Status Survey and Conservation Action Plan

Canids: Foxes, Wolves, Jackals and Dogs

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IUCN/SSC Canid Specialist Group

IUCN
The World Conservation Union

PART 2

Species Status Accounts

Edited by M. Hoffmann and C. Sillero-Zubiri

Species Status Accounts: an Introduction

M. Hoffmann and C. Sillero-Zubiri

The species' accounts represent the core of the Action Plan. Each species' account consists of a detailed entry summarising the information available on the biology, abundance, population trends and threats facing the species.

Some readers may balk at the amount of information presented for each species. Ordinarily, species action plans restrict the amount of information they include on basic ecology and behaviour and emphasise the sections on conservation, abundance, threats and so on. This is still very much the policy followed here; however, the viewpoint of the editors was that the conservation, status and threats facing a species cannot be viewed independently of a species' biology. Much of the information contained within the pages of this action plan has never appeared in published form before, and certainly never in such a summarised format. We believe that the inclusion of basic life-history information in this plan is crucial to fostering a clearer understanding of the sections on conservation and status, and that this information will, in itself, serve as important reference for future canid biologists. For this reason, the editors have sought to ensure that this action plan represents a detailed summary of all aspects of a species' life history, without sacrificing on the real "meat and bones" of the plan.

Each species' account has been prepared by one or more contributors, at the invitation of the editors. We have endeavoured to draw on the expertise of biologists and naturalists from many countries and, as far as possible, those with first-hand experience and knowledge of the species concerned. The species' accounts are based primarily on published information (i.e., from books and journals), supplemented as far as possible with reliable unpublished material and personal observations from the author's own studies or other sources. The use of grey literature has been strongly recommended, and authors were also encouraged to correspond with other colleagues likely to have unpublished material or to be able to contribute unpublished data. Accounts on African canids benefited from our linking in with the *Mammals of Africa* project, being edited by Jonathan Kingdon, David Happold and Tom Butynski. For the most part, the information contained in the species accounts is derived from free-living populations. Occasionally, this has been supplemented by information from captivity (for example, details of longevity which often are not available for wild populations); for other species that have never been studied in the wild, information on captive animals has been consulted more extensively where available. Each profile was reviewed by two or more appropriate reviewers, either chosen by the authors or suggested by the editors.

Regional sections

To respect evolutionary affiliations and facilitate access to the reader, we follow a biogeographical approach (*sensu* Sclater and Sclater 1899), with species accounts listed under the relevant regional regions.

Thus, we have organised the species accounts in seven chapters that follow the major biogeographical regions recognised for mammals by Wallace (1876). For the sake of convenience, the names of the biogeographical regions are paired with the relevant geographical regions covered by the Canid Specialist Group various Regional Sections (Table 1). The Ethiopian region is divided into two distinct groups of species. Those species that occur in more than one such region are included in the region that encompasses the largest area of the species range.

Table 1. Biogeographical regions are paired with the relevant geographical regions covered by the CSG various Regional Sections.

Biogeographic Region	CSG Regional Section
Neotropical (up to south Mexico)	South America/North and Central America
Nearctic	North and Central America
Palearctic	Europe/North and Central Asia
Ethiopian	Sub-Saharan Africa
Ethiopian	North Africa and Middle East
Oriental (south of the Himalayas)	South Asia and Australasia
Australasian	South Asia and Australasia

Outline of accounts

Because of the inconsistencies inherent in multi-author projects, the editors have requested authors to adhere to a strict set of guidelines in the compilation of the species accounts. While every effort has been made to make all species accounts conform to the same general structure and content, some idiosyncrasies remain evident. Far from detracting from the quality of the plan, we believe this only serves to make the plan a more interesting read! As far as possible then, and where available data allows, species accounts use the following format.

Scientific name (authority and year)
The currently accepted scientific name of the species is followed by the details of the author and the year in which the species was described. The latter appears in brackets where it is now included in a genus other than that in which the original author placed it.

IUCN Red List Category
The current (2003) Red List ranking, as assessed by the Canid Specialist Group using version 3.1 of the criteria (IUCN 2001). For information on the categories of canid species assessed by the Canid Specialist Group in 1996 see Appendix 1.

Preferred English name
Where more than one English name is commonly used, the preferred name appears.

Author(s)
The names of the author(s) responsible for researching and compiling the species account.

Other names
These include further English names, French, German, Spanish, Italian, Portuguese, and other names for any major language (and listed alphabetically). Names under indigenous languages are those in use in localised areas. The indigenous language is given, followed by the names used in that language and the country in which the indigenous language is used.

Taxonomy
This begins with the type species and description. This is the full and original citation of the species name, followed by the type locality. This information largely follows Wozencraft (1993), although in some cases the authors or editors have seen cause to deviate from this rule. Refer to Chapter 2 for a detailed treatment of modern canid systematics.

The taxonomy of the Family Canidae is dealt with in Chapter 2 of this volume. Within the species' accounts, this section is used where the taxonomy of a species requires clarification, particularly where recent studies may have challenged the accepted nomenclature of certain species. These are discussed here as relevant. Details of chromosome number are provided where available.

Description
The purpose of this section is to provide the reader with adequate information to identify the species. As far as possible, the description of a given species is based on live specimens and includes details of general appearance, followed with a detailed description beginning with the head, parts of the head, body, legs, feet and tail. This section includes notes on pelage characteristics (i.e., colour, length, variation in different parts of the body, pattern, areas of bare skin), and special attention is given to diagnostic features and the relative size of ears, eyes, muzzle, tail, etc. In addition, unique or characteristic cranial and dental features are noted, as well as the dental formula of adults (i/i-c/c-p/p-m/m = total number of teeth).

Body Measurements General body measurements are given separately in a table. These are either from previously published or unpublished sources and provide general morphometric data from a particular region within the range of the species.

HB	Head-Body length
T	Tail
E	Ear
SH	Shoulder height
WT	Weight

Subspecies The number of currently accepted subspecies is given here (followed by the source), with details of their geographical range. Where relevant, details important for diagnosis are provided. If no species are currently recognised, the species is regarded as monotypic.

Similar species The common name and scientific name of any similar species with which the current species could be confused, followed by details of how each similar species differs from the species being described (i.e., any description is for the similar species, not the one under the heading).

Current distribution
The geographical range of the species, described from west to east, and from north to south. Range extensions or reductions, reintroductions and introductions, and disagreements about the range of a species are discussed here. The ranges of rare species or those with a very restricted distribution (e.g., Ethiopian wolf) are described in more precise terms. The spelling of geographical names follows that given in *The Times Atlas* (2003). Where information pertaining to the historical range of a species exists, the distribution is given in two separate headings, namely historical distribution and current distribution:

Historical distribution Includes details and references for known historical data; evidence for assumed former range such as museum specimens, palaeontological and/or archaeological evidence, cave paintings and so on.

Current distribution The distribution of the species as currently understood.

Range countries A list of the range countries from which a species is known to occur (and listed alphabetically),

followed by the most important sources from which this information is derived. Possible, but unknown, occurrences are indicated by (?).

Distribution map

Each species account includes a map of distribution. The present distribution of the species is shadowed in a map of suitable scale. If the historic distribution of the species is known and differs significantly from present, it may be shown shaded in a lighter grain. Reliable single sightings within the last 10 years outside those areas are marked with crosses (X). Areas where species may be present but sightings unconfirmed are marked with a question mark (?).

Relative abundance

A general indication of abundance in the habitat, including details of density and frequency of observations whenever that is available. Whenever possible, a table is presented with site-specific populations/relative abundance and population trend, summarised for each of its range states. Quantitative population estimates are usually obtained from total counts, ground surveys, questionnaire surveys and informed guesses by knowledgeable observers. Population abundance is indicated by: abundant (A), common (C), uncommon (U), rare (R), vagrant (V), present but abundance unknown (x), presence not confirmed (?), absent (-), extinct (Ex), probably extinct (Ex?). Population trends are indicated by: increasing (I), stable (S), decreasing (D), unknown (?).

Habitat

The preferred habitat and range of habitats, including details of rainfall, altitude and seasonal shifts in habitat. Details of any association with a specific plant, terrain, water availability, and so on, are also mentioned.

Food and foraging behaviour

This section is divided into three subheadings:

Food Preferred food items; range of prey consumed; variation in diet in different ecosystems.

Foraging behaviour Location of food; time when foraging occurs, including notes on activity; whether solitary or group hunters; sex/age differences in foraging; nomadic movements in relation to food availability; scavenging; food caching; how the species kills and handles its prey.

Damage to livestock or game Whether species preys on domestic stock or impact on wild game, and associated economic significance.

Adaptations

Morphological (e.g., proportions, shape, dental structure), physiological (e.g., water metabolism, temperature regulation, moult), and behavioural (e.g., huddling, allo-suckling) adaptations that show how a species uniquely interacts with its environment.

Social behaviour

Details of group structure, group size and composition, home range, territorial behaviour, greeting or agonistic behaviour, use of secretions and vocalisations.

Reproduction and denning behaviour

Physiological and morphological characteristics related to reproduction, including: spermatogenesis and details of oestrous cycle; courtship and mating behaviour; length of gestation; time of birth, including peaks of births and relationship to rainfall or food availability; litter size; birth weight and size; spacing of litters; pup development, and time to weaning and sexual maturity; behaviour of young; presence of helpers. This section may be supplemented with information from captive animals. This section also includes details of dens and burrows, such as location, type, structure, use of bedding material and so on.

Competition

Details of those species with which the current species is known to compete for food, dens or other resources.

Mortality and pathogens

This section is divided into six subheadings:

Natural sources of mortality Sources of mortality that can be regarded as being natural (i.e., outside of the influence of man); for example, effects of major predators on populations, starvation, death of young animals during dispersal and so on.

Persecution Sources of mortality, with the exception of hunting and trapping for fur, which can be attributed to anthropogenic factors. For example, persecution of animals due to their preying on livestock and/or game, the capture of animals for the pet trade, and so on.

Hunting and trapping for fur The impact of the fur trade as a mortality factor in the species, including details of the quantities of animals affected by hunting or harvesting; fur harvests and yields; peak years in the fur trade; fur prices; exports and imports.

Road kills The impact of road traffic on populations, including information, where available, of numbers of animals killed.

Pathogens and parasites Effects of pathogens and parasites on populations; susceptibility to particular diseases, pathogens and parasites (endo- and ecto-

parasites); the importance of the species as a vector or reservoir of diseases of domestic stock and humans.

Longevity The known or estimated longevity of the species. Where data from the wild are not available, this is supplemented by known records from captive animals.

Historical perspective

The species' importance in culture; traditional uses; conservation measures taken in the past.

Conservation status

This section is divided into six subheadings:

Threats The most important tangible and potential threats the species faces for its immediate or long-term survival.

Commercial use Present human use and influence (e.g., fur trade, pet trade); international demand and marketing.

Occurrence in protected areas The species' known occurrence in protected areas within the normal distribution range of the species. This section is not intended to provide an exhaustive listing of protected areas from which a particular species is known to occur, although we have attempted to be as comprehensive as possible for threatened species (e.g., dhole). For other species, such as black-backed jackal, we list only a few of the larger and better-known protected areas. The lack of adequate survey data means that our knowledge of the occurrence of some species in protected areas is poor (e.g., pale fox). In some accounts, this information is arranged according to country, in others it is presented in a more generalised manner. A useful resource for readers, and one that is set to improve over coming years, is the ICE Biological Inventory Database (online at:), which features a searchable interface enabling users to find information on the occurrence of species in protected areas across the globe.

Protection status CITES listing; threat status in national or regional red data books.

Current legal protection Any protection status that is legally enacted or enforced for the express aim of protecting a species, including national legislation; whether hunting and trade are prohibited or regulated; legal protection; and legal status as problem animal.

Conservation measures taken International treaties and conventions; traditional protection due to cultural reasons; establishment of protected areas; action plans; vaccination trials; other specific actions being undertaken or completed.

Occurrence in captivity

Notes on whether the species is kept in captivity, and how successfully they breed in captive conditions. As far as possible, these have been checked with ISIS (International Species Information System based in Minnesota, USA, http://) and the International Zoo Yearbooks (Published by The Zoological Society of London as a service to zoos around the world since 1960). Captive breeding programmes, which have as their aim reintroduction of the species to areas in the wild, are discussed here.

Current or planned research projects

A list of research projects currently being conducted on the species, including brief details of the project, its coordinators and their institutional affiliations. Future projects are also listed.

Gaps in knowledge

Obvious gaps in our knowledge of the species that must receive priority in the next 10 years in order to improve our understanding of the respective species.

Core literature

A list of specific references that represent major works for the species. General references are not given unless they represent the primary source of information. Full citations of all references mentioned in the text are provided in the **References** section.

Reviewer(s)

The names of the reviewers responsible for reviewing and commenting on the species account.

Editor(s)

The names of the editors responsible for editing and ensuring the comprehensive nature of the species' account.

3.4 *Pseudalopex culpaeus* (Molina, 1782)
Least Concern (2004)
Culpeo

J.E. Jiménez and A.J. Novaro

Other names

English: Andean fox; **French:** Culpeau; **German:** Andenfuchs; **Spanish:** zorro colorado (Argentina); zorro Andino (Bolivia, Peru); zorro culpeo (Chile); lobo Andino (Ecuador); **Indigenous names:** Aymara: khamake (Peru, Bolivia, Chile); Mapuche: culpem (Chile, Argentina); Quechua: atoj (Peru).

According to Molina (1782 cited in Osgood 1943: 64) the name culpeo derives from the Mapuche word 'culpem' that means 'madness', because individuals expose themselves to hunters that easily kill them.

Taxonomy

Canis culpaeus Molina, 1782. Sagg. Stor. Nat. Chile, p. 293. Type locality: "Chili" restricted by Cabrera (1931) to the "Santiago Province" (*c.*71°00'W, 33°30'S; Osgood 1943, Novaro 1997a).

Due to their wide range in distribution, high phenetic variability and scarcity of material, the taxonomy of the South American canids has been a topic of much debate. During the last three decades, Clutton-Brock *et al.* (1976) and Wozencraft (1989) placed the culpeo in the genus *Dusicyon*, Langguth (1975) and Van Gelder (1978) in *Canis*, while Berta (1987), Wozencraft (1993) and Tedford *et al.* (1995) considered it as *Pseudalopex*. Finally, Zunino *et al.* (1995) proposed use of the genus *Lycalopex*. As a result, the taxonomic status of the culpeo is still unresolved (Novaro 1997a).

The culpeo separated from their closest relative, the chilla (*P. griseus*) between 250,000 and 500,000 years ago. Morphological evolution of these foxes, relative to other species, has been faster than genetic changes (Wayne *et al.* 1989). In fact, in both species, some populations within species are genetically more distinct than populations between species (Yahnke *et al.* 1996).

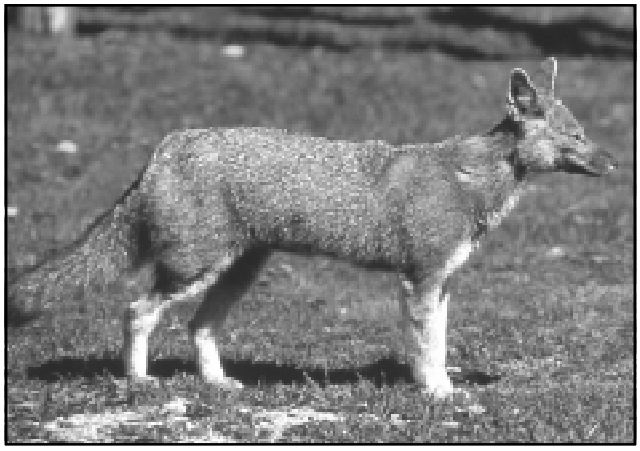
Chromosome number: 2n=74 (Vitullo and Zuleta 1992).

Description

The culpeo is the largest fox in the genus (Novaro 1997a; Table 3.4.1) and among South American canids, is only smaller than the maned wolf (*Chrysocyon brachyurus*). The head is broad and the muzzle is wide, which gives the culpeo a strong appearance. The species is dimorphic, males being larger and on average 1.5 times heavier than females (Johnson and Franklin 1994a; Travaini *et al.* 2000). It has a white to light tawny chin and body underparts. Dorsal parts of the head, including the ears

Table 3.4.1. Body measurements for the culpeo.

	Peru highlands (B.D. Patterson pers. comm.)	**Salar de Punta Negra** (highland desert, northern Chile) (M. Parada pers. comm.)	**Reserva Nacional Las Chinchillas** (matorral, north central Chile) (J.E. Jiménez unpubl.)	**Neuquén** (steppe, north Patagonia, Argentina) (A.J. Novaro unpubl.)	**Parque Nacional Torres del Paine** (steppe, south Patagonia, Chile) (W.E. Johnson pers. comm..)
HB male	700mm (613–752) n=6	715mm (660–790) n=8	586mm (545–635) n=6	879mm (810–925) n=11	729mm (445–840) n=6
HB female	680mm (675–685) n=2	641mm (490–705) n=8	675mm (610–720) n=4	832.3mm (765–890) n=15	756mm (742–770) n=4
T male	354mm (305–408) n=6	380mm (350–415) n=8	381mm (360–415) n=6	452mm (425–493) n=11	433mm (400–465) n=6
T female	360mm (340–380) n=2	362mm (310–400) n=8	355mm (340–370) n=4	414mm (370–450) n=15	397mm (380–410) n=4
HF male	163mm (153–175) n=6	156mm (144–170) n=10	149mm (145–152) n=6	173mm (160–184) n=9	174mm (165–180) n=6
HF female	152mm (149–155) n=2	150mm (137–157) n=8	139mm (130–145) n=4	162mm (145–177) n=13	155mm (148–160) n=4
E male	94mm (90–98) n=6	110mm n=1	84mm (79–88) n=6	89mm (82–95) n=11	91mm (85–96) n=6
E female	88mm (85–90) n=2	90mm n=1	83mm (79–87) n=4	82mm (75–90) n=15	83mm (78–88) n=4
WT male		6.5kg (5.4–8.6) n=10	4.0kg (3.4–4.9) n=3	11.0kg (8.5–12.3) n=11	10.5kg (7.3–13.8) n=6
WT female		5.4kg (4.6–6.8) n=9	4.6kg (3.9–5.1) n=4	8.5kg (7.4–10.0) n=15	7.8kg (6.8–9.0) n=4



Enrique Couve Montané

Culpeo, age and sex unknown. Magallanes, Southern Chile.

and neck, as well as legs and flanks are tawny or rufous. The rump is darker, ranging in colour from tawny to dark grey, according to the subspecies. The tail is long and bushy of grey colour with a black tip and a dark dorsal patch near its base. Feet and legs are bright tawny with no black (Osgood 1943). Specimens from northern ranges (i.e., *P. c. andina*) are lighter in colour (Osgood 1943; J.E. Jiménez pers. obs.). Compared to the chilla, culpeos have longer canines and shorter second molars (Wayne *et al.* 1989). The dental formula is 3/3-1/1-4/4-2/3=42 (Novaro 1997a).

Subspecies Six subspecies are recognised (Cabrera 1931).
— *P. c. andina* (altiplano)
— *P. c. culpaeus* (central Chile and west central Argentina)
— *P. c. lycoides* (island of Tierra del Fuego)
— *P. c. magellanica* (Magallanes and Patagonia)
— *P. c. reissii* (Andes of Ecuador)
— *P. c. smithersi* (mountains of Córdoba, Argentina)

Similar species Chilla (*P. griseus*): sympatric in Chile and northern, western, and southern Argentina; smaller, with dark chin and dark patch on the thighs. Pampas fox (*P. gymnocercus*): closest in size to the culpeo, but apparently not sympatric with it. Crab-eating fox (*Cerdocyon thous*): sympatric in southern Bolivia (L. Maffei pers. comm.); smaller with darker coat.

Current distribution

The culpeo is distributed along the Andes and hilly regions of South America from Nariño Province of Colombia in the north (Jiménez *et al.* 1995) to Tierra del Fuego in the south (Markham 1971; Redford and Eisenberg 1992). It ranges down to the Pacific shoreline in the desert of northern Chile (Mann 1945; J.E. Jiménez pers. obs.), south to about Valdivia (Osgood 1943), and then again in Magallanes. On the eastern slopes of the Andes, the culpeo is found in Argentina from Jujuy Province in the North, reaching the Atlantic shoreline from Río Negro and southwards. This extended eastward distribution is relatively recent and was apparently favoured by sheep ranching (Crespo and De Carlo 1963; Novaro 1997a). See also Relative Abundance.

Range countries Argentina, Bolivia, Chile, Colombia, Ecuador, Peru (Cabrera 1958; Novaro 1997a).

Relative abundance

Due to conflicts with humans (i.e., preying upon poultry and livestock; Crespo and De Carlo 1963; Bellati and von Thüngen 1990) and because of its value as a furbearer, the culpeo has been persecuted throughout its range for many decades (Jiménez 1993; Novaro 1995). Thus, current population numbers may be the result of past and present hunting pressure and food availability. The introduction of exotic prey species such as European hares (*Lepus europaeus*) and rabbits, as well as small-sized livestock into Chile and Argentina *c.* 100 years ago, probably led to increases in the distribution and abundance of culpeos, and facilitated their expansion towards the lowlands in

Figure 3.4.1. Current distribution of the culpio.

eastern Argentina (Crespo and De Carlo 1963; Crespo 1975; Jiménez 1993; Jaksic 1998; Novaro *et al*. 2000a). Currently, culpeos range over a much wider area in Patagonia than previously. Likewise, in several areas of the desert of northern Chile, recent mining activities provide the culpeo with resources such as food, water, and shelter that were in much shorter supply in the past, and hence have changed their local distribution and abundance (J.E. Jiménez pers. obs.).

Culpeos appear to withstand intense hunting levels as shown by fur harvest data from Argentina and still maintain viable regional populations (Novaro 1995). Culpeo populations that are harvested intensively may maintain viable levels through immigration from neighbouring unexploited areas that act as refugia (Novaro 1995). The culpeo population in Neuquén Province in north-west Patagonia for example, appears to function as a source-sink system in areas where cattle and sheep ranches are intermixed (Novaro 1997b). Cattle ranches where no hunting occurs supply disperser foxes that repopulate sheep ranches with intense hunting. Changes in sex ratio may be another mechanism that allows culpeo populations to withstand intense hunting (Novaro 1995). Furthermore, large litter size and early maturity (Crespo and De Carlo 1963) could explain the culpeo's high resilience to hunting.

When hunting pressure is reduced, culpeo populations usually can recover quickly (Crespo and De Carlo 1963). This increase was observed at the Chinchilla National Reserve (Jiménez 1993) and at Fray Jorge National Park (Meserve *et al*. 1987; Salvatori *et al*. 1999), both in north central Chile. Culpeo densities also have increased in many areas of Argentine Patagonia following the reduction of fur prices and hunting pressure in the late 1980s and early 1990s (Novaro 1997b; A.J. Novaro and M.C. Funes unpubl.). An exception to this response is the culpeo population in Tierra del Fuego, where they are still declining in spite of several years of reduced hunting pressure (N. Loekemeyer and A. Iriarte pers. comm.).

Estimates from intensive trapping by Crespo and De Carlo (1963) provided a density of 0.7 individuals/km² for north-west Patagonia, Argentina. Thirty years later, Novaro *et al*. (2000b), using line transects, reported densities of 0.2–1.3 individuals/km² for the same area. In north central Chile, the ecological density of culpeos in ravines is 2.6 individuals/km², whereas the crude density (throughout the study site) is 0.3 individuals/km² (Jiménez 1993). In Torres del Paine, a crude density of 1.3 individuals/km² was reported based on sightings (J. Rau pers. comm.). Interestingly, a later estimate for the same area, based on telemetry, rendered an ecological density of 1.2 individuals/km² (Johnson 1992, in Jiménez 1993).

Based on radio telemetry, sightings and abundance of faeces, Salvatori *et al*. (1999) concluded that culpeos respond numerically to a decline in the availability of their prey in north central Chile. Earlier, based on abundance of faeces, Jaksic *et al*. (1993) reached the same conclusion for the same culpeo population. In contrast, culpeos (not distinguished from sympatric chillas) did not show a numerical or a functional response during a decline of their main prey at another site in north central Chile (Jaksic *et al*. 1992).

Habitat

Throughout its wide distribution, the culpeo uses many habitat types ranging from rugged and mountain terrain up to the tree line, deep valleys and open deserts, scrubby pampas, sclerophyllous matorral, to broad-leaved temperate southern beech forest in the south. The culpeo uses all the range of habitat moisture gradients from the driest desert to the broad-leaved rainforest. In the Andes of Peru, Chile, Bolivia, and Argentina, the culpeo reaches elevations of up to 4,800m (Redford and Eisenberg 1992; Romo 1995; A.J. Novaro *et al*. unpubl.; J.E. Jiménez pers. obs.). Redford and Eisenberg (1992) placed the culpeo in the coldest and driest environments of South America relative to other South American canids.

Food and foraging behaviour

Food Trophic ecology is perhaps the best-studied aspect of culpeo biology (Medel and Jaksic 1988; Jaksic 1997). The culpeo diet, based mainly on faecal analysis, has been described for northern Chile (Marquet *et al*. 1993), north central Chile (Meserve *et al*. 1987; Jaksic *et al*. 1993; Jiménez 1993), central Chile (Yáñez and Jaksic 1978; Jaksic *et al*. 1980; Simonetti 1986; Iriarte *et al*. 1989; Ebensperger *et al*. 1991), northern Argentinean Patagonia (Crespo and De Carlo 1963; Crespo 1975; Novaro *et al*. 2000a), southern Patagonia (Yáñez and Rau 1980; Jaksic *et al*. 1983; Johnson 1992; Johnson and Franklin 1994b), and for the Island of Tierra del Fuego (Jaksic and Yáñez 1983; Jaksic *et al*. 1983). Most of these studies are from areas where only culpeo foxes are present, given that their faeces cannot be easily distinguished from those of the chilla (Jiménez *et al*. 1996a; but see Capurro *et al*. 1997).

Their main prey ranges from wild ungulates in Peru, European hares and domestic sheep in northern Patagonia, hares in southern Patagonia, small mammals and European rabbits (*Oryctolagus cuniculus*) in central Chile and Tierra del Fuego, to small mammals, ungulates, and insects in the highlands of northern Chile. Other vertebrates such as lizards, birds, and insects, make up a small component of this fox's diet. Although it is an opportunistic predator, the culpeo is considered more carnivorous and a consumer of larger mammalian prey than the other South American foxes (Crespo 1975; Langguth 1975; Redford and Eisenberg 1992). When seasonality was examined, almost all studies found differences in diet composition, likely in response to prey availability. In Argentine Patagonia, culpeos prey on hares more than would be expected from

their availability (Novaro *et al*. 2000a) and selected among rodent species for those that may be more vulnerable (Corley *et al*. 1995). Culpeos in central Chile select the largest small mammals available (Meserve *et al*. 1987; Iriarte *et al*. 1989; Jaksic *et al*. 1993).

Although the bulk of the diet is made up of animal prey, it is often described as a consumer of fruits and berries and is, therefore, considered a disperser of a variety of seed species (Yáñez and Jaksic 1978; Jaksic *et al*. 1980; Bustamante *et al*. 1992; Castro *et al*. 1994; Leon-Lobos and Kalin-Arroyo 1994). Highest fruit consumption occurs when small mammals are the least abundant and vice versa (Castro *et al*. 1994).

Foraging behaviour Culpeos appear to be solitary foragers (W. Johnson pers. comm.). Culpeo foraging may be influenced by the nocturnal activity of its main prey (Iriarte *et al*. 1989; Johnson and Franklin 1994a) but also by persecution. In Argentina, highland Peru, (where it is intensively persecuted), the Chilean desert and Magallanes, the culpeo has an almost completely nocturnal activity pattern (Crespo and De Carlo 1963; Crespo 1975; Johnson 1992; Novaro 1997b; M. Parada unpubl.). This contrasts with the diurnal activity patterns in north central Chile (Jiménez 1993; Salvatori *et al*. 1999), where it is protected. The reason for the nocturnal activity in Magallanes is perhaps because they are hunted in the surrounding areas. Culpeos have been recorded moving linear distances of about 7km in Fray Jorge National Park (Salvatori *et al*. 1999) and north-west Patagonia (A.J. Novaro *et al*. unpubl.), but movements three times as large have been documented for desert-dwelling foxes in northern Chile (M. Parada pers. comm.). This high variability is likely associated with the spatial distribution and abundance of its food and water sources.

Damage to livestock and game Bellati and von Thüngen (1990) indicate that foxes, mainly culpeos, are involved in predation of lambs during parturition and account for 60% of the attacks by predators in Patagonia. Lamb mortality by foxes ranges from 5–40%, but it may be mainly compensatory (Bellati and von Thüngen 1990). Up to 83% of the biomass of the culpeo diet in some areas is from exotic mammals, mainly from European hares and sheep, but most of the sheep could be taken as carrion (Crespo and De Carlo 1963; Miller and Rottmann 1976; Novaro *et al*. 2000a). Offending individuals attack the throat, the neck, or the scapular area on the back of their victims. A collared juvenile culpeo (weighing 3.6kg) attacked and killed a 24kg goat by biting and hanging from the throat (J.E. Jiménez pers. obs.).

Adaptations

The culpeo has the smallest molars of all South American foxes, which reflects its highly carnivorous diet (Kraglievich 1930). Its relatively longer canines also indicate carnivory (Wayne *et al*. 1989).

Culpeo fur quality changes between seasons (Osgood 1943), becoming longer and denser during the winter (Crespo and De Carlo 1963). The increase in body size towards the south (Jiménez *et al*. 1995) and to higher elevations (Miller and Rottmann 1976; J.E. Jiménez unpubl.) may be the result of a bio-energetic adaptation to lower temperatures and harsher conditions.

Social behaviour

Culpeos seem to be solitary foxes. Spatial studies throughout their range indicate that they have inter- and intra-sexually non-overlapping home ranges (Johnson 1992; Jiménez 1993; Salvatori *et al*. 1999; M. Parada pers. comm.). Small areas of spatial overlap occur at sites of human refuse, but foxes still segregate temporally (Salvatori *et al*. 1999). Females are apparently more spatially intolerant than males in the wild (Salvatori *et al*. 1999) as well as in captivity.

In north central Chile, home ranges of females averaged 8.9km^2 and were 2.5 times larger than those of males (Salvatori *et al*. 1999). In contrast, culpeo home ranges in Torres del Paine were only 4.5km^2 in size and similar for males and females (Johnson and Franklin 1994a). Desert-dwelling culpeos show high variability in home range size, ranging from 10km^2 for culpeos living in ravines to 800km^2 for foxes associated with highland salt flats and lakes (M. Parada unpubl.).

Reproduction and denning behaviour

In the Patagonian steppe of Argentina, male culpeos produce sperm between June and mid-October (early winter to early spring). Females are monoestrous and mating occurs from the beginning of August through October (Crespo and De Carlo 1963). Gestation is 58 days. Based on embryo counts, Crespo and De Carlo (1963) estimated a mean litter size of 5.2 (range=3–8). At birth pups weight *c.*170g and reach up to 13kg when adults. Juveniles reach adult size within seven months and can reproduce during the first year. Although the sex ratio of 253 individuals was skewed in favour of males in the Neuquén population (Crespo and De Carlo 1963), some 30 years later the sex ratio approached parity, as expected for intensively hunted populations (Novaro 1995).

Competition

For evidence of potential competition between culpeo and chilla, please refer to the corresponding section of the latter species account.

In the steppe of Argentina, Crespo (1975) proposed that an increase in food availability through the introduction of sheep and hares may have relaxed potential competition between culpeos and other carnivores such as

chilla, little grisons (*Galictis cuja*), mountain cats (*Oncifelis colocolo*), and Geoffroy's cats (*O. geoffroyi*). A study in the same region indicates that culpeos, chillas, Geoffroy's cats, and pumas (*Puma concolor*), all select European hares as one of their main prey items. Hares undergo periods of low abundance, when competition may be intense and consumption of native prey may increase (Novaro *et al*. 2000a).

Ebensperger *et al*. (1991) found that in central Chile, despite an eight-fold body mass difference, culpeos prey on similar prey and in similar proportions to little grisons, suggesting potential competition for food. In contrast, a study of a carnivore community in highland Peru shows that sympatric predators such as culpeos, pumas, and mountain cats feed on similar prey items, but in very different proportions, rendering different mean prey sizes (Romo 1995).

Mortality and pathogens

Natural sources of mortality Crespo and De Carlo (1963) state that with the exception of pumas, the culpeo lacks natural enemies.

Persecution One of the prime causes of mortality in the species has been persecution by farmers through hunting and trapping because of their reputation for preying on lambs; they are also controlled by using strychnine (Bellati and von Thüngen 1990; Novaro 1995). See Relative Abundance.

Hunting and trapping for fur Until the early 1990s the main cause of mortality was hunting and trapping for fur (Miller and Rottmann 1976; Novaro 1995). During 1986, in excess of 2,100 fox skins (culpeo and chilla) were exported from Chile (Iriarte *et al*. 1997). An average of 4,600 culpeo pelts were exported annually from Argentina between 1976 and 1982, with a peak of 8,524 in 1977. Legal exports declined to an average of approximately 1,000 between 1983 and 1996 with peaks of 2,421 in 1990 and 4,745 in 1996 and have been negligible since 1997 (Novaro 1995; Dirección de Fauna y Flora Silvestres and M. Elisetch pers. comm.). See Relative Abundance.

Road kills Road kills occur frequently in Neuquén, Argentina (A.J. Novaro pers. obs.).

Pathogens and parasites In central Chile, one culpeo tested for *Trypanosoma cruzi*, the protozoan of Chagas disease, gave negative results (Jiménez and Lorca 1990).

Stein *et al*. (1994) found a low prevalence of the nematodes *Physolaptera clausa*, *Toxascaris leonina*, and *Protospirula numidica* in the 129 culpeos examined from Argentine Patagonia. In addition, in culpeos from the same general area, the cestode *Echinoccocus patagonicus* and the tick *Toxocara canis* were reported (Crespo and De Carlo 1963). In Peru, culpeos had *Taenia hydiatigena* and *T. multiceps* (Moro *et al*. 1998). In Chile, a *Taenia* sp. was also found in the intestine (Medel and Jaksic 1988) and adults of *Linguatula serrata* were detected in the trachea of culpeos (Alvarez 1960 in Medel and Jaksic 1988).

Longevity The oldest wild-caught individual based on cementum annuli was 11 years old (Novaro 1997b).

Historical perspective

Remains of the prey of culpeo (in the form of faeces and large bones) complicate studies by archaeologists at rock shelters that were co-used by humans in the past (Mondini 2000).

Conservation status

Threats Main threats to culpeos have been hunting for fur and persecution to reduce predation on livestock and poultry. Habitat loss does not appear to be an important threat to this species. Predation by feral and domestic dogs may be important in some areas (Novaro 1997b).

Commercial use This has usually taken the form of hunting and trapping for fur, although trade has decreased in the last decade. See Hunting and trapping for fur; see also Relative Abundance.

Occurrence in protected areas

— In Chile, the culpeo occurs in 38 protected areas distributed throughout the country, encompassing all the habitats where it can be found. However, only 14% are large enough to support viable populations.
— In Argentina, the species occurs in 12 national parks and several provincial reserves, the majority of which probably support viable populations.
— In Peru, culpeos occur in 13 protected areas (D. Cossios pers. comm.).

Protection status CITES – Appendix II

Current legal protection In Chile, the species is considered as "Insufficiently Known" and the subspecies *P. c. lycoides* is considered as "Endangered" by Glade (1993). According to Cofré and Marquet (1999), the culpeo is not in need of immediate conservation action. Hunting has been banned since 1980, although law enforcement is not strict.

The Argentine legislation about culpeos is contradictory. Culpeos were considered "Endangered" by a 1983 decree of the Argentine Wildlife Board (Dirección de Fauna y Flora Silvestres), due to the numbers of culpeo pelts traded during the 1970s and early 1980s. Trade at the national level and export of culpeo pelts, however, was legal during that entire period and currently remains legal. The culpeo's endangered status has never been revised in

spite of marked changes in the fur trade and reports from monitoring programmes (see Relative Abundance). The Tierra del Fuego population has been legally protected since 1985 (N. Loekemeyer pers. comm.).

In Peru, the culpeo is not considered endangered and culpeo hunting may be legal if a management plan is approved by the government (D. Cossios pers. comm.). In Bolivia, although the fur export was banned in 1986, the species is not protected (Tarifa 1996; L. Pacheco pers. comm.).

Conservation measures taken The Argentine Wildlife Board is starting to develop a management plan for canids that will include the culpeo (V. Lichschein and M. Eliseth pers. comm.). Five regional workshops that included wildlife agency officials from provincial governments, wildlife traders, conservationists, and scientists have been held in Argentine Patagonia during recent years (the last one in 2002) to coordinate efforts to manage culpeo populations in a sustainable manner and reduce sheep predation. Similarly, in Chile, two national carnivore workshops have been organised by the Livestock and Agricultural Bureau during recent years. These were aimed at presenting new findings on the natural history of canids, including culpeos, and wildlife-livestock issues and to discuss ways of improving our knowledge and better protecting Chilean carnivore populations.

Occurrence in captivity

The culpeo is common in zoos throughout Chile and Argentina.

Current or planned research projects

In Chile, the culpeo is one of three species being studied in Nahuelbuta National Park as part of a doctoral dissertation by E. McMahon (University of Massachusetts).

Ongoing research at Salar de Punta Negra in the highland desert of northern Chile (conducted by Minera Escondida and Chile's Forest Service) has been focusing on culpeo ecology and its impact on flamingo reproduction. The monitoring programme, which has been running since 1986, includes examining the diet and a study of movement patterns using satellite and standard telemetry.

There are two other long-term monitoring projects in north central Chile at Fray Jorge and at Aucó, led, respectively, by P. Meserve (Northern Illinois University) and F. Jaksic (Universidad Católica de Chile). In addition, researchers from Universidad Austral de Chile are studying the ecology of culpeos on Tierra del Fuego (M. Briones pers. comm.).

Biologists from Córdoba University in central Argentina are conducting a study of the diet and prey availability of the little-known *P. c. smithersi* population of Pampa de Achala (M. Pía and S. López pers. comm.).

In Neuquén Province, A.J. Novaro (Centro de Ecología Aplicada del Neuquén), is in charge of an ongoing project investigating the role of culpeos in regulating European hare populations.

Throughout Argentine Patagonia, researchers from several agencies have been evaluating population trends of culpeos and other carnivores using standardised scent-stations and other methods since 1989 (A.J. Novaro and M.C. Funes of Centro de Ecología Aplicada del Neuquén, C. Chehebar of Parques Nacionales, A. Travaini of Universidad Austral, and N. Loeckemeyer of Dirección de Recursos Naturales of Tierra del Fuego).

Gaps in knowledge

1. It appears that conservation measures (e.g., hunting and trapping regulations) to protect culpeos are not effective to prevent poaching. There is a need for science-based information to aid management decisions and formulation of conservation regulations.
2. Studies on and long-term monitoring of population dynamics are needed to manage culpeos as a furbearer species. Given the wide distributional range of the species, research that encompasses the entire range of variability of the species is required. This is also true with regards to the genetic makeup of the species, especially as concerns the status of the currently recognised subspecies.
3. It is essential to develop means of making sheep-ranching activities compatible with sympatric wildlife including culpeos. Research aimed at better understanding culpeo behaviour as a sheep predator combined with sheep husbandry could help in decreasing the impact of predation. Bounty systems to kill culpeos are still in place in some Argentine provinces to reduce predation on sheep. This control system has proven to be widely ineffective with other carnivores. Research is needed to determine whether sheep predation is carried out only by certain individuals as is the case with coyotes (*Canis latrans*), in which case selective removal may be a more effective system of control (J. Bellati pers. comm.).
4. A study is urgently needed to determine the causes of decline of the Tierra del Fuego population and measures to reverse it.

Core literature

Crespo and De Carlo 1963; Jiménez 1993; Jiménez *et al.* 1996b; Johnson 1992; Johnson and Franklin 1994a,b; Medel and Jaksic 1988; Novaro 1997a,b; Novaro *et al.* 2000a; Salvatori *et al.* 1999.

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