

3.5 Darwin's fox
***Pseudalopex fulvipes* (Martin, 1837)**
Critically Endangered – CR: C2a(ii) (2004)

J.E. Jiménez and E. McMahon

Other names

Spanish: zorro de Darwin, zorro de Chiloé, zorro chilote;

Indigenous names: Huilliche: payneguru (i.e., blue fox) (Chile).

Taxonomy

Vulpes fulvipes Martin, 1837. Proc. Zool. Soc. Lond., p.11. Type locality: near the mouth of San Pedro Channel on the southern end of Chiloé Island, Chile (c. 73°45'W, 43°20'S; Osgood 1943).

Until recently the Darwin's fox was known only from the Island of Chiloé. Its taxonomic status was uncertain and confusing, mainly due to a paucity of museum material from which to make an accurate taxonomic assessment. It has been considered alternatively as an island form of the chilla (*P. griseus*) (Langguth 1969; Clutton-Brock *et al.* 1976; Pine *et al.* 1979; Corbet and Hill 1980; Honacki *et al.* 1982; Redford and Eisenberg 1992; Wozencraft 1993) or as a distinct species (Martin 1837; Osgood 1943; Cabrera 1958; Miller *et al.* 1983; Tamayo *et al.* 1987).

However, the discovery of a mainland population in sympatry with the chilla (Medel *et al.* 1990), and the analysis of mitochondrial DNA of the three Chilean foxes (i.e., including culpeo *P. culpaeus*), provides strong evidence for considering the Darwin's fox as a legitimate species (Yahnke *et al.* 1996). This study found that: (1) Darwin's fox separated from the chilla 275,000 to 667,000 years ago; (2) the mainland population is a relict population (and not a founder group that escaped from captivity as has been suggested; Medel *et al.* 1990) and was probably distributed over a larger area in south central Chile; and (3) the mainland stock separated from the island stock about 15,000 years ago. In other words, current populations of Darwin's fox are relicts of a former, more widely distributed species (Yahnke 1995; Yahnke *et al.* 1996). Yahnke (1995), based on pelage coloration, found some similarities between the Darwin's fox and the Sechuran fox (*P. sechurae*) from the coastal desert of Perú (2,000km to the north), supporting Osgood's (1943) speculations of a phylogenetic relationship.

Chromosome number is not known.

Description

Darwin's fox is a small, stout fox possessing an elongated body and short legs (Table 3.5.1). Its muzzle is short and thin and extends into a rather rounded forehead. The agouti hair on the torso is a mixture of grey and black that contributes to its dark appearance. It has rufous markings on the ears and along the legs below the knees

and elbows (i.e., *fulvipes*). White markings are found under the chin, along the lower mandible, on the under belly and on the upper and inner part of the legs. The tail is dark grey, relatively short and quite bushy, a useful diagnostic character for distinguishing this species from congenetics (Novaro 1997). Compared to the chilla, the skull is shorter and the auditory bulla smaller, but the dentition is heavier (Osgood 1943). Dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Monotypic.

Table 3.5.1. Body measurements for Darwin's fox.

	Chiloé Island (J.E. Jiménez unpubl.)	Nahuelbuta National Park (E. McMahon unpubl.)
HB male	540mm (525–557) n=6	538mm (482–561) n=9
HB female	514mm (480–550) n=9	522mm (495–591) n=7
T male	224mm (195–240) n=7	220mm (195–255) n=9
T female	219mm (175–250) n=9	221mm (199–235) n=7
HF male	107mm (99–111) n=7	110mm (101–117) n=9
HF female	103mm (93–110.5) n=9	105mm (101–114) n=7
E male	67mm (61–75) n=6	69mm (62–81) n=5
E female	64mm (52–71) n=9	60mm (56–66) n=3
WT male	3.26kg (2.8–3.95) n=7	2.44kg (1.9–2.8) n=9
WT female	2.91kg (2.55–3.7) n=9	2.26kg (1.8–2.5) n=7

Darwin's foxes. Radio-collared ~four-year-old male with five-month-old male pups. Parque Nacional Nahuelbuta, Chile, 2000.



Elise McMahon

Similar species Sechuran fox (*P. sechurae*): smaller in size; inhabits open areas and sandy coastal deserts of Perú. Chilla (*P. griseus*): larger in size, with longer legs and lighter colour; sympatric only in Nahuelbuta National Park.

Current distribution

Darwin’s fox is endemic to Chile (Figure 3.5.1). It has a disjunct distribution with two populations: one found in the forests of Chiloé Island (42°S, 74°W), and another on the coastal mountains in Nahuelbuta National Park of mainland Chile (37°45’S, 73°00’W).

There are few records for the species. Charles Darwin collected the first specimen in 1834 from the south-eastern end of Chiloé Island. Osgood (1943) later captured it at the mouth of the Inio River, on the southern shore of the same island. On the Pacific shore of Chiloé, the species has been trapped on Playa Tricolor (in June 1999; J.E. Jiménez pers. obs.) and intensively monitored since November 2001 at Ahuenco; on the Cordillera del Piuché, the fox has

been monitored since 1989 (Jiménez *et al.* 1990). On the northern part of Chiloé Island, one fox was captured in November 1999 and at Tepuhueico, on the central part, two adults were observed in June 2002 (J.E. Jiménez pers. obs.). On the north-western part of the same island, a local recently killed a female and her two cubs; and there have been additional sightings in the same area (C. Muñoz pers. comm.). Thus, Darwin’s fox occurs on most of Chiloé Island (about 200km long x 62km wide), especially where forest remains, with the exception of the most populated areas on the eastern and north-eastern parts.

On mainland Chile, Jaime Jiménez has observed a small population since 1975 in Nahuelbuta National Park; this population was first reported to science in the early 1990s (Medel *et al.* 1990). It appears that Darwin’s foxes are restricted to the park and the native forest surrounding the park (McMahon *et al.* 1999). This park, only 68.3km² in size, is a small habitat island of highland forest surrounded by degraded farmlands and plantations of exotic trees (Greer 1966). This population is located about 600km north of the island population and, to date, no other populations have been found in the remaining forest in between (W.E. Johnson pers. comm.).

Figure 3.5.1. Current distribution of Darwin’s fox.



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Range countries Chile (Osgood 1943).

Relative abundance

Darwin’s fox was reported to be scarce and restricted to the southern end of Chiloé Island (Osgood 1943). The comparison of such older accounts (reporting the scarcity of Darwin’s fox), with recent repeated observations, conveys the impression that the Darwin’s fox has increased in abundance, although this might simply be a sampling bias.

Estimated populations/relative abundance and population trends

Yahnke *et al.* (1996) speculated that 500 foxes live on the Island of Chiloé. Based on home range estimates of six foxes, and considering their extensive range overlaps (42–99%) Jiménez (2000) calculated that the ecological density of the Darwin’s fox is 0.95 individuals/km² at the Piruquina study site (c. 9km²) on Chiloé. Although difficult to estimate the overall density on the island, the species is rare on the northern part and around towns on the north-eastern and eastern part of Chiloé. Otherwise, the species is fairly common for a wild canid in forested environments, especially on the mountain terrain and lowland beaches on the Pacific Ocean side.

Table 3.5.2. The status of Darwin’s fox populations in Chile (Trend: I=increasing, S=stable, D=declining, ?=Unknown).

Region	Protected areas		Other areas		Total	
	Population size	Trend	Population size	Trend	Population size	Trend
Mainland	~78	?	10	D	<100	?
Chiloé Island	250	S	250	D	500	S

Based on intensive captures in Nahuelbuta National Park, E. McMahon (unpubl.) estimated a density of 1.14 individuals/km² and extrapolated an abundance of 78 individuals in this isolated population. This estimate is similar to the figure of 50 foxes given by Cofré and Marquet (1999). This number is quite small considering it is the only known mainland population. Nevertheless, the mainland population appears to have increased in numbers since 1986, apparently as a response to a decrease in chillas (Jaksic *et al.* 1990). Recent quantitative information (Table 3.5.2) does not agree with a previous study that reported that the Darwin's fox was about twice as abundant on Chiloé as in Nahuelbuta (Jiménez *et al.* 1990).

Habitat

Darwin's fox is generally believed to be a forest obligate species found only in southern temperate rainforests (Jaksic *et al.* 1990; Medel *et al.* 1990). Recent research on Chiloé, based on trapping and telemetry data on a disturbance gradient, indicates that, in decreasing order, foxes use old-growth forest followed by secondary forest followed by pastures and openings (Jiménez 2000). Although variable among individuals, about 70% of their home ranges comprised old-growth forest. However, compared with the amount available, foxes preferred secondary forest and avoided old growth. Selection of openings varied among individuals. The forest is of Valdivian type, comprising a few native conifers and several species of broad-leaved evergreen species, and dominated by fruit-bearing trees of the Mirtaceae family. This forest is dense, with different strata and very moist all year round (Jiménez *et al.* 1990).

On the Pacific coast of Chiloé, Darwin's fox lives in a fragmented environment of coastal sand dunes mixed with dense evergreen forest. On the northern part of the island, Darwin's fox uses a relatively flat, but fragmented landscape of broad-leaf forest and dairy cow pastures. Research on the mainland population supports the notion of the species using primarily dense forest (Jaksic *et al.* 1990; Jiménez *et al.* 1990). Capture and telemetry data indicate that animals are found in dense *Araucaria-Nothofagus* forest, open *Nothofagus* forest and open pasture with decreasing frequency (McMahon *et al.* 1999). The forest comprises mainly monkey-puzzle trees (*Araucaria araucaria*) and five species of southern beech (*Nothofagus* spp.), one of which is non-deciduous.

Food and foraging behaviour

Food Darwin's fox is omnivorous, has a broad diet spectrum, and is highly opportunistic; these traits facilitate its survival in a prey-poor and highly fluctuating environment (such as Nahuelbuta and Chiloé; Jaksic *et al.* 1990; Jiménez *et al.* 1990). It changes its diet as the availability of food items changes in the environment, which renders marked seasonal changes. Based on faecal

analysis, Jiménez *et al.* (1990) reported that the mainland population ate mainly small mammals, reptiles, insects, birds, and arachnids (in that order of importance). The proportions of these prey classes fluctuated strongly among seasons. More recently, analysis of faeces of trapped foxes indicated that, by number, insects were the most abundant prey in the diet, followed by small mammals and reptiles (although small mammals constituted most of the diet biomass). Berries were also included in the diet, showing up in c. 20% of the faeces.

On the mainland, Darwin's foxes rely heavily on the seeds of monkey-puzzle trees from March to May (E. McMahon unpubl.). During the summer months, droppings are filled with insect remains and seeds. Further content and genetic analysis of scats collected in Nahuelbuta National Park over a four-year period will provide more detailed information on seasonal fluctuations in diet and the dietary separation between the Darwin's fox and the other carnivores in the system.

On Chiloé, during the warm season insects were the most abundant in the diet by number, followed by amphibians, mammals, birds and reptiles (Jiménez *et al.* 1990); 49% of faeces had seeds. A recent dietary study of three different fox populations on the island found that in the summer, foxes fed mainly on insects, which were replaced by small mammals during the winter (J. Jiménez and J. Rau unpubl.). During late summer and fall, the diet was comprised almost entirely of fruits of Mirtaceae trees. Armesto *et al.* (1987) speculated that foxes could be considered a key species because of their role in dispersing seeds of forest species. An ongoing experiment indicates that at least for one tree species (*Amomyrtus luma*), a high percentage of seeds collected from faeces germinate under field conditions. A small amount of the diet consists of carrion, as evidenced by the remains (e.g., hair) of sheep, pigs, cattle, and horse in faeces.

Foraging behaviour Our telemetry data indicate that up to four foxes may concentrate on a carcass for a few days, but that they are otherwise solitary hunters. Jiménez *et al.* (1990) stated that foxes would scavenge opportunistically. Local settlers reported that lone Darwin's foxes would kill Southern pudu deer (*Pudu puda*) (about 10kg in weight) by biting their ankles and then the throat. They have been observed hunting ducks in a marsh during midday in the coastal range at Playa Ahuenco (October 2000; J.E. Jiménez pers. obs.). In addition, coastal foxes feed on shellfish and shorebirds, and up to nine individuals have been observed feeding on large brown algae on the beach. In Nahuelbuta National Park, where the Darwin's fox is sympatric with the chilla, McMahon (2002) has found that Darwin's fox forage in habitats rich in small mammals mainly at night, when the larger chilla is less active. Daytime activity of the Darwin's fox seems to be concentrated in forested areas where they may feed on

reptiles, amphibians, and forest-floor dwelling birds species such as the tapaculos (Rhinocrytids).

Damage to livestock or game On Chiloé, foxes are well known for killing poultry and raiding garbage dumps, apparently with little fear of people and dogs to the point that they enter houses at night in search for food (J.E. Jiménez pers. obs.). In the farmlands surrounding Nahuelbuta National Park, interviews with the local farmers indicate that Darwin's foxes are not involved in livestock or poultry predation (E. McMahon unpubl.).

Adaptations

Small size and short limbs and tail appear to be adaptations for living in the dense forest understorey. Short extremities and compact body shape might also serve to decrease heat loss in cold and wet environments (Allen's rule) such as those favoured by Darwin's fox. The dark pigmentation pattern of the body corresponds with subsistence in a moisture-saturated environment (conforming to Gloger's rule). Dark coloration might also serve as camouflage in the dark environment close to the forest floor. The fox has been observed swimming across a river in excess of 15m wide on Chiloé. This aquatic ability might enable the Darwin's fox to move and disperse in a landscape where water bodies are a common landscape feature.

Social behaviour

Telemetric information on Chiloé indicates that when not breeding, Darwin's foxes are solitary carnivores (J.E. Jiménez unpubl.). They would, however, congregate at a food source when faced with concentrated resources (e.g., carcasses and seaweed stranded on beaches). A pair appears to be the standard unit during the breeding season. In the island population, home ranges are about 1.6km² for males and 1.5km² for females (J. Jiménez and J. Rau unpubl.). Given the very large range overlaps among neighbouring foxes, and that individuals share their home range with an average of 4.7 males and 3.3 females, the Darwin's fox appears to be a non-territorial species (Jiménez 2000).

On the mainland, pairs persist throughout the year, often being found within close proximity (E. McMahon unpubl.). Pairs have been known to share their home range with offspring from previous years. All family members associate closely with each other, showing very little aggressive behaviour between the parents and yearling offspring. Although one family has been observed for over three years, we have not seen any evidence of older siblings serving as helpers to new litters. Two yearling male siblings have been observed foraging and frolicking together (E. McMahon pers. obs.). Other known pairs (n=4) have juvenile males and females using their home range. Telemetry results from the mainland population indicate that there are groups of individuals with overlapping home ranges. However, there is little overlap between groups.

The maintenance of a large family group may be influenced by a paucity of suitable territories for potentially dispersing juveniles. Dispersal appears to be delayed and may be opportunistic such as in the case of one female, monitored since first captured as a yearling. She remained in association with her putative family group until three years of age, when she dispersed into an adjoining area with an adult male who had lost his mate. In another case, two males marked and radio-collared as pups, dispersed from their familial home range at two years of age. Their dispersal was six months post the death of their mother and coincided with the breeding season and the arrival of an adult female who subsequently paired with their father (E. McMahon unpubl.).

Reproduction and denning behaviour

On the mainland, lactating females have been caught in October (austral spring) and pups have been documented leaving the den area and venturing out with both parents in December (austral summer) (E. McMahon unpubl.). Litter size is estimated to be 2–3 pups based on observations of parents with litters and capture data. Weaning occurs in February. During weaning, the female spends relatively less time with the pups and a greater portion of their interactions are antagonistic, whereas the male spends more time playing with and grooming the pups (E. McMahon pers. obs.). Jaksic *et al.* (1990) described a den as a rock cavity (2m deep, 1.8m wide, and 0.7m high), located in *Araucaria-Nothofagus* forest with a bamboo understorey.

On Chiloé, reproduction occurs at least between October and January, when lactating females have been found. A small pup was found denning in a rotten and hollow log on the ground in late December (J.E. Jiménez pers. obs.). During mating, males and females are together for a few days. During the few weeks after parturition occurs, females do not move much and appear to stay in the den.

Competition

The only other terrestrial carnivores that live on Chiloé Island are the kod-kod or guiña (*Oncifelis guigna*), the hog-nosed skunk (*Conepatus chinga*), and the little grison (*Galictis cuja*). However, there are no data to support potential competition of these carnivores with the fox. The sympatric rufous-legged owl (*Strix rufipes*) is another potential competitor of Darwin's fox for small mammal prey.

The mainland population overlaps geographically with six carnivore species. These include the puma (*Puma concolor*), the culpeo and the chilla, the guiña, the hog-nosed skunk and the grison. The first three carnivores are larger and represent not only potential competitors, but also potential predators. Preliminary results of the current investigation of the ecological overlap between Darwin's fox and the chilla indicate that they exhibit some degree of

overlap in home ranges and activity patterns (E. McMahon unpubl.). Clearly, the potential exists for competition between these two species.

It appears that when in sympatry with other carnivores, such as on the mainland, Darwin's fox moves into the open forest/grassy areas mainly at night, when the small mammals are active and when the grey fox is less active (E. McMahon pers. obs.). Thus, nocturnal behaviour may be related to avoidance of competitors as well as potential predators.

Mortality and pathogens

Natural sources of mortality In Nahuelbuta National Park, puma, culpeo, and chilla are all potential predators of the Darwin's fox. The larger culpeo has also been trapped in the same area as the Darwin's fox, but based on telemetry data, these individuals were passing through the area and therefore less likely to be serious competitors. Of the 29 radio-collared foxes we have followed over four years, there have been five mortalities attributed to larger carnivores, of which one was a puma. This latter fox had a home range adjacent to the park and was often in open patchy habitat. However, the main habitat of the Darwin's fox includes extremely dense undergrowth, which may prohibit serious pursuit by pumas (E. McMahon pers. obs.).

In Nahuelbuta National Park, survival rates of radio-collared juvenile and adult Darwin's foxes are 84% for females and 93% for males. Analysis of cause-specific mortality rate for the mainland population indicates that 74% of mortalities are due to natural causes while 26% are human caused (McMahon 2002).

Persecution Aside from reports by locals that they kill Darwin's foxes because they eat their poultry, and individuals killed by dogs, no other mortality causes have been detected on the island. On the mainland, radio-telemetry data and interviews with local people support the idea that the Darwin's fox does not venture far enough outside the park and forested area surrounding the park to be considered a nuisance by farmers.

Hunting and trapping for fur Although this fox is easily and repeatedly trapped, there is no known hunting or trapping for its fur.

Road kills In Nahuelbuta National Park, an adult, lactating female was killed by a tourist in the parking lot of the park's main attraction (McMahon 2002). Some foxes have become habituated to people by constant and unrestricted feeding by park visitors. These foxes spend much of their time under vehicles in the parking lot and are at risk of being killed by visitor's cars. Foxes have been observed climbing into visitor's cars, and there have been reports from CONAF park rangers of visitor's attempting to leave the park with Darwin's foxes in their vehicles. This lack of supervision

over tourists who feed and thereby encourage foxes to spend time in the parking lot is thought to be one of the main conservation concerns for this mainland population.

Pathogens and parasites No pathogens or parasites have been reported for the Darwin's fox.

Longevity In Nahuelbuta National Park, an adult male estimated to be three years old at capture has been monitored since 1998, making him now seven years of age. We have been following another male estimated to be 6–7 years old and a female who is five years old (McMahon 2002).

Historical perspective

No information available.

Conservation status

Threats and conservation measures taken Although the species is protected in Nahuelbuta National Park, substantial mortality sources exist when foxes move to lower, unprotected private areas in search of milder conditions during the winter. Some foxes even breed in these areas. This is one of the reasons why it is recommended that this park be expanded to secure buffer areas for the foxes that use these unprotected ranges (McMahon *et al.* 1999).

The presence of dogs in the park may be the greatest conservation threat in the form of potential vectors of disease or direct attack. There is a common practice to have unleashed dogs both on Chiloé and in Nahuelbuta; these have been caught within foxes' ranges in the forest. Although dogs are prohibited in the national park, visitors are often allowed in with their dogs that are then let loose in the park. There has been one documented account of a visitor's dog attacking a female fox while she was nursing her two pups (E. McMahon pers. obs.). In addition, local dogs from the surrounding farms are often brought in by their owners in search of their cattle or while gathering *Araucaria* seeds in the autumn. Park rangers even maintain dogs within the park, and the park administrator's dog killed a guiña in the park. Being relatively naive towards people and their dogs is seen as non-adaptive behaviour in this species' interactions with humans.

The island population appears to be relatively safe by being protected in Chiloé National Park. This 430km² protected area encompasses most of the still untouched rainforest of the island. Although the park appears to have a sizeable fox population, foxes also live in the surrounding areas, where substantial forest cover remains. These latter areas are vulnerable and continuously subjected to logging, forest fragmentation, and poaching by locals. In addition, being naive towards people places the foxes at risk when in contact with humans. If current relaxed attitudes continue in Nahuelbuta National Park,

Chiloé National Park may be the only long-term safe area for the Darwin's fox.

Commercial use None. However, captive animals have been kept illegally as pets on Chiloé Island (Jiménez pers. obs).

Occurrence in protected areas Nahuelbuta National Park (IX Administrative Region) protects the mainland population in *c.* 68km²; Chiloé National Park (X Administrative Region) protects the island population in *c.* 430km².

Protection status CITES – Appendix II

The conservation status in Chile is 'rare' on the mainland and 'vulnerable' on Chiloé Island (Glade 1993). More recently, Cofré and Marquet (1999) considered the Darwin's fox as 'critical', assigning it the second most urgent conservation priority among Chilean terrestrial mammals. Spotorno (1995) reported that the mainland population is vulnerable and its future survival uncertain if current environmental trends continue.

Current legal protection Protected by Chilean law since 1929 (Iriarte and Jaksic 1986), but enforcement is not always possible and some poaching occurs.

Occurrence in captivity

The Temuco Zoo held a male and a female until their release in October 2000 on Chiloé. No known specimens are kept elsewhere.

Current or planned research projects

J.E. Jiménez (Universidad de Los Lagos, Osorno, Chile) has studied the Darwin's fox since 1989 on Chiloé. He is currently conducting a study on the ecology of the species and the effects of forest fragmentation on the behaviour and habitat use of Darwin's fox. In 2001, he began an outreach programme with local farmers to help protect the species. In August 2002, a three-year Darwin Initiative to focus on the conservation of the Chiloé population was initiated by J.E. Jiménez and S.M. Funk. It is addressing questions on the ecology, genetic structure, spatial modelling of distribution and abundance, and an assessment of risks of disease transmission by dogs, in addition to having a strong education programme with local people.

E. McMahon (University of Massachusetts, Amherst, USA) has been studying the behavioural ecology of the Darwin's fox in Nahuelbuta National Park since 1998. One aspect of this study is an investigation of interspecific interactions with sympatric chillas, culpeos, and guñas. A further initiative concerns conservation education in the local schools involving both children and their parents.

E. McMahon (University of Massachusetts) has conducted a study on disease and parasites affecting the

Darwin's fox in the mainland population since January 2002. Since potential interaction with domestic dogs appears to be one of the primary conservation threats to the mainland population, a study is planned to determine the presence of rabies, parvovirus, and distemper in the dogs living in the area surrounding the park.

E. McMahon (University of Massachusetts) and W.E. Johnson (National Cancer Institute, Maryland, USA) will be examining levels of inbreeding in the mainland population and conducting further investigation of the phylogenetic relationships between the Darwin's fox and other South American canids.

Gaps in knowledge

A high priority would be to conduct intensive searches for other populations between Nahuelbuta and Chiloé. There are many remote pockets that are little explored where isolated populations could still be found.

The behavioural ecology of a forest-specialist or forest-dependent species is of utmost interest. Research topics to be explored include: social behaviour (e.g., tolerance to conspecifics), large home range overlaps, presence of helpers, and small litter sizes. In addition, little is known as concerns population dynamics, dispersal behaviour, and metapopulation structure.

Genetic aspects, including levels of inbreeding and inbreeding depression, and past population bottlenecks, are little known and important for future management.

Impacts of and resilience to human-related disturbances, the effects of free-ranging dogs, the foxes ecological naiveté to people, and forest disappearance and fragmentation are all of interest for fox survival. The impact of habitat loss (through forest conversion) on fox populations is also of interest. At least in Chiloé, habitat disturbance *per se* seems to play little, if any, role in population dynamics. On the mainland, however, fragmentation might increase risk of predation by other native predators.

Considering the potential disease threat posed by domestic dogs, an investigation into diseases and pathogens (and other allied mortality causes) is crucial.

If Darwin's fox is so closely related to the Sechuran fox of southern Perú as the circumstantial evidence suggests, then how did the two species diverge and become separated? These two ranges have been separated by the Atacama Desert for a long time. Exploring this question, in connection with other puzzling biogeographical patterns, could provide evidence to better understand canid speciation and species interactions.

Core literature

Jaksic *et al.* 1990; Jiménez *et al.* 1990; Medel *et al.* 1990; Yahnke *et al.* 1996.

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