

REVIEW

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The rare Fuegian fox (*Lycalopex culpaeus*) from the Tierra del Fuego Archipelago: history of discovery, geographic distribution, and socio-ecological aspects

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Abstract

Background The Fuegian fox (*Lycalopex culpaeus*) is a rare inhabitant of the Tierra del Fuego Archipelago on account of: (a) It is the southernmost Canid in the world. (b) It is the second largest, heaviest, and tallest native Canid in South America. (c) It is currently scarce in northern Tierra del Fuego. (d) It may have been tamed by the Selk'nam natives.

Methods and results Based on chronicles and scientific reports we document the timeline since discovery of the distinctive and island-confined Fuegian fox. We pay attention to its patchwork distribution within the Fuegian archipelago, with populations spread on the large Tierra del Fuego Island (Fuegia) and on two smaller ones, Hoste and Gable. This fox seems to have disappeared recently from the latter and historic records from Navarino Island are dubious. We provide new distributional records and unpublished photographs. Among the socio-ecological aspects studied, we highlight the relationships of this fox with two local indigenous people: The Yahgan and the Selk'nam.

Discussion The introduction of sheep *Ovis aries* in 1885 and the ensuing persecution of its putative predators apparently caused the fox decline from the northern half of Fuegia. The introduction of the continental Chilla fox *Lycalopex griseus* in 1951 further impacted the Fuegian fox, apparently by competition for food but perhaps also by diseases. It is currently concentrated in the southern half of Tierra del Fuego Island. The possibility that the Selk'nam introduced this fox from the mainland and that they tamed it, is also discussed.

Keywords Argentina, Chile, Fuegia, Magallanes, Patagonia, Tierra del Fuego Island

Background

The Fuegian fox (*Lycalopex culpaeus*) is a rare inhabitant of the Tierra del Fuego Archipelago in several ways [1–6]: First, it is the southernmost Canid in the world. Second, it is the second largest, heaviest, and tallest native Canid in South America. Third, it is rare in the sense of being scarce nowadays in northern Tierra del Fuego. Fourth, but not least, it may have been tamed or domesticated by the almost vanished Selk'nam natives. This rare combination of qualifications calls for further attention from scientists of all walks, from anthropologists to zoologists. Here, we summarize what concerns its history of

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discovery, geographic distribution, and socio-ecological aspects.

Methods

Literature search and screening

We mostly back-tracked references from current to older sources, using mainstream journals, monographs, books, and relevant grey literature (typically, governmental-agency technical reports). Some new sources emerged when engine-searching the internet without time or language constraints for vernacular keywords such as Fuegian fox or zorro fueguino, both in singular and plural forms; or scientific names such as *Canis*, *Dusicyon*, *Lycalopex*, *Pseudalopex*, and *Vulpes*, in combination with *culpaeus*, *lycoides*, and *magellanicus*. In keeping with customs of the times, sometimes a scientific species name was capitalized (which we ignored) or not italicized, but when clear misspellings or egregious meanings were expressed, we attached to them the Latin adverb *sic* in square brackets [*sic*]. When we were doubtful as to a given assertion, we added a question mark in square brackets [?]. All the vernacular and scientific terms we filtered first by country or region: Argentina, Chile, Magallanes, Patagonia, Tierra del Fuego, and in all usable conjugates (e.g., Argentinian, binational, Chilean, Fuegian, Magellan, Magellanic, and/or Patagonian). We distinguished between first-hand information and secondary use of primary literature sources to avoid redundancies; instead of quoting review papers, book chapters, or books, we preferred to read and cite the original sources and secondarily the compilation ones. In quoting authors, we did not correct grammar or taxonomic mistakes, but did standardize fonts by eliminating those in all capitals or boldface, and kept the italicized style when present. When we could not access an original source, i.e., Pigafetta (originally published in 1584), or Molina (originally published in 1782), we denoted the actual version consulted in square brackets [Pigafetta 1922] [7], or [Molina 1788] [8]. Darwin's [9] classic book underwent several editions and had so many small variations over the years that one has to be careful in citing which exact edition was used to lift quotations; we used the internet rendition (http://darwin-online.org.uk/converted/publicshed/1839_Voyage_F10.3/1839_Voyage_F10.3.html) of the original 1839 version of the book. We ignored congress reports --abstracts or posters--, because they did not provide enough details and were eventually published as full papers or chapters, after peer review. This literature search is undeniably non-systematic (e.g., the grey and older literature is not usually archived electronically) and relies on the authority and expert judgment of the authors of this review. It is not exhaustive, but selective of those higher-quality items judged on our expertise.

Study area

At a broad scale, the Magallanes Region of Chile has a continental and an insular part. The latter is called Tierra del Fuego, which is an ambiguous geographic term: It may refer to the Fuegian archipelago (Archipiélago de Tierra del Fuego or Archipiélago fueguino) or the island proper, Tierra del Fuego Island (Isla Grande de Tierra del Fuego). This latter isolate is situated within a polygon ca. 52–55°S and 65–72°W, bound by the Strait of Magellan to the north, the Pacific Ocean to the west, the Atlantic Ocean to the east, and the Beagle Channel to the south. This large island is split east-west between Argentina and Chile (40:60, respectively), at meridian 68°34'W (both sides are called Province of Tierra del Fuego, one in Chile and the other in Argentina). The Fuegian archipelago contains the large island itself (ca. 48,000 km²), seven medium-sized islands (Hoste, Santa Inés, Navarino, Dawson, Aracena, Clarence, and Staten, ranging from 4,100 to 500 km² in the same sequence), and ca. 3,000 smaller islands and islets, the best-known being Cape Horn or Cabo de Hornos, Gable, Lennox, Nueva, and Picton (in alphabetical sequence). Most of these smaller islands are located to the southwest of Tierra del Fuego Island (Argentina's Staten Island excepted) and thus, are in Chilean territory.

Fuegian foxes

Evolutionarily and systematically speaking, there are no foxes in all South America [10, 11]. In addition, those in the southern part of the continent are more closely related to wolves (*Canis* spp.) than to foxes (*Vulpes* spp.). Indeed, one of the original names of South American "foxes" in the diverse genus *Lycalopex* was *Dusicyon*, meaning "almost a dog." Whatever their phylogeny, those "foxes" have had a long history of interactions with humans [12–17], but not to the point of becoming domesticated [18, 19], although possibly of being tamed and even trained as hunting aids [11, 17] and moved around in canoes by humans [12, 14, 20].

The systematics of South American foxes seems to be in constant flux since early on [1–6, 21–23]. The foxes of our interest have over the years been classified in the genera *Vulpes*, *Canis*, *Dusicyon*, *Pseudalopex*, and more recently *Lycalopex*. According to Iriarte and Jaksic [2] *Lycalopex culpaeus* in Chile encompasses four subspecies: *andinus*, *culpaeus*, *magellanicus*, and *lycoides*, ordered from north to south. But Guzmán et al. [24] and Pizarro et al. [23] proposed that the latter should be considered as part of the nominal subspecies *culpaeus*. Because we do not intend to discuss systematics, we do not assign the current Fuegian fox to any subspecies.

Lycalopex culpaeus has been called fox or wolf or even dog [3], while being neither. Still, we prefer the former denomination, thus calling it the Fuegian fox. And to shorten the denomination Tierra del Fuego Island, we sometimes substitute it for Fuegia.

Indigenous peoples

The Fuegian archipelago hosted until the 20th century four different peoples: Kawesqar or Alacalufe, Manek'enk or Haush, Selk'nam or Ona, and Yahgan or Yamana; the former denominations being more favored. The Selk'nam branched out from the "Patagones" (= Aonikenk or Tehuelche people) on the South American mainland and migrated across the Strait of Magellan to the large Tierra del Fuego Island, where they concentrated on the north-eastern area of the island (ca. 54°S, 68°W), although they sporadically reached southward to the Beagle channel (ca. 55°S, 68°W). The Manek'enk lived on the Mitre peninsula (around 54°46'S, 65°46'W) in southeastern Tierra del Fuego Island and were culturally and linguistically related to the more northerly Selk'nam. Unlike these three peoples ("foot Indians"), two others were nomadic seafaring, or "canoe Indians." The Kawesqar concentrated mostly on islands to the south of the Gulf of Penas (47°22'S, 74°50'W) down to Brunswick peninsula (53°30'S, 71°25'W) and Cockburn Channel (54°20'S, 71°30'W). The Yahgan traditional territory included the lands to the southeast of that channel, mostly around the Beagle Channel (54°52'S, 68°08'W), extending their presence into Cape Horn (55°59'S, 67°17'W), making them the world's southernmost human population. All these five peoples overlapped geographically to some extent and traded goods among them. Detailed information may be found in Gallardo [25], Gusinde [26], Bridges [27], Laming [28], Chapman [29], and Martinic [30–32].

Results

Historical account and geographic distribution

Archeological records demonstrate the presence of two foxes on Tierra del Fuego Island during the Late Pleistocene, but remains from Tres Arroyos 1, dated ca. 10,500 year ago, are not able to distinguish between the extant *Lycalopex culpaeus* and the recently extinct *Dusicyon avus* [17, 33–35]. Franklin [20], noting that Tierra del Fuego currently has few large vertebrates, proposed that they were decimated by the major eruption of the Hudson volcano 7,750 year before present, which eradicated indigenous peoples and most terrestrial vertebrates from the island (guanacos and foxes included). And that neither vertebrates nor humans returned from the mainland for 1,000 years because the Strait of Magellan had become a biogeographical barrier. He then proposed that when humans recolonized Tierra del Fuego, they

selectively introduced two 'utility species': the guanaco (*Lama guanicoe*) because of its importance for meat and skin and the Fuegian dog for companionship and hunting abilities. The latter denomination seems to correspond to a tame *Lycalopex culpaeus* (but see below, under Socio-ecological aspects).

The first historical record by Europeans of foxes in Patagonia was that by Pigafetta ([7], page 6), who reported having seen foxes at San Julian Bay (49°18', 67°42'W) in 1520, in what is now Argentina. They could have been *Lycalopex culpaeus* or *Lycalopex griseus* ([36], page 16). De Bougainville ([37], page 185) while visiting a Fuegian area 29 km east across Le Maire Strait from Staten Island (Isla de los Estados, 54°47'S, 64°15'W, 534 km²) reported that his crew killed a fox "very similar to those in Europe." Byron ([38], page 242) referred having seen "Patagon" natives accompanied by dogs (*Canis lupus familiaris*) "with a pointy muzzle as that of a fox," but no foxes properly. Darwin in 1834 ([9], pages 300–301) reported foxes on Navarino Island (Isla Navarino, 55°04'S, 67°39'W, 2,473 km²) and stated that his shipmate Jemmy Button (a Yahgan native) told him that no foxes existed on neighboring Hoste Island (Isla Hoste, 55°15'S, 69°00'W, 4,117 km²). Both Darwin and Button seem to have been mistaken; it is the opposite (see below). In J. Jiménez's experience, who has been conducting intensive research for a decade on Navarino Island and monitoring vertebrates with camera traps, he has never detected any fox on the island, and it has never been reported by local people. Darwin ([9], footnote in page 250) stated that the fox "is the *Vulpes Magellanicus* [sic.] brought home by Captain King from the Strait of Magellan. It is common in Chile." He was referring to a previous visit by the HRS Beagle (1826–1830) under the command of Captain Phillip Parker King, to Port Famine (Puerto del Hambre, 53°37'S, 70°56'W) in the Brunswick Peninsula of continental Magallanes [39].

Hamilton Smith ([40], pages 266–267) wrote about the "Magellanic Aguara fox" referring to it as *Cerdocyon magellanicus* and tracing it back to *Vulpes magellanicus*, currently named *Lycalopex culpaeus*. He stated that it "inhabits Magellanic Straits" probably referring to its eastern and continental side. Cunningham ([41], pages 110–111) reported having seen a fox at Possession Bay (Bahía Posesión) on the mainland side of the Strait; being unsure of its identity, either *Canis magellanicus* or *Canis azarae*. The former is now called *Lycalopex culpaeus*, while the latter is an all-purpose name better applied to *Lycalopex gymnocercus*, which does not occur so far south. Martial [42] edited a book on the Mission scientifique du Cap Horn, 1882–1883 --carried out by the ship Romanche-- and therein Milne Edwards ([43], page 29) stated that "*Canis magellanicus* is not uncommon in

Tierra del Fuego” and that officers of the Mission killed some foxes at Orange Bay (Hoste Island) in 1882 and noted their presence on the banks of the Beagle Channel at Banner Cove (Caleta Banner on Picton Island, 55°05'S, 66°53'W, 105 km²) [?]. In JEJ's experience, who visited that cove and set camera traps, no foxes were observed.

Philippi ([44], pages 542–545) described *Canis (Pseudalopex) lycoides*, noting that it was the largest fox of the South American tip of the continent, and that in comparison with *Canis magellanicus* it was not as grey (see [1] and our Figs. 1 and 2). He stated that *Canis lycoides* inhabits Tierra del Fuego Island, tacitly indicating that *Canis magellanicus* was described from the continent (Port Famine or Puerto del Hambre). Señoret ([45], page 11) reported that the fox in Tierra del Fuego Island reaches a large size and that its fur is valuable. Ohlin ([46], page 177) stated that in 1895–6 “From the eastern pampas of Tierra del Fuego I secured a few specimens of a fox (*Canis magellanicus*), which occurs also in Patagonia.” Thus, Ohlin was unaware of the description of *Canis lycoides* by Philippi [44]. Dabbene ([47], page 349) stated that there were two species of foxes: *Canis (Lupulus) magellanicus* and *Canis (Thous) griseus*, “...both spread over all islands down to the Cape Horn...” This is certainly not true according to our experience. He [47] added “It may be that in other times there were neither guanacos nor foxes in Tierra del Fuego and that these animals have been introduced in it from the Patagonian

region by the indigenous people.” Franklin [20] made the same argument; see below.

Wolffsohn ([48], page 62) clearly distinguished *Canis magellanicus* from *Canis lycoides*, the former from the continent and the latter from the island, adding that furs of *Canis lycoides* were sold in Punta Arenas, that they were captured with traps during winter, and were more difficult to catch than *Canis magellanicus*. Thomas ([49], page 357) noted that the muzzle of *Pseudalopex culpaeus* increased relatively in *Pseudalopex culpaeus magellanicus* and it peaked in *Pseudalopex lycoides*. Lönnberg ([50], page 1) emphasized that “the differences between the species of Tierra del Fuego, and the one of the mainland, generally known as *Pseudalopex magellanicus* which for a long time have been mixed up.” He elaborated profusely on the distinctive characteristics (size and cranial proportions) of the island fox versus its mainland ancestor and ended by stating that (page 10) “This comparison proves that the present *Pseudalopex lycoides* is not only a geographic relict on Tierra del Fuego, ... This has been made possible, no doubt, by the fact that it has been without competitors on its isolated native island.” Cabrera ([51], page 63) recognized *Pseudalopex culpaeus lycoides* as a subspecies (=not a full species) different form *Pseudalopex culpaeus magellanica* [sic].

Osgood ([22], page 38) commented that “The larger land mammals of Tierra del Fuego consist only of the guanaco and the wolf (*Dusicyon culpaeus lycoides*). Of



Fig. 1 Pictures of different individuals of *Lycalopex culpaeus* from Karukinka Natural Park (ca. 53°42'S, 69°18'W) on southern Tierra del Fuego Island during the winters of 2008–2009



Fig. 2 Pictures of an individual of *Lycalopex culpaeus* from Lapataia Bay (ca. 54°52'S, 68°33'W) on southern Tierra del Fuego Island, taken on March 2004 by Beth Branthaver

these, the wolf appears to be somewhat peculiar in size and cranial characters, but material representing it is scanty and comparisons so far made are with only one or two specimens from the mainland." On pages 66–67 he stated that "This form, which is supposed to be confined to the island of Tierra del Fuego, is thought by Lönnberg (l.c.) to be distinguished from *Lycoides magellanicus* of the mainland by larger size and by certain cranial characters among which a relatively narrow braincase is perhaps most important. Material representing it is still very scanty and its obviously close relationship to *magellanicus* is at best indicated by the subspecific status given it by Cabrera. During several weeks spent on Tierra del Fuego, Mr. Sanborn and myself could only learn that it is now very scarce although a few skins from remote parts of the island annually come into the fur market. A mounted skin is in the Museo Regional Salesiano at Punta Arenas."

Olrog ([52], page 509) reported that the Fuegian fox was rather scarce on Tierra del Fuego Island, but that on Hoste Island it was still common to the point of being a nuisance for sheep ranchers; and that it was not known on Navarino Island (*contra* Darwin [9], pages 300–301). Bridges ([27], page 157) reported that foxes were very abundant on Gable Island (Isla Gable, 54°53'S, 67°29'W, ca. 22 km²), 200 m from Fuegia proper across a branch of the Beagle Channel and 1.4 km from Navarino Island. When 1,500 sheep were introduced there, the foxes escaped [?] to Fuegia by swimming and did not return

until 12 years later. Upon their return they started killing sheep and their owners reciprocated, to the point of having exported on one occasion over 300 choice furs – not necessarily from that island only– to the London market, where they were sold at the price of 2 to 2.5 shillings each. Martinic ([53], pages 21–22) commented that this fox was persecuted by sheep ranchers because of its predation on lambs and that owing to this, by then it was already in population decline.

Markham [54] recognized three subspecies of *Dusicyon culpaeus* (currently *Lycalopex culpaeus*) in the Magallanes Region: *culpaeus* in Puerto Eden (49°7'S, 74°24'W), *magellanicus* in continental Magallanes, and *lycoides* on Tierra del Fuego Island. Markham [54] noticed that the subspecies from Fuegia was larger in both body size and skull length and with a different skull morphology than the continental ones. Markham [55] recognized the presence of *Lycalopex culpaeus* on Hoste Island, "likely *lycoides*," and commented on its puzzling absence from neighboring Navarino Island. Sielfeld [56] captured three of these foxes on Hoste Island but did not commit as to the subspecies involved. Briceño [57] live-trapped a juvenile male on this island on April 2012 and assigned it to the former *lycoides* subspecies, but based solely on its geographic origin. Pine et al. ([58], page 100) reported several fox skulls from San Sebastian Bay (Argentinian side of Fuegia) but did not decide whether they were from the island native *Lycalopex culpaeus* or the introduced *Lycalopex griseus* (brought from the Magellanic

continent in 1951; see Jaksic and Yáñez [59], Zurita et al. [60]). Pine et al. ([61], pages 367–368) collected a good number of foxes from around Useless Bay (Bahía Inútil) and doubtlessly attributed them to *Lycalopex griseus*. Prosser-Goodall ([62], page 67) reported that the Fuegian fox was rather scarce on the northern part of the large island but that it was “fairly common” on the southern portion and on Hoste and Navarino [?] Islands. The latter assertion may have been picked up from Darwin [9] or Bridges [27].

The most complete account on this putative subspecies is in Massoia and Chebez ([63], pages 35–40). Regarding geographic distribution, to the previous records described above, they added a substantial number of others from all over Tierra del Fuego Island, mostly from the Argentinian side. In addition, they discarded its presence on Navarino Island and confirmed previous observations of this fox on Hoste and Gable Islands. But also warned that in a visit by Chebez to the latter island in 1982, he was unable to find evidence of its presence, and the locals reported that they did not know of this fox in such a small setting (ca. 22 km²).

To date the only detailed research on the genetics and diseases of Fuegian foxes was conducted by Briceño [57] based on samples from 14 wild-caught foxes on Tierra del Fuego Island and one on Hoste Island in 2012. Through using mitochondrial DNA and major histocompatibility complex genes, he found very limited diversity for functional and neutral genes --the lowest detected among culpeo foxes. Interestingly, he found that the haplotypes of the specimen from Hoste had a closer genetic distance with specimens from the Metropolitan Region in central Chile. He thus speculated whether foxes on Hoste Island were translocated from the mainland by humans. Finally, through data obtained from antibody prevalence and questionnaires, Briceño [57] found that Fuegian foxes may have been exposed to distemper and parvovirus, likely transmitted by domestic dogs. Moya et al. [64] found that Fuegian foxes had higher seroprevalence to *Leptospira* sp. than did introduced Chilla foxes or domestic dogs. Briceño et al. [65] reported that the ear mite

Otodectes cynotis was found among Fuegian foxes but not among Chillas or dogs.

Because little information on Fuegian fox morphology is available [24], here we report measurements obtained by C. Briceño in Karukinka Natural Park (53°42'S, 69°18'W; 2,720 km²; see Table 1 and map in Fig. 3). We also report unpublished sightings/photographs or catch/release captures of this species as recorded by C. Briceño, J. Jiménez, and C. Zurita over southern Tierra del Fuego Island (Table 2; Figs. 1 and 2, and map in Fig. 3). Notice that we also report one capture from Hoste Island (Fox No. 17 in Table 2 and in Fig. 3). An estimate of the relative abundance of this fox may be obtained from the capture success of using Tomahawk live trap-nights by the same operator, C. Briceño. In Karukinka 142 trap-nights yielded 24 individuals = 16.9% trap success from August 2008 to December 2009. On Hoste Island the respective figures were 19 and 1 = 5.3% in March 2012.

Socio-ecological aspects

Four rather recent species accounts on *Lycalopex culpaeus* contain relevant information on biological, ecological, and evolutionary features of the Fuegian fox, namely, Novaro [6], Jiménez and Novaro [4], Lucherini [5], Castelló [1], and Guntiñas [66]. Our intent is not to repeat what is already published, and thus, we concentrate on the relatively untouched socio-ecological aspects of the Fuegian fox. García Oteiza [67] provided an overview of the different explorations of Tierra del Fuego, which contributes to determining who the early explorers were and where and when they went. Historiographic research of their surviving documents may yield unpublished information on their fox sightings, if any.

Molina ([8], pages 331–332), though likely referring to the subspecies *culpaeus* in central Chile, stated that its name came from the native Mapuche word *culpem*, which in the words of Osgood ([22], page 64) “...it signifies madness or folly and is strikingly applicable to the conduct of this animal, which constantly exposes itself to be shot by hunters.” This may partly explain why the Selk’nam people are said to have tamed or even

Table 1 Body measurements of *Lycalopex culpaeus* from Karukinka Natural Park (ca. 53°42'S, 69°18'W) on southern Tierra del Fuego Island during the winters of 2008–2009

Body features	Mean male, female	Range male, female	N male, female
Head and body length (mm)	928, 873	800–1000, 800–950	6, 6
Tail (from body insertion to tip) length (mm)	391, 389	345–430, 340–425	6, 6
Hind foot (from tarsus to toes without claws) length (mm)	172, 162	165–180, 150–167	7, 6
Mean inner ear (from cartilage edge to endpoint) length (mm)	98, 95	95–100, 80–105	4, 5
Weight (kg)	12.9, 10.0	11.4–14.5, 8.8–11.0	7, 6

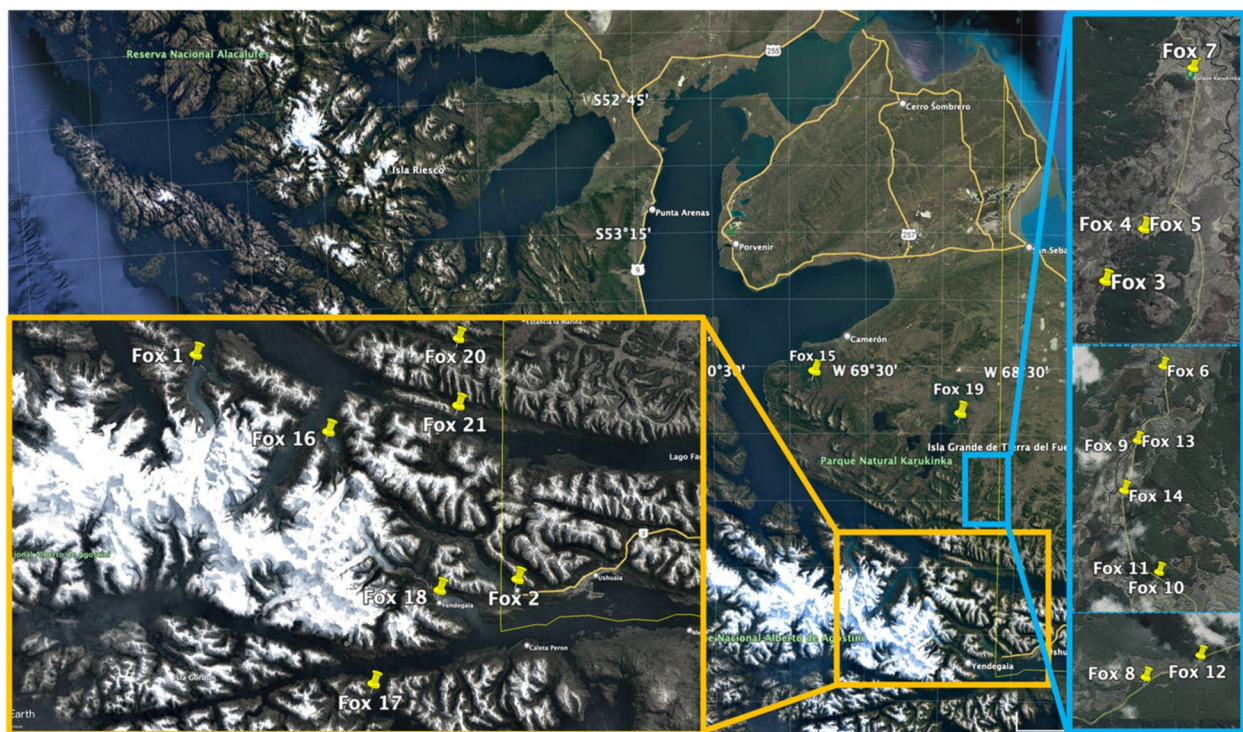


Fig. 3 Sights/captures of *Lycalopex culpaeus* on southern Tierra del Fuego Island. The yellow wavy lines are the main (paved) roads. White dots are human settlements of different sizes, from cities > 85,000 inhabitants (Punta Arenas, Río Grande, Ushuaia) through towns ca. 10,000 people (Porvenir, Puerto Williams, Tolhuín), through villages < 1,000 inhabitants (Cerro Sombrero, San Sebastián), to miscellaneous settlements including large sheep stations

domesticated the Fuegian fox (see detailed review in Jaksic and Castro [3]).

Gallardo [25] described the customs of who he called the Onas (technically, Selk'nam people) in Tierra del Fuego. In that book there are so many mentions to the use of Fuegian foxes by these natives, that it better be summarized as follows: Foxes were hunted with bow and arrow, sometimes aided by dogs. Fox skins were used for clothing, especially for making capes called “quillangos,” which were longer for men (weighing ca. 2.6 kg) than for women, and for making triangular hats and squarish purses. Also, for warming and caring of newborn babies and for polishing arrowheads and staffs. Fox bones were used for making harpoon points, and their meat was enjoyed especially when fat.

Gusinde ([26], page 564 as cited in Stahl [16], pages 523–524) seems to be the first who took notice of the accounts by early Europeans visiting the Tierra del Fuego Archipelago, that Yahgan dogs resembled small foxes. Nevertheless, Lönnberg's [50] study of such a dog skull obtained during the Nordenskjöld's 1885–1886 expedition indicated that it was simply a domestic dog, *Canis lupus familiaris*. Of the Selk'nam's dogs, Gusinde [26] did not contribute much information about their tamed or

domesticated animal. Gusinde ([68], page 92), reported that [our free translation from Spanish]: “Of the mammals it deserves mention only the fox (*Cerdocyon magellanicus*), a large and beautiful animal, and the otter; these latter are not hunted by the Selk'nam.” The unfortunate wording may include the two species or only the last. The scientific name given in the original, currently corresponds to *Lycalopex culpaeus*. Gusinde ([68], page 252) stated that the Yahgan people used fox fur for wrapping up and when nursing their newborn babies.

Bridges [27] memorialized his life in Harberton sheep station (Estancia Harberton, 54°52'S, 67°19'W) —on the Argentinian (northern) side of the Beagle Channel—and surroundings during the early 1900s. He was a keen observer, and at the risk of being slightly repetitive, we prefer to deal with his comments on Fuegian foxes as the reading of his book proceeds. (a) The Yahgan natives did not eat fox, even if in famine conditions, but the Selk'nam did and regarded it as a delicacy (page 28). (b) The Yahgan covered their body with fox or otter (*Lontra felina*) furs, rarely with those of guanacos (page 56). (c) The Haush (technically speaking, Manek'enk) from Mitre Peninsula on the southeastern seaboard of Fuegia occasionally visited Harberton station to exchange with

Table 2 Unpublished records of *Lycalopex culpaeus* on southern Tierra del Fuego Island, 2003–2023. The exception is Fox 17, which is from Hoste Island, 2012. These geographic records are mapped in Fig. 3

Fox ID	Observer	Latitude S	Longitude W	Date
Fox 01	J. Jiménez	54°24'20.89"	69°37'18.59"	February 2003
Fox 02	"	54°49'53.47"	68°33'44.85"	January 2004
Fox 03	C. Briceño	54°10'58.39"	68°43'59.07"	August 2008
Fox 04	"	54°10'21.05"	68°43'13.26"	"
Fox 05	"	54°10'21.05"	68°43'13.26"	"
Fox 06	"	54°13'57.13"	68°43'33.45"	"
Fox 07	"	54°08'20.12"	68°42'14.07"	September 2009
Fox 08	"	54°18'13.09"	68°46'57.61"	"
Fox 09	"	54°14'47.35"	68°44'01.02"	"
Fox 10	"	54°16'09.86"	68°43'36.39"	"
Fox 11	"	54°16'09.86"	68°43'36.39"	"
Fox 12	"	54°17'59.88"	68°46'02.97"	"
Fox 13	"	54°14'47.35"	68°44'01.02"	"
Fox 14	"	54°15'19.83"	68°44'14.79"	"
Fox 15	"	53°45'35.19"	69°56'25.20"	"
Fox 16	"	54°33'11.10"	69°11'15.39"	December 2009
Fox 17	"	55°01'55.43"	69°02'11.40"	March 2012
Fox 18	J. Jiménez	54°51'13.11"	68°49'09.71"	December 2014
Fox 19	C. Zurita	54°01'33.86"	68°55'51.17"	September 2021
Fox 20	"	54°22'23.91"	68°45'46.86"	September 2022
Fox 21	"	54°30'07.21"	68°45'44.66"	January 2023

Yahgans their fox furs for knives and axes (page 297). (d) According to Bridges’ travel mate Ahnikin (a Selk’nam), foxes occasionally gathered in packs --as if they were wolves--, to hunt for guanacos, but neither E. Lucas Bridges nor his father Thomas had ever watched this and indeed doubted it (page 360). (e) The Selk’nam valued fox fur for making their ample capes --but they also favored guanaco-- (page 377), used fox fur to polish their arrow tips or arrowheads (pages 386–387), and traded it with Caucasian miners for rifles (page 405). (f) This fox was abundant in Fuegia and on Navarino Island [?], was larger on Hoste Island, and was absent everywhere else in the Fuegian archipelago (page 456). (g) The Selk’nam enjoyed fat fox meat, unlike their dogs --which vomited if they accidentally ingested it (pages 456–457). And finally, an ecological comment (h): Because sheep ranching had increased over the years and foxes had been massively killed on suspicions of being lamb predators, native geese (*Chloephaga* spp.) had increased, eating, or spoiling up to 20% of the pastures (page 461).

According to Martinic ([30], page 56) sheep raising in Tierra del Fuego Island started in 1885 with 600 sheep brought from the Malvinas or Falkland Islands to Gente Grande Bay (northeastern Fuegia) and expanded in all

directions where pastures existed. Conflicts with the Selk’nam soon started as they found it easier to hunt for sheep --the “white guanaco”-- than for guanaco proper (pages 80–99). Fuegian foxes fell under the same disapproval from ranchers, as they preyed on sheep particularly during the lambing season, although no tallies were recorded. Fuegian fox received a double whammy when its potential competitor *Lycalopex griseus* was introduced to central Fuegia in 1951 to control an existing rabbit (*Oryctolagus cuniculus*) infestation [59, 60, 69]. Indeed, Jaksic et al. [70] reported that both foxes used the same prey categories though in slightly different proportions, and that their overall overlap in diet was 63%, rather high. Gómez et al. [71] analyzed the diets of both invading *Lycalopex griseus* and resident *Lycalopex culpaeus* and found that their prey profiles and other trophic characteristics were almost identical, thus pointing to potential competition between them. Novaro et al. [72] thoroughly documented the attack of a Fuegian fox on a 6-month-old guanaco and Tadich et al. [73] that on an introduced Canadian beaver (*Cas-tor canadensis*) by direct observation and scavenging of beaver remains through camera traps. Castillo et al. [74] documented that the Fuegian fox may be a key species in providing biotic resistance to invaders such as the muskrat (*Ondatra zibethicus*), on which they frequently preyed.

Radic et al. [75] reported that between 2012 and 2017 in the Magallanes Region 2,259 livestock animals (cattle, horses, sheep) were killed by different carnivores, mainly pumas (*Puma concolor*), foxes (*Lycalopex* spp.), and domestic dogs (*Canis lupus familiaris*). Of those livestock killed, 83% were sheep *Ovis aries* (1,887 individuals). Most of those attacks were reported on Tierra del Fuego Island (59%). Here, 78% of attacks corresponded to dogs (55 events) accounting for 1,855 killings of livestock (82%). Foxes (*Lycalopex* spp.) were reported to kill 208 livestock (9%), and puma 13 animals (1%) [sic]. WCS [76] focused on livestock attacks as reported by sheep ranchers within Chilean Tierra del Fuego Island and were able to discriminate among free-ranging dogs, *Lycalopex griseus*, and *Lycalopex culpaeus*, showing that their impacts decreased in the same sequence. While dog attacks were reported homogeneously all over the island, those of *Lycalopex griseus* were prevalent in the northern half, and those of Fuegian fox on the southern part. It should be considered that the latter fox is currently scarce in the sheep-intensive northern half of the island, and that the introduced *Lycalopex griseus* is thus the premier fox predator [60]. Coupled with this predation pattern, which apparently released northern guanaco populations from predator attacks, the latter species has increased, causing new human-wildlife conflicts [77].

Jaksic and Castro [3] addressed the issue of whether the Fuegian fox may have been tamed or domesticated by the Selk'nam, thus becoming the Patagonian “dog.” They discussed that the original Fuegian dog was indeed a *Canis lupus familiaris* brought along ca. 9,000 year by the incoming natives after the Bering's crossing and that the Patagonian “dog” was a tame Fuegian fox *Lycalopex culpaeus*. The latter was progressively replaced by the more gregarious, human-friendly, and colorful domestic dogs brought by European explorers, adventurers, colonizers, and settlers of Patagonia and Tierra del Fuego during the mid to late 1800s [78]. Jaksic and Castro [3] did not consider the possibility that the Patagonian “dog” may have been *Dusicyon avus*, an issue which is still unresolved [17, 64].

The possibility that the Patagonian “dog” was a cross between a domestic dog and a Fuegian fox (either *Lycalopex culpaeus* or *Dusicyon avus*) cannot be ruled out, but the only specimen genetically analyzed was closest to being the former and not a hybrid [79]. It should be called to attention that hybridization between *Canis lupus familiaris* and *Lycalopex gymnocercus* was reported by Krieg ([80]; cited in Stahl [16], page 523), with a hybrid having been created from a domestic Fox terrier father and a tamed Pampas fox mother. “Interestingly it could not bark, but it growled like a fox, and although not particularly obedient, it knew its name.” Attempts to breed the hybrid were unsuccessful and Krieg ([80], page 706) suspected that it was sterile. Stahl ([16], page 523) further reasoned that differences in chromosome number ($2n=78$ for *Canis* and $2n=74$ for *Lycalopex*; see [81]) should result in any offspring most likely being sterile. Another case of presumed hybridization between these two species was reported by Szyrwelski et al. [82]: The resulting female was melanistic, with an intermediate karyotype of $n=76$, and other midway genomic characteristics. Nevertheless, hybridization between *Canis lupus familiaris* and *Dusicyon avus* was discarded by Prevosti et al. [17] on the basis of differential cranial features.

A final interesting aspect is that raised by Franklin [20], better explained in his own words: “Although the Fuegian dog was a tame companion under the stewardship of peoples of Tierra del Fuego for thousands of years, its close genetic and phenotypic similarities to culpeo foxes and wild behavioural tendencies indicate it was not truly domesticated in the classical, domestic dog sense, but only partially as an intermediate between domestic and wild —strongly favouring the latter. Culpeo foxes lack the gregariousness of wolves and its solitary social system except for reproduction is considered to have been a major stumbling block in the way of full domestication ... The reversion of lost or abandoned Fuegian dogs back

to culpeo foxes is intriguing but was most likely an easy transition that paralleled today's equivalent examples of domestic horses in North America ... and dromedary camels in the Australia Outback ... successfully reverting to ancestral wild populations when returned to compatible environments. Based upon what we know to date, I suggest that the semi-domestic Fuegian dog is best recognised and referred to as the ‘culpeo dog.’ It is noteworthy that the ‘domestication’ of the culpeo dog by Stone-Age, Patagonia hunter-gatherer societies was a special case and atypical of canid domestication, different from the dual wolf-to-dog domestications in the northern hemisphere. While species of endemic wild foxes (avus and culpeo) in South America might not have been fully domesticated as the domestic dog, Patagonia archaeological records suggest an intimate and enduring relationship with humans...” Following Franklin's [20] reasoning, the Patagonian or Fuegian “dog” may not have become fully extinct, but simply regressed from being a tamed Fuegian fox harbored by the Selk'nam people, back into its wild form —which still subsists on Tierra del Fuego Island: the extant *Lycalopex culpaeus* or the extinct *Dusicyon avus*. Genetic studies are urgently needed to resolve this important issue.

Discussion

The historical account of this rare fox suffers from several geographic imprecisions: While Darwin [9], Bridges [27], and Prosser-Goodall [62] stated that it was abundant on Navarino Island, Olrog [52] asserted that it was not known there, and J. Jiménez has never recorded it over 10 year of fieldwork on that island. Again, according to Darwin [9], this fox was not on Hoste Island, while Prosser-Goodall [62] declared the opposite. Indeed, Milne Edwards [43] reported that some foxes were killed at Orange Bay (Hoste Island), Markham [55] recognized their presence there, Sielfeld [56] captured three, and Briceño [57] one on that same island. Dabbene's [47] assertion that this fox was “...spread over all islands down to the Cape Horn” seems totally off the mark. Up to now, Bridges [27] is the only source for the presence of this fox on Gable Island. And Milne Edwards [43] reported its presence at Banner Cove on Picton Island, but in J. Jiménez's experience, it is not there nowadays. Another geographic puzzle deserves noting: Although there are foxes on Hoste Island, there are no guanacos there, while the opposite happens on Navarino Island.

In Chile, according to the country's bylaws providing protection to species of conservation concern (https://clasificacionespecies.mma.gob.cl/wp-content/uploads/2019/10/Pseudalopex_culpaeus_P05_R5-9_RCE.pdf), *Lycalopex culpaeus lycoides* (the subspecies is recognized) is catalogued as Vulnerable by

criteria B1ab(iii) + 2ab(iii) (DS N°151 of 2007 of MIN-SEGPRES). In Argentina, this Fuegian variety is considered either as Least Concern (<https://www.iucnredlist.org/search/map?query=Lycalopex%20culpaeus&searchType=species>) or as Endangered (<https://cma.sarem.org.ar/es/especie-nativa/lycalopex-culpaeus>), mostly because of illegal shooting, poisoning, and running over by buses, cars, and trucks, with interference by domestic dogs also playing an unmeasured part. A consideration that seems to be missing is that the advance of a penetration route from Pampa Guanaco on the Chilean side of Fuegia toward Yendegaia on the northern shore of the Beagle Channel, is facilitating the spread of the invading Chilla fox toward the south, with potential competitive consequences for the native Fuegian fox [70, 71]. Another threat may be the potential cross-infections between these two species and also with stray domestic dogs [65, 83–85].

In general, there is an ominous lack of data on the geographic distribution and abundance of the Fuegian *Lycalopex culpaeus*, and of the enforcement of no-poaching, no-poisoning, no-shooting, no-trapping regulations. It is unfortunate that no estimates exist on previous --before, during, and after the increase phase of sheep ranching and of rabbit *Oryctolagus cuniculus* infestation-- and current Fuegian fox abundance and distribution [59, 70]. They appear to first have been pushed southwards because of hunting pressure by sheep ranchers and later by the introduction of --and interactions with-- its congener *Lycalopex griseus* [71]. It would also be desirable to explore whether the invasive beaver *Castor canadensis* somehow subsidizes as prey the Fuegian fox population [73, 74]. An effort to monitor both *Lycalopex* foxes' populations would be welcome, especially considering their binational character, given that the nature of the Argentina/Chile border is artificial, and Fuegian foxes move around unimpeded.

And finally, the “resurrection” of the Patagonian or Fuegian “dog” by means of retro-selection of ancestral characteristics seems a worthy enterprise, in line with the very recent official Chilean recognition that the Selk’nam people are not extinct: Their genes are still out there, same as those of the “dog” and its putative ancestor, the Fuegian fox.

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Authors' contributions

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The authors declare no conflict of interest.

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