species of coyote-sized *Dusicyon*, one insular (*D. australis*) and one continental (*D. avus*). The extinction of the former is a resolved matter, but that of *D. avus*, found in the Patagonian and Pampean regions, is still poorly understood. Using the Gaussian-Resampled Inverse-Weighted McInerny method we present new radiocarbon evidence indicating that its disappearance occurred in very recent times (about 324–496 years cal yr). We found no evidence to support a role for hybridization with domestic dogs in causing the extirpation of this fox. Climatic change may have reduced its distributional range, as has happened with other mammals, although not to the extent of explaining its extinction. Climatic change, however, coupled with increased anthropogenic impacts such as hunting, domestic dogs, and/or other aspects relating to the impact of European colonization in South America’s southern cone, were the probable main drivers of the recent extinction of *D. avus*. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, 116, 704–720.

ADDITIONAL KEYWORDS: carnivorans – environmental changes – Holocene – human impact.

INTRODUCTION

Recent extinctions, i.e. those taking place in comparatively modern times (after AD 1500), and their study...
are important in that they may herald the onset of a sixth mass extinction (Leakey & Lewin, 1992; MacPhee & Flemming, 1999; Ceballos & Ehrlich, 2002; Barnosky et al., 2011; Teta et al., 2014). These extinctions, which have impacted a wide array of organisms, principally affected small-sized, island-dwelling species (body mass < 10 kg) in the case of mammals, and were apparently not related to climatic change (MacPhee & Flemming, 1999). Continental South American mammals showed few extinctions after the Early Holocene (MacPhee & Flemming, 1999; Turvey, 2009; Turvey & Fritz, 2011). Since the arrival of Europeans, some ten species mostly small rodents and marsupials- are thought to have become extinct (Teta et al., 2014) although taxonomic uncertainties make the true number uncertain.

South America suffered a large extinction during the Late Pleistocene–Early Holocene, mostly affecting large and mega-mammals (Barnosky et al., 2004; Borrero, 2008a; Cione, Tonni & Soibelzon, 2008). Mammalian predators were also affected, and several large carnivores – including sabre-tooth cats (Smilodon spp.), a large jaguar (Panthera onca mesembrina), short faced bears (Aerotherium spp.), and large hypercarnivorous canids (e.g. Canis dirus, Procyon spp.) – disappeared during the Pleistocene–Holocene transition. The surviving depauperate assemblage of large carnivores includes only two large felids (> 50 kg; Puma concolor, Panthera onca), a large omnivorous canid (> 20 kg; Chrysocyon brachyurus), and a small bear (> 50 kg; Tremarctos ornatus; Prevosti & Rincón, 2007; Cione et al., 2008; Prevosti, Ubilla & Perea, 2009; Prevosti & Soibelzon, 2012). During the late Holocene, the fox Dusicyon avus (10–15 kg) disappeared in the Pampean region and Patagonia (Prevosti et al., 2011). The cause of the extinction of Dusicyon australis – the endemic Malvinas fox or Falklands wolf – in the late 19th century is a resolved matter (Cabrera & Yepes, 1940; Clutton-Brock, Corbet & Hills, 1976; Slater et al., 2009; Prevosti et al., 2011; Austin et al., 2013), but the processes that triggered the disappearance of their continental counterpart, D. avus, are still controversial.

Slater et al. (2009) and Austin et al. (2013) established that D. avus is the sister taxon of D. australis, and that this clade is related to the living maned wolf (Chrysocyon brachyurus). Dusicyon avus has a rich fossil record, based on several Late Pleistocene (Lujanian) localities in Southern Brazil, Uruguay, Argentina and Chile, but there are also Holocene records from the Patagonian and Pampean regions (Argentina and Chile, Fig. 1, Supporting Information, Appendix S1; see Prevosti et al., 2011; for a review). According to recent studies, the Dusicyon lineage became extinct in the late Holocene, first with the fading of D. avus around 3000 cal years BP (Prevosti et al., 2011), and then in the 19th century when D. australis was hunted to extinction (Darwin, 1839; Clutton-Brock et al., 1976; Slater et al., 2009; Turvey, 2009). Hypotheses advanced to explain the extinction of D. avus include a change to drier climate and open vegetation or hybridization with domestic dogs, but neither are supported by published data; human expansion in South America during the late Holocene (< 3000 years BP) is gaining merit as a potential cause (Prevosti et al., 2011).

Here we describe new specimens of D. avus, dated between 700 and 400 cal years BP, from localities in the Pampean and Patagonian regions of Argentina and southern Chile. Using the Gaussian-Resampled Inverse-Weighted McInerny (GRIWM) method (Bradshaw et al., 2012), we estimated the time of extinction of this fox, and determined its occurrence in historical times. Based on this emerging evidence we revisited the potential factors that may have accounted for the extinction of D. avus.

**MATERIAL AND METHODS**

**Taxonomic identification**

Taxonomic assignment of the specimens was based upon a combination of qualitative and quantitative approaches (Kraglievich, 1930; Berman & Tonni, 1987; Trejo & Jackson, 1998; Amorosi & Prevosti, 2008; Prevosti et al., 2009, 2011). A list of specimens and definition of measurements utilized are provided in Supporting Information (Appendix S2). We performed a Principal Component Analysis (PCA) from the variance-covariance matrix of the ln transformed measurements following Prevosti et al. (2009, 2011) to evaluate the identification of the new specimens. A biplot between the length of first and second lower molar follows Prevosti et al. (2009, 2011). See Supporting Information, Appendix S7 for more details of these analyses. To improve sample sizes we included a large number of unpublished archaeological/paleontological specimens of Lycalopex culpaeus, L. griseus and Dusicyon avus (Supporting Information, Appendix S2).

**NEW TAXON DATES, EXTINCTION AGE ESTIMATION, AND STABLE ISOTOPES**

New accelerator mass spectrometry (AMS) 14C dates produced by the National Science Foundation (NSF) – Arizona Accelerator Mass Spectrometry Laboratory (AA: University of Arizona, Tucson, USA), Centro de Datazione e Diagnostica (LTL: Università del Salento, Brindisi, Italy), and Beta Analytic (Beta; Miami,
USA), were obtained from five *D. avus* specimens. Calibrations of $^{14}$C dates were calculated with the program CALIB 7 available at http://intcal.qub.ac.uk/calib/ (Stuiver & Reimer, 1993; Reimer et al., 2009), using the SHCal13 curve (Hogg et al., 2013) and two sigma ranges. To estimate the age of extinction of *D. avus* we used the GRIWM method, with an R 3.0.1 script (R Core Team, 2013) obtained from C. Bradshaw and F. Saltre, which weighs observations inversely according to the temporal distance from the last confirmed observation of a species (Bradshaw et al., 2012). As some of the dates had large errors, and there were few dates between 4000 and 1000 years cal BP (Supporting Information, Appendix S3) that could bias the GRIWM results (F. Saltre, pers. comm.), we first ran a model analysis reducing the error of four dates with values larger than 150 to 90 cal years. To address the second source of bias we used the younger eight dates, all of which are <4000 cal BP (Supporting Information, Appendix S4).

Stable isotopes ($\delta^{13}$C, $\delta^{15}$N) data were obtained from the dated specimens and compared with published data for *D. avus* to determine the potential existence of dietary variability (Supporting Information, Appendix S8; for the interpretation of dietary signals with these isotopes, see Bocherens & Drucker, 2003; Fox-Dobbs et al., 2007; Yeakel et al., 2013).

**POTENTIAL DISTRIBUTION MAPS**

To explore the role that climate change may have had in affecting the distribution of *D. avus*, we performed potential distribution models using MaxEnt v.3.3.e (Elith et al., 2006; Phillips, Anderson & Schapire, 2006), using specimens of different ages and two different climatic variable datasets. This software was chosen because it performs better than...
alternatives with presence-only data (Elith et al., 2006). We used the WorldClim database for present climatic conditions (Hijmans et al., 2005), with a spatial resolution of ~ 1 km², and the CCSM4 database (Gent et al., 2011) for climatic information for the middle Holocene (i.e. 6000 years), with a spatial resolution of 2.5 km². Both environmental datasets contain monthly precipitation and temperature information, and 19 bioclimatic variables. We generated two potential distribution models: one including only middle Holocene localities and the 6000 years BP database (6 ka), and the other including only late Holocene localities and the ‘actual’ database (0 ka). Because there is an appreciable interval between the late Holocene fossils themselves and the modern environmental conditions in the WorldClim database, there was a risk that the distribution of D. avus in the 0 k model would be biased by greater present-day humidity. To explore this alternative we ran an analysis using the middle Holocene database and the late Holocene localities of D. avus (6 kaB). Ten replicates were performed for each model, with 25% of localities used as test data, random seed and 10 000 background points. We used the cumulative output and assigned predictive values of 100–51, 50–26, 25–11, 10–2 and 1–0 (Fig. 6). Variable contributions were analyzed with jackknife tests and model predictions with a threshold independent measure, the area under the receiver operator curve (AUC) (Phillips et al., 2006). The AUC is interpreted as the probability that a randomly chosen present location is ranked higher that a randomly chosen background point (Merow, Smith & Silander, 2013). It varies between 0 and 1, with an AUC of 0.5 meaning that the model does not perform better than would a random model (Hernández et al., 2006).

To evaluate the effects of climatic change across time, we extracted climatic information (i.e. mean annual temperature, and annual precipitation) for each recorded in D. avus locality from three climatic databases, the two mentioned above as well as a third for the Last Glacial Maximum database (Collins et al., 2006).

RESULTS

TAXONOMIC IDENTIFICATION

MCA 81-VI-1-1 is composed of an incomplete rostrum with part of the maxillary and premaxillary bones and left and right I3-M2; incomplete left and right mandibles with right c1-p1, broken p2 and p3-m1, and left c1-p2 and p4-m2 (m1 is broken; Figs 2–4, Supporting Information, Appendices S5, S6). The left p3 alveolus was reabsorbed, indicating that this tooth was lost while the animal was alive; the permanent dentition is in its final position and is moderately worn, suggesting an adult individual. CEH 5131 is a nearly complete skull (right zygomatic arch and pterygoid bones are broken) with broken right P4, nearly complete left P4 and complete left M2 (Figs 2–4, Supporting Information, Appendices S5, S6). MC 787 and MPEF-PV 10887 are right and left mandibles, respectively. The dentition is nearly complete, but the i1-3, p1 and m3 were not preserved in the MC 787, while the m3 was missing in MPEF-PV 10887 (Figs 2–4, Supporting Information, Appendices S5, S6).

The new specimens are clearly separable from domestic dogs due to the presence of several cranial and dental traits that separate Dusicyon and Canis (see Pocock, 1913; Berta, 1989; Tedford, Taylor & Wang, 1995; Prevosti, 2010). These include: (1) the occipital forming a more rounded inion that is not so expanded posteriorly, while in Canis the inion is very pointed and posteriorly projecting; and (2) the jugal bone has a scar for the superficial masseter m. that is wider in Dusicyon than Canis, which instead exhibits a steeper forehead front with a more developed frontal sinus (Figs 2–4, Supporting Information, Appendices S5–S7). The dentition of Canis familiaris is more robust, with more bunodont teeth (e.g. molars, premolars), lower and more robust principal cusps in the premolars (especially the p4), shorter and more robust canines, and I3 with a strong mesiolingual cingulum. The M1 has a more reduced labial cingulum and a proportionally larger and more bunodont paracone, while the m1 has a stouter trigonid and a more reduced metaconid and entoconid (Figs 2–4, Supporting Information, Appendices S5–S7; Prates, Prevosti & Berón, 2010; Prevosti, 2010).

Similarly Chrysocyon brachyurus is easily distinguished from D. avus due to a larger skull, with proportionally narrower palate and rostrum, stronger sagittal crest, slender zygomatic arches, more hypocarnivorous dentition (proportionally smaller carnassials and larger M1–2 and m2–3; proportionally larger protocone in the P4, and talonid and metaconid in the m1) with taller premolars (Kraglievich, 1930; Langguth, 1970; Figs 2–4, Supporting Information, Appendices S5–S7).

ABBREVIATIONS

i/I: lower/upper incisor, respectively; c/C: lower/upper canine, respectively; p/P: lower/upper premolar, respectively; m/M: lower/upper molar, respectively; CEHA: Centro de Estudio del Hombre Austral, Instituto de la Patagonia, Universidad de Magallanes, Punta Arenas, Chile; MC: Colección Marcelo Carrera, Puerto Madryn, Chubut Argentina; MCA: Museo ‘Carlos Ameghino’, Mercedes, Buenos Aires, Argentina; MPEF-PV: Museo Paleontológico ‘Egidio Feruglio’, Trelew, Chubut, Argentina.

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Using size and evidence of a more carnivorous dentition, we were able to separate the new specimens from other South American living foxes (e.g. *Cerdocyon thous*, *Lycalopex gymnocercus*). We then differentially compared them with *L. culpaeus*, *Dusicyon australis* and *D. avus*. The new specimens present a set of characters that are diagnostic of *D. avus*. These include the presence of a well developed hypoconulid in the m1, a second accessory cusp and a narrowed distal cingulum in the p4 (in *L. culpaeus* is low and wide), and a protocone placed lingually in the P4 (in *L. culpaeus* is placed mesially or mesiolingually; Prevosti et al., 2011; Figs 2–4, Supporting Information, Appendices S5–S7). The new specimens have proportionally wider postorbital constrictions and processes, larger m1 in relation to m2 and a wider bulla, which are characters that are shared with *D. australis* (Prevosti et al., 2011; Figs 2–4, Supporting Information, Appendices S5–S7). *D. australis* has a more reduced protocone in the P4 and smaller metaconid in the m1 than *D. avus*. The principal cusps of the premolars are taller and more acute in *D. australis* (specially the p4), the distal cingulum of the p4 is narrower and more acute in *D. australis*. In some specimens the cingulum was raised and cusp-like, but a true second accessory distal cusp is not present (Prevosti et al., 2011; Figs 2–4, Supporting Information, Appendices S5–S7). The secondary palate is posteriorly extended just at the level of the distal border of the M2, while in *D. avus* it ends more anteriorly (at the level of the distal half of the M2; Figs 2–4, Supporting Information, Appendices S5–S7; Berta, 1989). The sagittal crest is more developed in several specimens of *D. avus*, while the studied *D. australis* presents a lyriform area delimited by the temporal crests (Figs 2–4, Supporting Information, Appendices S5–S7; Berta, 1989).

Morphometric analyses (i.e. Principal Component Analysis and biplot graph) were compatible with this comparison and supported the separation of *D. avus* from other similar sized South American wild canids (see Supporting Information, Appendix S7).

**Figure 2.** Specimens of *Dusicyon avus* included in this study. A, Skull in ventral view (CEHA 5131). B, Skull in lateral view (CEHA 5131). C, Right mandible in lateral view (MCA 81-VI-1-1). D, Palate in ventral view (MCA 81-VI-1-1). E, Left mandible in lateral view (MPEF-PV 10887; reflected). F, Right mandible in lateral view (MC 787). Scale bar = 10 mm.

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**SITE INFORMATION, NEW TAXON DATES, ESTIMATED AGE OF EXTINCTION, AND STABLE ISOTOPES**

MCA 81-VI-1-1 was discovered at the archaeological site of Río Luján 1; it was never fully described, and was initially tentatively associated with *Chrysocyon brachyurus* (Kriskautzky, 1975), later with *Canis familiaris* (Tonni & Politis, 1981). Here we conclusively refer it to *D. avus* (see also Prevosti, Bonomo & Tonni, 2004; Prevosti et al., 2011). Río Luján 1 was a burial site containing six humans, one of them associated with both a jaguar (*Panthera onca*) and MCA 81-VI-1-1 (Petrocelli, 1975). The site is located in northeast Buenos Aires province (34°17′S, 58°52′30″W; Argentina), near the Parana fan (Petrocelli, 1975; Salemme & Tonni, 1983; Fig. 1); the burial was dated to c. 600 cal years BP (Toledo, 2009; Bonaparte, Migale & Buide, 2011). This is in good agreement with the date for the *D. avus* specimen, 724 ± 52 14C year BP (AA102584; 553–718 cal years BP; Supporting Information, Appendix S3).
Figure 3. Dorsal view of a skull of *Dusicyon avus* compared with other canids. A, *Dusicyon avus* (CEHA 5131). B, *Dusicyon australis*. C, *Chrysocyon brachyurus*. D, *Lycalopex culpaeus*. E, *Canis familiaris*. Scale bar = 10 mm.

Figure 4. Lateral view of a skull of *Dusicyon avus* compared with other canids. A, *Dusicyon avus* (CEHA 5131). B, *Dusicyon australis*. C, *Chrysocyon brachyurus*. D, *Lycalopex culpaeus*. E, *Canis familiaris*. Scale bar = 10 mm.

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CEHA 5131 was recovered from the northern site of Dinamarquero, situated on the northern margin of the Magellan Strait in southern Patagonia (52°24′57″ S, 70°35′02″W, Chile; Martinic & Prieto, 1986; Fig. 1). This site is an Aonikenk base camp characterized by abundant glass and metal tools, in use during the 19th century between at least 1833 and 1896 (Martinic & Prieto, 1986; Martinic, 1995). Even though CEHA 5131 was found near a peat bog close to the centre of Dinamarquero, there was no evidence that it is linked with the Aonikenk occupation in any way. CEHA 5131 was dated to 400 ± 30 14C years BP (Beta365051; 324–496 cal years BP; Supporting Information, Appendix S3).

MC 787 and MPEF-PV 10887 were found in sand dune deposits in Peninsula Valdés (Chubut, Argentina; Fig. 1), Punta Buenos Aires (42°14′3″S, 64°21′3″ W) and Playa Colombo (42°38′1″S, 64°12′1″W), all of which contain important vertebrate remains in surface assemblages (Udrizar Sauthier, 2009). MC 787 includes postcranical elements, and some ribs were used to dated it in 1112 ± 14C years BP (LTL13408A; 922–1060 cal years BP; Supporting Information, Appendix S3). MPEF-PV 10887 was dated to 589 ± 45 14C years BP (LTL13407A; 503–638 cal years BP; Supporting Information, Appendix S3).

A fifth D. avus specimen, consisting of a lower mandible with p2-m1 (CEHA CP B.B2) was found in Cueva del Puma in the Pali Aike volcanic field (52°05′37″S, 69°44′31″W; Magallanes, Chile; Martin, 2013), and was dated to 2030 ± 44 14C years BP (Beta276516; 2091–2326 cal years BP), within the previously published date range for this species (Supporting Information, Appendix S3).

GRIWM analysis using all samples indicated that D. avus would have become extinct during the 20th century (c. 1950), with a median date of 0 cal years BP. Such an analytical result theoretically implies that it might still be extant, since the upper confidence limit (2.5%) is 441 cal years after 1950. The lower confidence limit (CI; 97.5%) is 463 cal years BP. Additional GRIWM runs gave similar results (see Fig. 5; Supporting Information, Appendix S4).

Stable isotope ratios collected from Río Luján δ13C: −12.8, δ15N: 9.6, and Dinamarquero specimens exhibit values of δ13C: −20.2 and δ15N: 9.6. The δ13C values for MC 787 and MPEF-PV 10,887 were −18.9 and −19.9, respectively. These values were within the previously published data range (see Supporting Information, Appendix S8), with the exception of the Río Luján specimen which was more positive (δ13C value, −16.8; Supporting Information, Appendix S8).

DISTRIBUTION AND POTENTIAL DISTRIBUTION MODELS

A potential distribution model 6 ka was performed with eight middle Holocene localities (Fig. 6, Supporting Information, Appendix S9). High predictive values were attained for southern and central Patagonia and western Argentina at 29°S, and mean predictive values along northern Patagonia and the Argentine Pampas (Fig. 6). Model 0 ka was performed with 13 late Holocene localities (Supporting Information, Appendix S9), and returned a southern displacement of high predictive values for Buenos Aires province, while southern Patagonia remained with high predictive values (Fig. 6). Model 6 kaB showed a pattern more similar to model 6 ka than to model 0 ka.

Jackknife tests suggested that for the 6 ka model the most important environmental variables were temperature seasonality, isothermality and January maximum average temperature, whereas altitude and August minimum temperature were more relevant for models 0 ka and 6 kaB (Supporting Information,
Appendix S9). All models presented better predictions that those randomly generated, with high AUC values: 6 ka, 0.997 ± 0.002; 0 ka, 0.957 ± 0.049; 6 kaB, 0.997 ± 0.002.

Considering all the Holocene localities studied, mean annual temperature during the Late Glacial Maximum (LGM) was 5.7 °C (−3.3 to 12.8 °C) and annual precipitation was 446 mm (152–1159 mm). Mean annual temperature of record localities in 6 ka was 9.8 °C (4.4–16.4 °C) and annual precipitation was 483 mm (186–977 mm; Supporting Information, Appendix S10). Mean annual temperature of record localities in the actual database was 10.5 °C (5.3–16.8 °C) and annual precipitation was 517 mm (197–1085 mm). The upper precipitation limit was smaller when only the localities used in the model 6 ka and model 0 ka were included: 765 mm for the middle Holocene, and 995 mm for the actual climatic database (Supporting Information, Appendix S10). Due to some uncertainty we excluded the Río Luján specimens, that could have been collected elsewhere and brought in by humans (see below), and the northern Pampas specimens (Laguna El Doce and Estación J. M. García), that lacked chronological data (they had a ‘Holocene’ age and the last one could be from the Early Holocene, see Prevosti & Pardiñas, 2001). Using this reduced sample we found a decrease of ~1 °C in the maximum of the mean annual temperature and >100 mm in the maximum annual precipitation.

**DISCUSSION**

**AGE OF EXTINCTION**

Based on an archaeological context a late Holocene extinction of *Dusicyon avus* was proposed in the 1970s and 1980s, (Caviglia, 1978, 1986; Berman & Tonni, 1987; Berman, 1994; Mansur, 2006, 2007), but was only recently confirmed by direct taxon dates using 14C. Absolute chronology places *D. avus* last occurrence at c. 3000 years 14C BP (Prevosti et al., 2011). Martin (2013) published a taxon date of 1600 ± 40 years 14C BP (1361–1536 cal years BP) based on remains found in Cueva de los Chingue, near the Magellan Strait in Chile. Similarly, Prates & Di Prado (2013) obtained a date of 2057 ± 38 years 14C BP (1885–2081 cal years BP) from material recovered in Negro Muerto 2 in northern Patagonia, Argentina (Fig. 1). Our new data extend *D. avus* biochron to <1000 years 14C BP, with the last record in the Pampuan region at c. 700 14C years BP (AD 1232–1397 years), and the most recent record in southernmost Patagonia with an age of c. 400 years 14C BP (AD 1454–1626 years). These dates would suggest that *D. avus* extinction could have occurred after the arrival of Europeans to South America (Fig. 5; Supporting Information, Appendix S3). The extinction estimate using GRIWM overlaps with the younger 14C, suggesting that the extinction could have happened since 463 cal years BP (AD 1482 years). Indeed, the species could even be living.
today, since the estimated age of extinction lays in the future, with a median value that falls in the middle of the 20th century (Fig. 5; Supporting Information, Appendix S3), supporting the idea that D. avus disappearance might have happened after the European arrival. If this is correct, D. avus might have been living in historical times, and even observed by naturalists and explorers travelling the southern portion of the subcontinent during the last few centuries. Unfortunately, there is no solid evidence reported from diaries and notes written during the 18th to 20th centuries to support the occurrence of a large canid attributable to D. avus then. The most intriguing observation was noted by George Musters who, inspired by Charles Darwin’s diary, crossed 3000 km of Patagonian territory between 1869 and 1870 (Rey Balmaceda, 1976). Musters (1871) wrote ‘On another occasion, when hunting, we made a circle, finishing off in the wooded district near the banks of the river [= Tecka river]. On our return we hunted over a park-like country, with alternate open glades and woods. Here we killed a doe red deer and a large description of fox, apparently identical with the Falkland Island species – Lupus antarcticus [= D. australis]’. This observation was made about 43°S, in the western portion of Chubut province near the Andean forest piedmont (Rey Balmaceda, 1976) and might have been one of the last observations of D. avus. An unusual large fox was also mentioned for Tierra del Fuego (Lothrop, 1928). Together with ‘Aguaras’ reported in the 19th century in northern Patagonia and the Pampean region (and uncritically assigned to Chrysocyon brachyurus; Prevosti et al., 2004), these could have been in fact D. avus specimens. However attractive this interpretation is, and bearing the support of the GRIWM results, the available information is not enough to corroborate this hypothesis (Prevosti et al., 2004, 2011).

**DISCLOSING THE CAUSE FOR D. AVUS EXTINCTION**

Three hypotheses have been advanced to explain the extinction of D. avus (Berman & Tonni, 1987), namely either (a) change toward a more humid climate, (b) hybridization with domestic dogs, or (c) the impact of native human population. Prevosti et al. (2011) showed that between the Late Pleistocene and late Holocene, D. avus occupied a large area (estimated at 762 351 km²) that encompassed the Pampean region and Patagonia (including Tierra del Fuego) that experienced significant climatic and environmental changes, particularly in the Holocene (Clapperton, 1993; Markgraf, 1993; Prieto & Stutz, 1996; Tonni, Cione & Figini, 1999, 2001; Mancini, 2003; Schäbitz, 2003; Grill et al., 2007; Mancini et al., 2008; Borromei et al., 2010; Pardiñas & Teta, 2013; Tammonne et al., 2014). Climatic variations recorded in the last 1000 cal years, including the Medieval Warm Period and the Little Ice Age ‘events’ impacted the southern cone of South America (Politis, 1984; Tonni et al., 1999, 2001; Deschamps, Otero & Tonni, 2003; Favier-Dubois, 2007; Borromei & Quattrocchio, 2008; Waldmann, 2008; Tonello & Prieto, 2010; Ponce et al., 2011; Pardiñas, Udrizar Sauthier & Teta, 2012; Del Puerto et al., 2013; Mancini & Graham, 2014; Teta et al., 2014), but there is no evidence to suggest that these climatic anomalies were more deleterious than those which characterized the Late Pleistocene–Holocene, the middle Holocene, or even the Neoglacial advance (Mancini et al., 2008; Tonello & Prieto, 2010; Mancini & Graham, 2014). In conclusion, there is no compelling linkage between climatic changes and the extinction of this hitherto widespread fox species (Prevosti et al., 2011; Fig. 5).

The climatic parameters obtained from the climatic databases and the distribution models are congruent with the interpretation that D. avus inhabited open areas (e.g. grass steppe, shrub steppes) under a wide range of climatic conditions (Fig. 5). The models also show that most recorded localities experienced arid to semiarid conditions (i.e. annual precipitation < 800 mm), with variable temperature and precipitation, and high seasonality and isothermality (Supporting Information, Appendix S9). This would support the hypothesis that at least in Buenos Aires province the distribution of D. avus was related to more arid conditions, as has been suggested for the middle and late Holocene (e.g. Tonni et al., 1999; Mancini et al., 2005). Several mammal species presently associated with dry environments disappeared from their Pampean ranges during the late Holocene, including ungulates (e.g. Lama guanicoe; Tonni & Politis, 1980; Politis & Pedrotta, 2006; Politis et al., 2011), mustelids (Lyncodon patagonicus; Prevosti & Pardiñas, 2001; Schiaffini et al., 2013), and marsupials (Lestodelphys halli; Prado, Goin & Tonni, 1985; Goin, 1995, 2001). A plausible explanation would be that these range retractions were triggered by a regional change to more humid conditions (Tonni et al., 1999; Stutz, Prieto & Isla, 2006; Tonello & Prieto, 2010; Del Puerto et al., 2011). We verified an additional regional extirpation of D. avus during the late Holocene for the northeastern portion of Chubut province, probably connected with the southward advance of the Monte shrubland during warmer and drier conditions (Medieval Warm Period and present). A similar situation involving small marsupials and rodents (e.g. Abrothrix olivacea, Lestodelphys halli) has been documented for eastern Patagonia (Pardiñas et al., 2012; Udrizar Sauthier & Pardiñas, 2014). However, although these climatic changes
could be linked with local retractions, they were arguably not enough to trigger the extinction of a widespread fox species.

The presence of *D. avus* in a burial site in Río Luján 1 around 700 14C years BP contravenes the climate hypothesis, as warmer and wetter conditions related to the Medieval Warm Period were prevalent in the Pampean region at this time. This specimen might have been transported for ritual purposes from elsewhere, or might have been a tame animal (Prates, 2014). A similar explanation has been invoked for a late Holocene *Lama guanicoe* record in northeast Buenos Aires province (Politis & Pedrotta, 2006; Politis et al., 2011).

The second hypothesis advanced to explain the extinction of *D. avus* by Berman & Tonni (1987) – through hybridization with domestic dogs – was also discarded, as there is no evidence of hybridization in the morphology of the skull and dentition of *D. avus* nor in its mitochondrial DNA (Prevosti et al., 2011; Austin et al., 2013). We also failed to find any evidence of hybridization in the morphology of the new specimens, but this hypothesis remains unlikely, as hybridization with domestic dogs seems to be restricted only to the genus *Canis* (e.g. *Canis lupus, C. simensis*; Gottelli et al., 1994; Vila & Wayne, 1999; Macdonald & Sillero-Zubiri, 2004; Sillero-Zubiri, Hoffmann & Macdonald, 2004), and there are no records of such hybridization in living South American canids. More ancient DNA sequencing (including nuclear DNA) will be needed to further test this hypothesis.

*Dusicyon avus* were used by humans during the Holocene for ritual purposes, as suggested by its inclusion in burials, and its teeth were probably utilized in necklaces (Messineo & Politis, 2007; Prates et al., 2010; Prevosti et al., 2011; Laporte, 2014; Politis, Barrientos & Scabuzzo, 2014; Prates, 2014). Based on the frequency and the skeletal elements (mostly teeth) found in archaeological sites, Bonomo (2006) surmised that the species had a high symbolic value for aboriginal peoples. Prates (2014) inferred that a specimen from Loma de los Muertos was intentionally buried, and may have been tamed, a practice recorded elsewhere, or might have been a tame animal (Prates, 2014). A similar explanation has been invoked for a late Holocene *Lama guanicoe* record in northeast Buenos Aires province (Politis & Pedrotta, 2006; Politis et al., 2011).

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to small geographic areas (e.g. *C. simensis*), are more likely to be heavily affected by burgeoning human populations, and to suffer range and population reductions, but they still manage to subsist in more remote, wilderness areas (Mech & Boitani, 2003; Macdonald & Sillero-Zubiri, 2004; Sillero-Zubiri *et al.*, 2004). In contrast, other more generalist canids (e.g. *Canis latrans*, *C. aureus*, *Lycalopex culpaeus*) have experienced recent population or distribution expansions (Novaro, 1997; Sillero-Zubiri *et al.*, 2004). Thus, it is difficult to understand why these threats could be the cause of the extinction of *D. avus*.

Stable isotopes suggest that *D. avus* in the Late Pleistocene of southern Patagonia had a more carnivorous diet than living foxes, and could scavenge large and mega-mammals (Prevosti & Martin, 2013). The δ13C and δ15N values are consistent with a carnivorous diet (Supporting Information, Appendix S8), but display some variability (especially in δ13C values). Río Luján 1 specimen has a much higher δ13C values which indicate the consumption of C4 rather than C3 plant feeders. This could be a valid interpretation because C4 plant feeders (i.e. cervids) were present in the limited isotopic data currently available is congruent with some degree of generalization in the fox’s diet and large areal distribution (see above).

**A COMBINATION OF CAUSAL FACTORS?**

Changes in population densities and the behavior of early settlers in the southern cone of South America, followed by the impact of the European colonization and a climatic trend to more humid conditions, could have come together during the late Holocene in such a manner that there was a strong impact upon *D. avus* populations that had probably already suffered some reduction, as has been proposed for the Pleistocene-Holocene megafauna extinction (Cione *et al.*, 2008). In this scenario *D. avus* would have been more heavily affected because it was more carnivorous and larger than other South American foxes (Prevosti & Vizcaíno, 2006; Prevosti *et al.*, 2011; Prevosti & Martin, 2013). Furthermore, the few genetic data available would indicate that the species had low genetic variability (Austin *et al.*, 2013), something that could be related to low population densities or a population bottleneck (Chan *et al.*, 2005; Chan, Anderson & Hadly, 2006). If this inference is correct, *D. avus* would have been more sensitive to external threats (e.g. human impact, climatic change, or in combination; Frankham, 2005; Jansson *et al.*, 2012; Frankham, Bradshaw & Brook, 2014; Marris, 2014; but see Rodriguez *et al.*, 2011) than other canids. Conversely, *D. avus* had a wide distribution, apparently restricted to open environments (e.g. Patagonian steppe, Pampas), while *Lycalopex culpaeus* is also present in forested region in Patagonia and widely distributed along the Andes to northeastern South America (Macdonald & Sillero-Zubiri, 2004; Sillero-Zubiri *et al.*, 2004). Other living southern cone canids are also restricted to open environments and their distributions are not necessarily larger, but also occur in more closed environments such as the Monte or Chaco (e.g. *Lycalopex gymnocercus*; Macdonald & Sillero-Zubiri, 2004; Sillero-Zubiri *et al.*, 2004). The more open and non-forested environments would have had fewer areas offering refuges for this species, exposing it to human impact.

Summing up, the new data and the available information clearly support a ‘multi-causal’ process, in which environmental change and human impact interacted causing the recent extinction of *D. avus*.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

Appendix S1. List of localities of *Dusicyon avus* used in this study.

Appendix S2. List of studied canids with their respective locality, age, collection number, and measurements (in mm), collection names and measurement definitions.

Appendix S3. New and published 14C taxon dates for *Dusicyon avus*. New taxon dates in bold.

Appendix S4. Estimation of extinction age of *Dusicyon avus* using the GRIWM method. (1) Analysis of the whole sample with the original data; (2) analysis of the whole sample but artificially reducing the error of four dates with values larger than 150 to 90 cal years BP; (3) analysis including only the unmodified data of late Holocene age.

Appendix S5. Ventral view of a skull of *Dusicyon avus* compared with other canids. A, *Dusicyon avus* (MCA 81-VI-1-1). B, *Dusicyon avus* (CEHA 5131). C, *Dusicyon australis*. D, *Lycalopex culpaeus*. E, *Chrysocyon brachyurus*. F, *Canis familiaris*. Scale = 10 mm.

Appendix S6. Lateral view of mandible of *Dusicyon avus* compared with other canids. A, *Dusicyon avus* (MCA 81-VI-1-1). B, *Dusicyon avus* (MPEF-PV 10887). C, *Dusicyon avus* (MC 787). D, *Dusicyon australis*. E, *Lycalopex culpaeus*. F, *Chrysocyon brachyurus*. G, *Canis familiaris*. The MPEF-PV 10887 was reflected. Scale = 10 mm.

Appendix S7. Morphometric analysis (Principal Component Analysis and biplots) comparing *Dusicyon avus* remains with other canids.

Appendix S8. Stable isotope values (δ13C, δ15N) of *Dusicyon avus*. New data in bold.

Appendix S9. Contribution of each variable to the potential distribution models for *Dusicyon avus*. Value of the variables with the highest contribution for each model are in bold.

Appendix S10. Value of some climatic variables for the *Dusicyon avus* localities used in each potential distribution model.