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 an 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based primarily on published information (i.e., from books and journals), supplemented as far as possible with reliable unpublished material and personal observations from the author's own studies or other sources.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has been strongly recommended, and authors were also encouraged to correspond with other colleagues likely to have unpublished material or to be able to contribute unpublished data.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's 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 Regional Sections.

Biogeographical Region	CSG Regional Section
Neotropical (up to south Mexico)	South America/North and Central America
Nearctic	North and Central America
Palearctic Ethiopian	Europe/North and Central Asia Sub-Saharan Africa
Ethiopian	North Africa and Middle East
Oriental (south of the Himalaya)	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 allow, species accounts use the following format.

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

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.

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.

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, 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 subspecies 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 (http://www.ice.ucdavis/bioinventory/bioinventory.html), 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://www.isis.org) 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.

South America (Neotropical)

3.1 Short-eared dog
Atelocynus microtis (Sclater, 1883)
Data Deficient (2004)

M.R.P. Leite Pitman and R.S.R. Williams

Other names
English: short-eared fox, small-eared dog, small-eared zorro; **French:** renard à petites oreilles; **German:** kurzohriger hund; **Portuguese:** cachorro-do-mato-de-orelhas-curtas; **Spanish:** perro de monte; perro de orejas cortas, zorro negro, zorro ojizarco; **Indigenous names:** Ayoreo: divequena; Chiquitano: nomensarixi; Guarayo: cuachi yaguar; More: quinamco; Ninim, Moseten: achuj jhirith; Siriono: ecoijok; Tsimane: achuj foij (Bolivia); Kaiabi: awara (Brazil); Yucuna: uálaca; Huitoto: urúbui; Yebá masá o Barasana: búyaíro; Bora: wipe; Okaima: juhxuutsoonna; Carijona: karejuqué (Colombia); Achuar: kuap yawa; Cofán: tsampi'su ain; Huaorani: babei guinta; Quechua: sacha alcu, jujunda, puma; Iona-Secoya: wë yai (Ecuador); Guarani: aguerau (Paraguay); Amarakaeri: huiwa toto; Matsiguenga: machit; Quechua: monte alcu; Shipibo: caman ino; Cashinaua: kama, kama inu; Amahuaca: kama, shindokama; Sharanahua: padoshoinca (Peru).

Taxonomy
Canis microtis Sclater, 1883. Proc. Zool. Soc. Lond., 1882:631 [1983]. Type locality: "Amazons", restricted by Hershkovitz (1961) to "south bank of the Rio Amazonas, Pará, Brazil."

Atelocynus is a monotypic genus. The species *A. microtis* has been placed in the genus *Lycalopex* (Studer 1905), *Cerdocyon* (Pocock 1914), *Dusicyon* (Osgood 1934; Clutton-Brock *et al.* 1976), and *Atelocynus* (Cabrera 1931; Languth 1975; Stains 1975). Van Gelder (1978) considered *Atelocynus* a subgenus of *Canis*. Berta's (1987) phylogenetic analysis showed *Atelocynus microtis* to be a distinct taxon most closely related to another monotypic Amazonian canid genus, *Speothos*, and this hypothesis is now widely accepted (Wozencraft 1993; Nowak 1999).

Chromosome number: 2n=76 (Wurster and Benirschke 1968). The only individual studied was a female and the karyotype included 36 pairs of acro- or subacrocentric autosomes and one pair of large submetracentric chromosomes, probably X-chromosomes.

Description
The short-eared dog is a medium-sized canid, averaging about 10kg as an adult (Table 3.1.1). According to Hershkovitz (1961), a captive adult female was a third larger than a captive adult male. The animal's head is fox-like, with a long, slender muzzle and rounded, relatively short ears. The pelt colour can range from black to brown to rufous grey. Pelage is often darkest in a dorsal line from the head to the tail. However, various colour patterns are observed in different individuals, and it is not clear whether colour varies with age, habitat, or moult; in
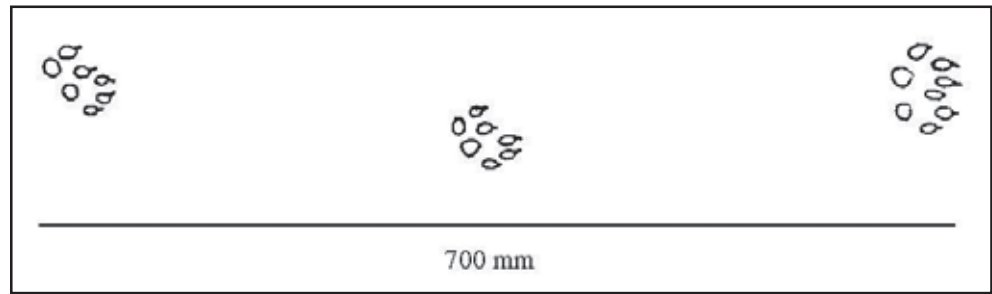

Adult male short-eared dog, taken by automatic camera. Alto Purus, Peruvian Amazon, 2002.

M.R.P. Leite Pitman and M. Swarner
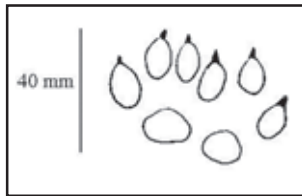
Figure 3.1.1. Footprint of adult short-eared dog recorded in Cocha Cashu, Peru (Leite 2000).

Figure 3.1.2. Tracks of adult short-eared dog in Cocha Cashu, Peru (Leite 2000).

Cocha Cashu Biological Station, Madre de Dios, Peru, both reddish and black individuals have been observed (Leite 2000). A complete moult lasting three weeks was observed in July 1960, when a captive animal was transported from Colombia to a zoo in the United States. During the moult, large flakes of orange-brown oily exudates appeared with the falling hairs. A subsequent moult was observed in March (Hershkovitz 1961; A. Gardner pers. comm.). The tail is bushy, particularly in comparison to the short pelage on the rest of the body, with a dark mid-dorsal band of thick erectile hairs and light-coloured underside.

The nasals are short; the forehead slightly convex; the frontal sinus small; the presphenoid very narrow with lateral wings and large bulla. The dental formula is 3/3-1/1-4/4-2/3=42. The lower third incisor is short and not caniniform. The upper canines are distinctively long, their tips projecting outside the closed mouth for about 50mm. The upper molars are narrow for their length (Hershkovitz 1961; Berta 1986).

Table 3.1.1. Combined body measurements for the short-eared dog from across the species' range (Nowak 1999).

|	
HB	720–1,000mm
T	250–350mm
E	34–52mm
SH	356mm
WT	9–10kg

Subspecies Monotypic (Berta 1986).

Similar species Only one other species of wild dog is known to inhabit lowland Amazonian forest, namely the bush dog (*Speothos venaticus*). Confusing the two species is unlikely due to unambiguous physical and behavioural differences. Bush dogs are smaller, light-coloured, with a very short muzzle, legs, and tail; they live in packs and are seldom seen alone. Tracks may be distinguished by the bush dog's conspicuous interdigital membrane, with the middle toes fused, whereas the short-eared dog's interdigital membrane is only partial (Figures 3.1.1, 3.1.2, 3.1.3). The bush dog's stride is also shorter, and its tracks and pads larger than those of the short-eared dog.

Two additional species of wild canids whose ranges border Amazonia, the crab-eating fox (*Cerdocyon thous*) and the culpeo (*Pseudalopex culpaeus*), as well as domestic dogs, could potentially be mistaken for the short-eared dog, but none of these have the combination of a slender, long snout, short ears, and a bushy tail. Tayras (*Eira barbara*) are also brownish and have bushy tails, but differ in their much smaller ears, yellowish throat and mostly arboreal habits. The jaguarundi (*Herpailurus yaguarondi*), which is sometimes similar in colour, is smaller, more delicate, and has a very slender tail (Emmons and Feer 1990).

Figure 3.1.3. Comparison of bush dog and short-eared dog feet, based on dried skins (Pocock 1914).
A and B – Right fore foot and hind foot of bush-dog.
C and D – Right hind foot and fore foot of short-eared dog.
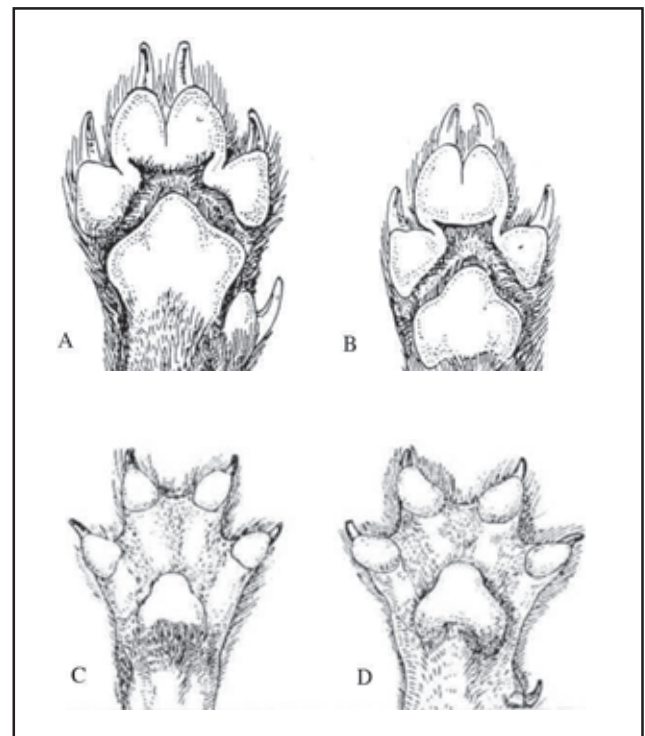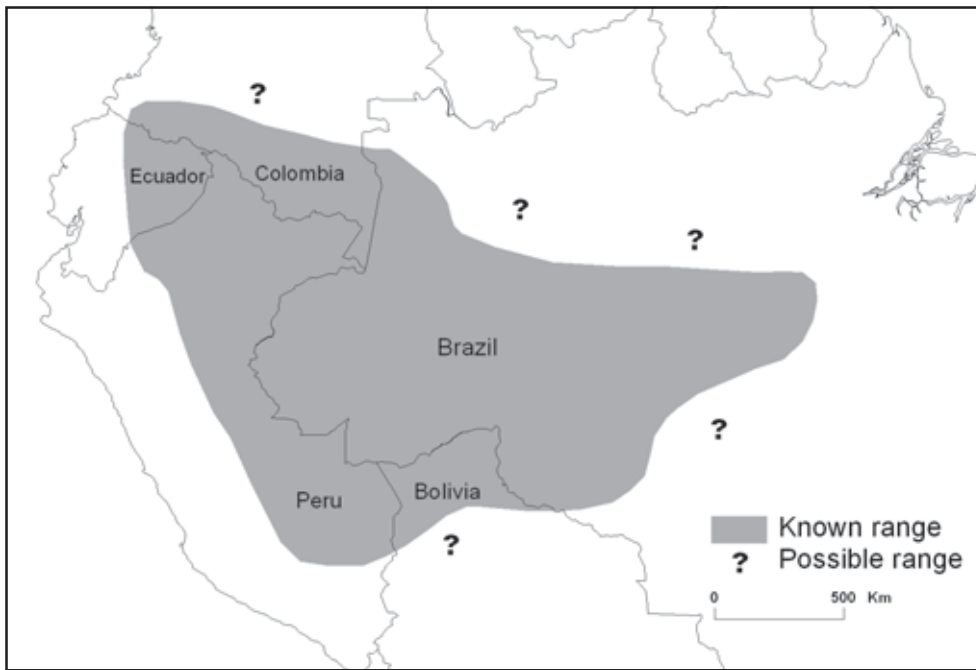
Figure 3.1.4. Current distribution of the short-eared dog.

Current distribution

The short-eared dog has been found in scattered sites from Colombia to Bolivia and Ecuador to Brazil (Figure 3.1.4). Its presence in Venezuela was suggested by Hershkovitz (1961) but never confirmed. Various distributional hypotheses for the species have been published, suggesting the presence of the species throughout the entire Amazonian lowland forest region, as well as Andean forests in Ecuador and savannah regions (Emmons and Feer 1990, 1997; Tirira 1999).

For this study, we rechecked museum specimens and carried out an extensive survey of field biologists doing long-term research in the species' putative range, constructing a new distributional map based only on specimens of proven origin and incontrovertible field sightings. Our results suggest a much smaller distribution range, limited to western lowland Amazonia. The northernmost record is in Mitú, Colombia, at 1°15'57"N, 70°13'19"W (Hershkovitz 1961), the southernmost on the west bank of the river Heath, Pampas del Heath, northwest Bolivia, at 12°57'S, 68°53'W (M. Romo pers. comm.). The easternmost record is from the vicinity of Itaituba, Brazil, at 4°20'S, 56°41'W (M. De Vivo pers. comm.), and the westernmost in the Rio Santiago, Peru, at 4°37'S, 77°55'W (Museum of Vertebrate Biology, University of California, Berkeley, collected 1979). Unfortunately, there is no information on the continuity of the species' distribution within its extent of occurrence; the absence of records from large areas suggests that its distribution may not be continuous throughout its range.

Range countries Bolivia, Brazil, Colombia, Ecuador, Peru (M.R.P. Leite unpubl.).

Relative abundance

The short-eared dog is notoriously rare, and sightings are uncommon across its range. However, this may not always have been the case. The first biologists to study the species found it relatively easy to trap during mammal surveys around Balta, Amazonian Peru, in 1969 (A.L. Gardner and J.L. Patton pers. comm.). Grimwood (1969) reported collecting specimens around the same time in Peru's Manu basin (now Manu National Park), suggesting that the species was also relatively common in that area.

Following these reports, the species went practically unrecorded in the Peruvian Amazon until 1987, despite intensive, long-term field surveys of mammals in the intervening years (Terborgh *et al.* 1984; Jason and Emmons 1990; Woodman *et al.* 1991; Pacheco *et al.* 1993, 1995). Even Louise Emmons, who carried out long-term projects monitoring and trapping ocelots (*Leopardus pardalis*) and other mammals at the Cocha Cashu Biological Station in Manu, never saw or trapped the short-eared dog (L. Emmons pers. comm.). For whatever reason, the species appears to have temporarily vanished from the region between 1970 and 1987.

Over the last decade, it appears that the species may be recovering in southern Peru and eastern Ecuador, with increasing numbers of sightings in recent years at both sites. Between 1987 and 1999, biologists working in the Peruvian department of Madre de Dios, mostly in the vicinity of Cocha Cashu Biological Station, have reported 15 encounters with the short-eared dog (M.R.P. Leite *et al.* unpubl.).

Estimated populations/relative abundance and population trends In an ongoing field study initiated at

Cocha Cashu in 2000, Leite and colleagues have sighted and followed five individuals in an area of 10km², giving an estimated density of 0.5 individuals/km². However, far too little is known about the species to extrapolate this estimate (itself preliminary) to the rest of the species' range. For the time being, the short-eared dog must be considered extremely rare throughout its range and certainly one of the rarest carnivores wherever it occurs.

Habitat

The short-eared dog favours undisturbed rainforest in the Amazonian lowlands. The species has been recorded in a wide variety of lowland habitats, including terra firme forest, swamp forest, stands of bamboo, and primary succession along rivers (M.R.P. Leite unpubl.). At Cocha Cashu, sightings and tracks of the species are strongly associated with rivers and creeks, and there are five reliable reports of short-eared dogs swimming in rivers. Records are very rare in areas with significant human disturbance, i.e., near towns or in agricultural areas. It is unclear whether the short-eared dog is able to utilise habitats outside wet lowland forests. One sighting in Rondonia, Brazil, was in lowland forest bordering savannah (M. Messias pers. comm.). Another, at the highest elevation yet documented for the species, was at 1,200m a.s.l. in the Ecuadorean Andes, in a transitional zone between lowland forest and cloud forest (Pitman 2002). Two specimens collected in 1930 are allegedly from even higher elevations in the same region – above 2,000m on Volcan Pichincha and Antisana (near Quito) – but the absence of any other reports from these well-studied areas leads us to believe that these represent mislabelled specimens.

Food and foraging behaviour

Food An ongoing study of the short-eared dog's diet, based on scat samples collected at Cocha Cashu since 2000 (M.R.P. Leite unpubl.), shows the species to be a generalist carnivore (Figure 3.1.5). Fish appear to be the most

Figure 3.1.5. Frequency of occurrence of various prey items in 21 scat samples from Cocha Cashu, Peru (Leite 2000).
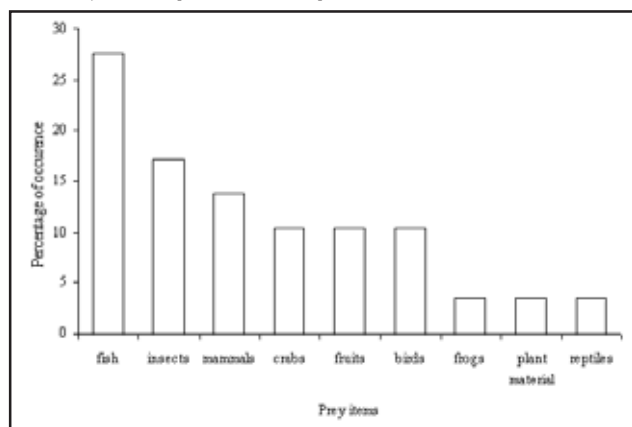
important item in their diet (present in 28% of samples; n=21). Defler and Santacruz (1994) had previously suggested that fish form part of the short-eared dog's diet, based on the discovery of a cestode (*Diphyllobothrium latum*) in a museum specimen's intestine (the parasite requires a fish as its intermediate host). Insects (mainly Coleoptera) were the second most important item in their diet (17% of samples), while mammal remains (agoutis, marsupials and small rodents) were present in 13% of the scats collected in Cocha Cashu. This corroborates earlier anecdotal evidence that small rodents, agoutis (*Dasyprocta* spp.), pacas (*Agouti paca*), and acouchis (*Myoprocta* spp.) are important components of the diet (Peres 1992; Defler and Santacruz 1994).

The remains of fruits, including *Borismenia japurensis*, *Strychnos asperula*, *Unonopsis floribunda*, *Pouteria procera*, *Sciadotenia toxifera*, *Socratea exorrhiza*, *Astrocaryum murumuru*, *Euterpe precatoria*, *Trattinnickia* sp., and various Cucurbitaceae and Moraceae were found in 10% of samples. Fruits of the palm *Euterpe precatoria* were found germinating in two scats. Defler and Santacruz (1994) report short-eared dogs eating fallen *Brosimum* fruits and the Cofan Indians of Ecuador report them being attracted to fallen bananas (R. Borman pers. comm.).

Close to 4% of droppings contained the remains of frogs, including *Osteocephalus taurinus* (see below). Parker and Bailey (1990) reported seeing a short-eared dog with a frog in its mouth in Madidi National Park in Bolivia. Crabs (10.3% of samples), birds (10.3%), reptiles (3.4%) and vegetable fibre (3.4%) were other components of the diet at Cocha Cashu.

Foraging behaviour The short-eared dog has been reported hunting alone and in pairs (Peres 1992; M.R.P. Leite unpubl.). Y. Campos (pers. comm.) described two adults hunting either a fish or a frog in a water hole in Ecuador; Peres (1992) observed an individual hunting a rodent (*Proechmys* sp.). M.R.P. Leite (unpubl.) observed an adult chasing a squirrel on the ground, and found a small waterhole where another adult had apparently killed, but not eaten, dozens of frogs (*Osteocephalus taurinus*).

Both diurnal and nocturnal activity patterns have been observed. Field reports (n=30) appear to indicate a diurnal or at least partly diurnal animal, with 95% of the observations made in daylight hours. However, the species has also been photographed at night walking on trails of Madidi National Park, Bolivia (R. Wallace pers. comm.), and one animal was captured swimming after a paca, in a river at 03:00 in Colombia (Defler and Santacruz 1994).

Damage to livestock or game A. Salas (pers. comm.) has documented a wild short-eared dog eating chickens near Tambopata National Reserve, Peru, and P. Santos *et al.* (unpubl.) reported two captive individuals in Brazil also killing poultry.

Adaptations

There is evidence, including the partial interdigital membrane, sleek, thick coat, and sightings on rivers, to suggest that the short-eared dog may be at least partly aquatic (Berta 1986). The short limbs (though not so short as those of the bush dog) likely facilitate movement in dense forests (Hershkovitz 1961).

Social behaviour

The short-eared dog is mainly solitary, although observations have been made of two adult animals walking together in October in Peru and between January and March in Ecuador (M.R.P. Leite unpubl.; Y. Campos pers. comm.). Since 2000, three individuals of adult size have been observed to use a 1.6km stretch of white sandy beach near Cocha Cashu, where two latrines are used infrequently by both short-eared dogs and river otters (*Lontra longicaudis*).

According to Hershkovitz (1961) and A.L. Gardner (pers. comm.), most observations of wild and captive individuals indicate that the species is very docile around humans, with the exceptions of a captive male in the Schönbrunner Zoo and a female in the Brookfield Zoo, which growled, snarled and attempted to bite when frightened. In addition, when a Brazilian hunting party with six domestic dogs found a pair of short-eared dogs with two puppies, "the mother protected the babies fiercely, having attacked one of the domestic dogs." Another female and two puppies were sufficiently docile to allow them to be carried in a basket with no attempt being made to bite the hunters (P. Santos *et al.* unpubl.). Hershkovitz (1961) and A.L. Gardner (pers. comm.) reported a strong musky odour in males for both wild and captive animals, this being hardly noticeable in females.

Reproduction and denning behaviour

Based on the fresh carcass of a three- or four-month-old juvenile found in September 2000 at Cocha Cashu Biological Station, short-eared dogs give birth in May or June in Peru. Breeding time is not known precisely, but pups have been found throughout the range in April to May, June, September, and November to December, suggesting that parturition occurs in the dry season.

Three dens have been found inside hollow logs, one of them containing two adults and two pups, another, the female and two pups (Defler and Santacruz 1994; P. Santos *et al.* unpubl.). Another den, containing three pups, was found in a paca burrow (M.R.P. Leite unpubl.). At Cocha Cashu Biological Station, the short-eared dog was found also to use several paca burrows along the steep banks of a creek.

Competition

Considering the short-eared dog's generalist diet, it is likely that all medium-sized sympatric carnivores, frugivorous monkeys, rodents, and ungulates, are competitors to some extent. Paca dens seem to be used often by short-eared dogs.

Mortality and pathogens

Natural sources of mortality Very little is known. Ocelot tracks found around the corpse of a dead juvenile in Cocha Cashu suggest it is a possible predator. Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are also potential predators.

Persecution There are only a few reports of the short-eared dog being hunted by man. In one case, the species was reportedly killed and eaten by the Yora indigenous people of Peru (Museum of Vertebrate Zoology, Berkeley, California MVZ No.: 181288 Accn No.: 12921). In another, A. Salas (pers. comm.) reported that villagers injured a male short-eared dog (which subsequently died) as it was killing chickens in the Tambopata river region, Peru. A recently captured and radio-collared animal was shot and killed by a hunter in the Alto Purus region of south-eastern Peru. The hunter claimed it was mistakenly shot.

Hunting and trapping for fur There are no known reports of the species being hunted or trapped for its fur.

Road kills The species avoids developed areas, and there are no known cases of road kills, so the impact of vehicles on population numbers is probably minimal.

Pathogens and parasites To date, no diseases have been reported in wild short-eared dogs. Common viral diseases such as canine distemper virus and canine parvovirus are widespread among domestic dogs in South America, even in the most pristine areas of the Amazon (Leite Pitman *et al.* 2003). Domestic dogs are kept throughout the region as pets or hunting companions and occur in a feral state around villages. Since potentially all wild canid species are susceptible to distemper, it is feasible that epidemics could occur, decimating or even locally eliminating populations of wild canids. P. Santos *et al.* (unpubl.) report the death of a captive, one year-old short-eared dog by canine distemper virus, and the possible death of another captive individual by the same means. These and other infectious diseases may represent a serious threat to wild populations of Neotropical canids. For example, one hypothesis to explain why this species largely disappeared from the Peruvian Amazon during the 1970s and 1980s (see Relative abundance) is that epidemics started by domestic dogs decimated the population over large areas. Clearly, the current and potential impacts of these diseases require further study.

The cestode, *Diphyllobothrium latum,* was found as an intestinal parasite of the short-eared dog (Defler and

Santacruz 1994). This tapeworm can cause pernicious anaemia and occasionally death in domestic dogs, as it competes with the host for vitamin B12.

Longevity Most captive animals survive for less than a year, with the exception of two animals that lived for nine years (Anon. 2000) and eleven years (Jones 1982). There is no data on longevity in the wild.

Historical perspective
The short-eared dog generally is poorly known by indigenous peoples of the Amazon basin and is not known to hold any special significance for them. Several Huaorani in Ecuador stated that it was one of the animals they did not hunt, but they could not offer a clear reason. The Amarakaeri indigenous people of Peru call the short-eared dog "huiwa toto", meaning solitary devil, and believe that it will attack men by biting their testicles (M. Swarner pers. comm.).

Conservation status
Threats Diseases from domestic dogs (see above) and habitat loss. There are no reports of widespread persecution of the species. An ongoing distribution survey (M.R.P. Leite unpubl.) suggests that the short-eared dog is rare throughout its range and threatened by the large-scale forest conversion underway in Amazonia.

Commercial use Reports of commercial use are scattered and few. In some cases, wild individuals have been captured for pets and occasionally for sale to local people and zoos.

Occurrence in protected areas The short-eared dog is likely to occur in most protected areas that encompass large tracts of undisturbed forest in western Amazonia. During the last decade, its presence has been confirmed in the following protected areas:
— *Bolivia*: Madidi National Park, Tahuamanu Ecological Reserve and Estación Biologica Beni;
— *Brazil*: Guajara Mirim State Park, Cristalino Reserve. The species has never been reported from Xingu National Park, Amanã Reserve, Mamirauá Reserve, Jaú National Park and Serra do Divisor National Park, but sightings close to these areas suggest the species is present at very low densities (M.R.P. Leite unpubl.);
— *Ecuador*: Yasuní National Park, Reserva Ecologica Cofanes de Bermejo and the Cuyabeno Wildlife Reserve;
— *Peru*: Manu National Park, Tambopata National Reserve, Alto Purus Reserved Zone, and Manu Wildlife Research Center.

Protection status CITES – not listed.
The species is on the Brazilian list of endangered species (see: www.ibama.gov.br/fauna/extincao.htm) and on the preliminary list of Colombian endangered species (Rodriguez 1998).

Current legal protection Protected by law in Brazil. Recently removed from the list of protected species in Peru.

Conservation measures taken Although protected on paper in some Amazonian countries, this has not yet been backed up by specific conservation action.

Occurrence in captivity
No short-eared dogs are known to be currently held in captivity, and only a dozen confirmed records of captive animals exist. The first recorded captive short-eared dog (eventually the holotype) was kept at the Zoological Society of London late in the 19th century (Sclater 1883). At around the same time, two males were kept at the Zoological Gardens of Para, Brazil, and in 1933 another one was present in the Schönbrunner Tiergarten, Germany (Hershkovitz 1961). Since then, individuals have been held in several U.S. zoos (including the Lincoln Park Zoo, the National Zoo, the Brookfield Zoo, the Oklahoma City Zoo, and the San Antonio Zoo), mostly during the 1960s and 1970s. Over the last decade, sporadic reports of captive animals have come from Peru (Pucallpa and Puerto Maldonado), Colombia (Medellin), Ecuador (Quito), and Brazil (Canaria and Itaboca in the Amazon).

Current or planned research projects
M.R.P. Leite (Duke University Center for Tropical Conservation, USA) is conducting an ongoing research programme on the ecology and conservation of the short-eared dog at Cocha Cashu Biological Station and the Alto Purus Reserved Zone, in south-eastern Peru. The project is currently seeking funding to establish a domestic dog vaccination programme in the Amazonian protected areas of Peru and to expand field work to other sites within the species' range, including western Brazil, Ecuador, Bolivia, Colombia, and northern Peru.

Gaps in knowledge
The biology, pathology, and ecology of the species are virtually unknown. Especially lacking is any estimate of population density and an understanding of the species' habitat requirements.

Core literature
Berta 1986; Defler and Santacruz 1994; Leite 2000; Peres 1992.

Reviewers: Annalisa Berta, Orin Courtenay, Louise Emmons, Alfred Gardner, James Patton, Pedro Santos, Matthew Swarner, John Terborgh. **Editors:** Claudio Sillero-Zubiri, Michael Hoffmann.

3.2 Crab-eating fox
Cerdocyon thous (Linnaeus, 1766)
Least Concern (2004)

O. Courtenay and L. Maffei

Other names

English: crab-eating zorro, common zorro, common fox, savannah fox, forest fox; **French**: renard crabier, chien des bois (Guyana); **German:** maikong, waldfüchse; **Italian:** volpe sciacallo; **Portuguese:** raposa, raposão, cachorro-do-mato, lobinho, graxaim, graxaim-do-mato, mata virgem, lobete, guancito, fusquinho, rabo fofo (Brazil); **Spanish:** zorro cangrejero, zorro carbonero, zorro de monte (Argentina); zorro de monte, zorro, zorro patas negras (Bolivia); zorro, lobo, zorro-lobo, perro-zorro, zorro-perro, zorro perruno, zorra baya, perro sabanero, perro de monte (Colombia); zorro perro (Uruguay); zorro común, zorro de monte, zorro sabanero (Venezuela); **Indigenous names:** Izoceno-Guarani: aguara (Bolivia). Guarani: aguará chai (Argentina); Guarani: aguara'i (Uruguay); Nações do Parque Indígena do Xingu (Kuikuro, Matipú, Naruótu, and Kalapalo people): sorokokusge; Ualapiti: tsunakatirre; Mehinaku and Uaurá: uáu; Suiá: roptó; Tumai: auaraí; Kamaiurá: uarain; Auetí: tovait; Xavante: waptsã'uwa (Brazil). Namo: guahibo; Oá: desano piratapuya, tukano; Perupa: chaké, yuko, yupa; Uá-kua: chimila; Yu: puinave; Fo/Fu: chibcha, muyska; Vescura: tunebo; Aguari/Awari: piaroa; Macadwimi: cubeo; Taimi: cuna; Gagaru: arhuaco; Maktu: kogui; Uá-kua: chimila; Uarir: wayú; Kiisoué: chimila (Colombia).

Taxonomy

Canis thous Linnaeus, 1766. Syst. Nat., 12th ed., 1:60. Type locality: "Surinamo" [Surinam].

Placed in genus *Cerdocyon* by Hamilton-Smith (1839), Cabrera (1931), Langguth (1975), Stains (1975) and Berta (1987). Placed in genus *Dusicyon* by Clutton-Brock *et al*. (1976), subgenus *Dusicyon* (*Cerdocyon*) by Osgood (1934), and subgenus *Canis* (*Cerdocyon*) by Van Gelder (1978).

Chromosome number: 2n=74 (Wurster-Hill 1973).

Description

A medium-sized (5–7kg) canid (Table 3.2.1), tail moderately bushy, often with black tip and dark at base. No sexual dimorphism. Rostrum long and pointed, head relatively short and narrow. Pelage generally dark grey to black along dorsum down to midline; midline to ventrum including legs grey or black, sometimes with yellow to

Table 3.2.1. Combined body measurements for the crab-eating fox from Brazil: Marajó (Pará state, n=28), São Miguel (Minas Gerais, n=5), Baturité (Ceará, n=3) (Courtenay *et al*. 1996, O. Courtenay unpubl.); Cuiabá, Chapada dos Guimarães, Poconé, Barra do Bugres, Jangada (Matto Grosso, n=26), Vila Boa (Goais, n=1) Altinópolis (São Paulo, n=1) (J. Dalponte unpubl.); Venezuela: Masaguaral (Guarico state, n=10) (Sunquist *et al*. 1989); various (data represent mean values of n=11–44 specimens from five different regions) (Bisbal 1988); Argentina: Sierras de Mal Abrigo (Colonia, n=6) (Cravino *et al*. 2000). Cranial and dental measurements are found in Berta (1982), Bisbal (1988), and Courtenay *et al*. (1996).

HB	658mm (570–775) n=61
T	310mm (220–410) n=52
HF	136mm (125–147) n=50
SH	368mm (330–415) n=34
E	69mm (55–86) n=47
WT	5.7kg (4.5–8.5) n=52

Crab-eating fox. Emas National Park, Goias, Brazil, 2002.

Adriano Gambarini

orange flecks; neck and underparts cream to buff white. Pelage notably bristly and coarse. Substantial inter- and intra-population pelage colour variation including dark to almost black (e.g., northern Venezuela, Amazonia, central Brazil), silver grey (e.g., Venezuelan llanos), and light grey-yellow rufous (e.g., Ceará, Brazil). Continuous black dorsal line from neck to tail tip variably present. The dental formula is 3/3-1/1-4/4-1/2=44.

Subspecies Five subspecies are recognised (Cabrera 1931, 1958; Berta 1982).
— *C. t. thous* (south-eastern Venezuela, Guyana, Surinam, French Guiana, northern Brazil)
— *C. t. azarae* (north-eastern and central Brazil)
— *C. t. entrerianus* (south Brazil, Bolivia, Uruguay, Paraguay, Argentina)
— *C. t. aquilus* (north Venezuela, Colombia)
— *C. t. germanus* (Bogotá region, Colombia)

Similar species Pampas fox (*Pseudalopex gymnocercus*): sympatric in southern Brazil, Bolivia, Uruguay, Paraguay and Argentina; similar build and weight (4–7kg); bushier tail, pelage mixed grey, with variable dark band running along dorsum; ears, neck, lower legs, and tail yellow to rufous. Culpeo (*Pseudalopex culpaeus*): sympatric in Bolivia and possibly Colombia; larger, sexually dimorphic (6–13kg); bushy coat, distinct reddish to agouti on head, limbs, and orange tinge on belly. Hoary fox (*P. vetulus*): sympatric in Brazil; smaller (2.5–4kg), less robust; pelage woolly not bristly; rostrum length shorter relative to rostrum width in *C. thous* (e.g., RL:RW ratio: *P. vetulus* 2.1 vs *C. thous* 2.5; Courtenay *et al*. 1996); confusion only likely with lighter pelage varieties of the crab-eating fox, or near melanic forms of the hoary fox. Short-eared dog (*Atelocynus microtis*): possible sympatry in undisturbed areas in lowland Amazonian forest of Brazil, Bolivia, Colombia and Venezuela; weight similar (6.5–7.5kg); rostrum long and narrow; small rounded ears; tail bushy relative to body pelage which is short; colour variable. Gray fox (*Urocyon cinereoargenteus*): sympatric in Colombia and north-west Venezuela; weight similar (3–7kg); distinct reddish pelage on shoulders, ears, legs, and ventrum below neck. Bush dog (*Speothos venaticus*): sympatric throughout most of range; similar weight (5–7kg), but much more robust with substantially shorter legs and tail, thicker neck, and broader head; brown to tawny. Tayra (*Eira barbara*): sympatric throughout most of range; weight similar (2.7–7kg); glossy brown to black over body with contrasting grey yellow brown head and neck; tail long, two-thirds of body length; ears small and round. Jaguarundi (*Felis yagouaroundi*): sympatric throughout most of range; weight similar (4.5–9kg); fur short and silky; legs short; body slender; tail relatively long; head and ears relatively small; silky black to tawny pelage.

Figure 3.2.1. Current distribution of the crab-eating fox.

Current distribution
The species is relatively common throughout its range from the coastal and montane regions in northern Colombia and Venezuela, south to the province of Entreríos, Argentina (35°S); and from the eastern Andean foothills (up to 2,000m) in Bolivia and Argentina (67°W) to the Atlantic forests of east Brazil to the western coast of Colombia (1°N) (Figure 3.2.1). Its known central distribution in lowland Amazon forest is limited to areas north-east of the Rio Amazon and Rio Negro (2°S, 61°W), south-east of the Rio Amazon and Rio Araguaia (2°S, 51°W), and south of Rio Beni, Bolivia (11°S).

Few records exist in Suriname and Guyana. Recent records in French Guyana (Hansen and Richard-Hansen 2000) have yet to be confirmed (F. Catzeflis pers. comm.). The previous citation of its occurrence in Peru (Pacheco *et al*. 1995) has since been retracted by the authors (D. Cossios pers. comm.).

Historical distribution Not dissimilar to current. Fossils found in deposits dating to the late Pleistocene (Lujanian 300,000–10,000 years before present) to Recent, in Lagoa Santa Caves, Minas Gerais, Brazil (Berta 1987).

Range countries Argentina, Colombia, Bolivia, Brazil, French Guiana(?), Guyana, Paraguay, Suriname, Uruguay, Venezuela (Cabrera 1958; Berta 1982).

Relative abundance
No precise estimates of population sizes are available, but populations generally are considered stable.

Estimated populations/relative abundance and population trends Average densities include 0.55 animals per km² (range: 0.273–0.769, n=7 territorial groups) in the savannah/scrub mosaic of Marajó, Brazil (Courtenay 1998); 4/km² in the Venezuelan llanos (Eisenberg *et al*. 1979), and 1/km² in dry forest in Santa Cruz, Bolivia (Maffei and Taber 2003). F. Michalski (pers. comm.) estimates <100 individuals in Ipanema National Forest (São Paulo) and Lami Ecological Reserve (Rio Grande do Sul), Brazil, and Hill *et al*. (1997) indicate high relative encounter rates in the Mbaracayu Forest Reserve, Paraguay. There is little documentation for Suriname, French Guiana, and periphery areas of lowland Amazon forest.

Habitat

Occupies most habitats including marshland, savannah, cerrado, caatinga, chaco-cerrado-caatinga transitions, scrubland, woodlands, dry and semi-deciduous forests, gallery forest, Atlantic forest, Araucaria forest, isolated savannah within lowland Amazon forest, and montane forest. Records up to 3,000m a.s.l. Readily adapts to deforestation, agricultural and horticultural development (e.g., sugarcane, eucalyptus, melon, pineapples) and habitats in regeneration. In the arid Chaco regions of Bolivia, Paraguay, and Argentina, confined to woodland edge; more open areas used by the Pampas fox.

Vegetative habitats generally utilised in proportion to abundance, varying with social status and climatic season. Radio-tagged foxes in seasonally flooded savannas of Marajó, Brazil, predominated in wooded savannah (34%) and regeneration scrub (31%); low-lying savannah was "avoided", and areas of wooded savannah "preferred", more by senior than junior foxes and more in the wet season than dry season (Macdonald and Courtenay 1996). In the central llanos of Venezuela, fox home ranges similarly shift to higher ground in response to seasonal flooding, though are generally located in open palm savannah (68% of sightings) and closed habitats (shrub, woodlands, deciduous forest, 32%) (Brady 1979; Sunquist *et al*. 1989). In Minas Gerais, Brazil, two radio-tagged foxes (1 male, 1 female) in different territories were observed most often at the interface of livestock pasture and gallery forest ("vereidas") (82%) and in eucalyptus/agricultural plantations (8%) (O. Courtenay unpubl.). Eighty-eight crab-eating fox specimens collected by the Smithsonian Venezuelan Project were taken from prairie and pasture (49%), deciduous and thorn forest (19%), evergreen forest (17%), and marshes, croplands and gardens (15%) (Handley 1976 as cited in Cordero-Rodríguez and Nassar 1999).

Food and foraging behaviour

Food Omnivorous, including fruit, vertebrates, insects, amphibians, crustaceans, birds, and carrion. An opportunistic predator; dietary components (and their relative frequency) at any one location varies according to availability, climatic season, and probably social status. In areas of human disturbance, a large proportion of the diet may comprise foods such as cultivated fruits, domestic fowl and refuse.

In the Venezuelan llanos, 104 stomach contents from four different locations comprised in percent volume: small mammals (26%), fruit (24%), amphibians (13%), insects (11%); the dry season diet was predominantly small mammals, reptiles and amphibians, with insect and fruit becoming more frequent in the wet season (Brady 1979; Eisenberg *et al*. 1979; Bisbal and Ojasti 1980; Motta-Junior *et al*. 1994). In one Venezuelan location, land crabs (*Dilocarcinus*) were the most frequent stomach content dietary item (frequency 33%, volume 17%) in the rainy season (Bisbal and Ojasti 1980), and in the wetlands of Laguna Ibera (Corrientes), Argentina, aquatic birds were identified in 87% of 23 fox scats collected in the vicinity of the bird's breeding colony (Parera 1996). Vertebrates were the most frequently encountered food item (69%) of 74 prey items identified in 22 scats collected at elevations of >2,600m in the eastern Colombian Andes (Delgado-V in press), but the least favoured food item (15%) in faeces collected from the lowland wooded savannahs of Marajó, Brazil, where cultivated and wild fruit (57%) and insects (86%) were more frequently encountered (Macdonald and Courtenay 1996). In Barlovento, Miranda state, Venezuela, the percentage volume of identifiable food items in nine fox stomachs was vegetable remains (80%), vertebrates (11%), and insects (5%) (Cordero-Rodríguez and Nassar 1999), whereas in Campinas, Brazil, the stomach contents of 19 road-killed foxes contained, by percent volume, fruit (44%), birds (17%), mammals (20%), arthropods (2%), fish (<1%), and amphibians (1%) (Facure and Monteiro-Filho 1996).

Foraging behaviour Crab-eating foxes are primarily nocturnal and crepuscular. They hunt individually, but most commonly as pairs; 1–3 adult-sized offspring may accompany them. Cooperative hunting apparently is rare, but was observed by a single pair in Masaguaral (Brady 1979). They will tolerate close proximity when foraging on concentrated, easily available food items such as turtle eggs, fruit, insects (e.g., termites), and sizeable carrion (e.g., goat carcass) (Montgomery and Lubin 1978; Brady 1979; O. Courtenay unpubl.). The young start to hunt with the parents at about six weeks old.

Hunting strategies include spring-pouncing to capture vertebrates, ground-level lateral head movements to snatch insects, and directional manoeuvres in chase of land crabs. Prior to consumption, Marajó foxes treat some food items (e.g., toads, eggs) with a series of shoulder blows with face up-turned. In the same region, foxes search for and consume small stones from specific open gravel sites presumably as a source of minerals (O. Courtenay pers. obs.). Foxes cache food items but do not regularly urine mark them (Brady 1979).

Crab-eating foxes probably act as seed dispersers of a range of wild and cultivated plant species, as indicated by the presence of germinating seeds in their scats. Examples include "tusca" (*Acacia aroma*) and "tala" (*Celtis tala*) in Chaco Serrano de Tucumán, Argentina (R. Varela pers. comm.), "butia" palm (*Butia capitata*) in Uruguay (Paz *et al*. 1995, R. Rodríguez-Mazzini and B. Espinosa pers. comm.), hovenia (*Hovenia dulcis*) in the Iguacu National Park (D. Rode pers. comm.), figs (*Ficus* spp.) in south-eastern Brazil (Motta-Junior *et al*. 1994), guava (*Psidium guineense*) in Maraca Ecological Station (M.R.P. Leite Pitman pers. comm.), and "miri" (*Humiria balsamifera*) and cashew (*Anacardium occidentale*) in Amazon Brazil (Macdonald and Courtenay 1996).

Damage to livestock or game Reports of poultry raiding by the crab-eating fox are widespread; however, there is no evidence that foxes represent a significant predator of lambs or cause of economic loss to farmers in wool-producing countries. In Colonia, Uruguay, predation by foxes (crab-eating fox and Pampas fox) contributed only 2.9% of the lamb mortality rate (0.4% of viable lamb mortality) (Cravino *et al*. 1997). Similarly, in Rio Grande do Sul, Brazil, only 1.9% of 1,468 lambs born in two months on six properties succumbed to fox predation, though foxes appeared to account for 57% of the 49 predatory attacks (Dotto *et al*. 2001). Sheep remains were identified in the stomach contents of 7% (1/14) crab-eating fox and 48.5% (16/33) Pampas fox examined in Rio Grande do Sul (M. Fabian pers. comm.). In Colonia 17% (1/6) crab-eating fox and 32% (5/16) Pampas fox examined had sheep remains in the stomach contents (Cravino *et al*. 2000: appendix 2).

The crab-eating fox predates incubating eggs of loggerhead sea turtles (*Caretta caretta*), hawksbill (*Eretmochelys imbricata*), olive ridley (*Lepidochelys olivacea*), and green turtles (*Chelonia mydas*) on Brazilian beaches including Praia do Forte, Bahia (Santos *et al*. 2000).

Adaptations
Crab-eating foxes are among the most versatile of canids, as evidenced by their ability to use a variety of habitat types and to exploit a number of different food sources.

Social behaviour
Monogamous. Social groups comprise a breeding pair and 1–5 offspring (older than one year). Family members travel around their home ranges usually in pairs or, if offspring are present, in loosely knit family groups. Separated foxes maintain contact by long distance, high-pitched, bird-like trill vocalisations. In Marajó, Brazil, territorial breeding pairs were located <100m apart on a mean 54% (n=7) of occasions during the period of activity, whereas close proximity of breeding adults and their adult-sized offspring varied from 7.2% to 93.3% between given pairings (Macdonald and Courtenay 1996).

Reported home range sizes are based on a variety of estimation techniques: in Marajó, Brazil, adult foxes occupied stable territories of 5.3km² (range=0.5–10.4km²; n=21; restricted polygon estimates (RP); Macdonald and Courtenay 1996). In pasture/eucalyptus habitats in Minas Gerais, Brazil, an adult male's range was 2.2km² (RP; O. Courtenay unpubl.); and in dry forest in Santa Cruz, Bolivia, an adult female and two adult males occupied mean home ranges of 2.2km² (range=1.1–2.8km²; minimum convex polygon estimates (MCP); Maffei and Taber 2003). In the central Venezuelan llanos (Masaguaral), Brady (1979) reported a joint home range size of 1.0km² for an adult M/F fox pair (convex polygon estimate CP); a more recent study of three adult foxes and three adult fox pairs in the same site (Sunquist *et al*. 1989) showed dry season home ranges (mean=0.7km²a; range=0.5–1.0km²) to be generally larger than wet season home ranges (mean=0.7km²; range=0.3–1.0km²; MCP). Shrinkage of fox range sizes in the wet season is thought to be in response to changes in availability of dry fox habitats and/or prey density, a phenomenon also observed in Marajó Island, Brazil (Macdonald and Courtenay 1996).

Dispersing offspring established territories adjoining or adjacent to their natal range, an average distance between range centres of 2.4km (range=1.9–2.9km; n=4) (Macdonald and Courtenay 1996). Post dispersal, these foxes interacted amicably with kin members both inside and outside their natal range. Four male foxes returned to their natal range 3–13 months after their dispersal, in two cases following the death of their mate and in one case after breeding (Macdonald and Courtenay 1996).

Group latrines are not usual features of crab-eating fox society; however, a latrine comprising >72 scats visited by at least four adult-sized individuals was observed in Maraca Ecological Station, Brazil (M.R.P. Leite Pitman pers. comm.). Brady (1979) also reports the use of scat latrines located near resting sites.

Reproduction and denning behaviour
In the wild, litters are produced once per breeding year, with litters observed in September/October in Marajó (n=6 litters; Macdonald and Courtenay 1996); June in Minas Gerais, Brazil (n=2; O. Courtenay unpubl.); December in Brasilia district (F. Rodrigues pers. comm.); between December and February in the Venezuelan llanos, with lactating females seen in June (Montgomery and Lubin 1978, Brady 1979), and year round (estimated in January, May, July, and October) in Barlovento, state of Miranda, Venezuela, with lactating foxes recorded in August (Cordero-Rodríguez and Nassar 1999). A pregnant female was caught in July in south-eastern Brazil (K. Facure and A. Giaretta pers. comm.), and a pair with three cubs approximately three months old were seen in late November

in Ipanema National Forest (SP) indicating parturition in August (F. Michalski pers. comm.). On emergence at 2–3 months, the mean litter size is 2.6 (range=2–3; n=6), with a male:female sex ratio of 5:1 (Macdonald and Courtenay 1996). It is not known whether the presence of a dominant female inhibits ovulation in subordinate females.

In captivity, births have been recorded in January, February, March, June and October, and foxes may breed twice annually at intervals of 7–8 months (Coimbra-Filho 1966; Brady 1978). The mean litter size is 4.5 (range=3–6; n=6) with male:female sex ratios of 3:6 (n=2 litters; Biben 1982) and 10:8 (range=5:1 to 1:4; n=4 litters; Brady 1978). The gestation period is 56 days (range=52–59 days), and neonatal weight 120–160g (Brady 1978).

Cub rearing is the responsibility of both breeding adults. Additional helpers have not been observed directly in the wild. However, the strong social affiliations between adults and dispersed returning offspring during subsequent breeding periods are strongly suggestive of sibling helpers (Macdonald and Courtenay 1996). In captivity, both sexes bring solid food (they do not regurgitate) to the young who consume solids from day 16–20 (Biben 1982, 1983; Brady 1978). The milk teeth start to erupt at day 14. Cubs first leave the den around day 28, but more regularly from day 45 when 1–1.5kg, at which time they develop the adult pelage. Lactation lasts for approximately 90 days (Brady 1978). Post-weaning dependency lasts for up to five months until sexual maturity which occurs at approximately nine months (Brady 1978). Offspring disperse when 18–24 months old (cf. Brady 1979), which in Marajó is between August and December.

Crab-eating foxes do not regularly excavate burrows, but rest above ground in dense undergrowth (including when rearing cubs), but occasionally adopt abandoned burrows of other animals such as armadillos (Brady 1979; Macdonald and Courtenay 1996; R. Cunha de Paula pers. comm.).

Competition
Potential competitors include the similarly sized hoary fox (2.5–4kg), Pampas fox (4–7kg), and larger-sized maned wolf (*Chrysocyon brachyurus*) (20–33kg). Interspecific divergence in dietary composition appears to allow these canid species to coexist (Juarez and Marinho 2002). Interspecific competition is unlikely to affect conservation status.

Mortality and pathogens
Natural sources of mortality One radio-tagged crab-eating fox was located inside the belly of a green anaconda (*Eunectes murinus*) in Emas National Park, Brazil (Jácomo and Silveira 1998), and an ocelot (*Leopardus pardalis*) was seen feeding on a carcass of this fox in Iguacu National Park (Crawshaw 1995). Domestic dogs are known to chase and kill foxes (Brady 1979), and cause cub deaths

when dens are located in peri-urban areas. Likely natural predators include caimans (*Caiman yacare* and *C. latirostris*), jaguar (*Panthera onca*) and puma (*Puma concolor*), though no cases have been reported.

Persecution The fox is perceived as a pest of poultry throughout much of its range (and in Uruguay as a predator of lambs), and they are thus shot, trapped, and poisoned indiscriminately (Cravino *et al*. 1997). In Marajó, 83% of 12 fox deaths between 1988 and 1991 were due to local hunters (Macdonald and Courtenay 1996). The mortality rate in the Marajó population was 0.325 per year (95% C.L. 0.180–0.587), corresponding to a mean life expectancy of 3.1 years (95% C.L. 1.70–5.56). This is reflected in a young population with 57% of the population aged =12 months (1988–1989, n=25; 1994–1995, n=37), and high population replacement (turnover) rate of 0.84 per year (Courtenay 1998).

Hunting and trapping for fur Young foxes are often taken as pets, and at least one hunting household in Marajó, Brazil, admitted to consuming a fox on one occasion. Heavy trapping occurred in dry forest regions in Bolivia before the early 1980s when single pelts were worth US$30 (L. Maffei pers. obs.).

Road kills In north-eastern São Paulo state, Brazil, 29 deaths (male:female ratio of 1:1.5) were recorded along 13,500km of surveyed road between January 1981 and December 1983; the ratio of crab-eating to hoary fox carcasses was about 10:1 (J. Dalponte and J. Tavares-Filho unpubl.; see also Dalponte and Courtenay this volume).

Pathogens and parasites The effect of pathogen infection on population status has been rarely monitored; there are currently no reports of population declines. Rabies was confirmed in 18 foxes in Ceará, Brazil between 1980 and 1986, 11 of which were from the same region and within a six month period (Barros *et al*. 1989). Two confirmed fatal cases of canine distemper virus (CDV) were passively detected in crab-eating foxes, both in Brazil, including one male from Santa Genebra forest (Universidade de Campinas, Sao Paulo state) in 1989 (M.R.P. Leite Pitman pers. comm.), and one male in Lami Biological Reserve (Rio Grande do Sul) in 1999 (R. Printes pers. comm.). Domestic dogs were the suspected source of infection in both cases. By contrast, serological and clinical screening of 37 foxes that had substantial contact with domestic dogs with past exposure to CDV and canine parvovirus (CPV) in Marajó, Brazil, revealed no serological or clinical evidence of infection (Courtenay *et al*. 2001). Similarly, there was no evidence of alopecia consistent with scabies infection in 16 animals observed in the Gran Chaco, Bolivia, despite 20% (19/94) of the sympatric Pampas fox presenting confirmed or suspected infection with *Sarcoptes scabiei* (S. Deem pers. comm.).

The involvement of the crab-eating fox in the epidemiology of the protozoan parasite *Leishmania infantum* causing human and canine leishmaniasis has been the subject of extensive field studies in Marajó, Brazil (Courtenay *et al*. 1994, 2002; Courtenay 1998). Foxes with confirmed infection do not usually suffer infection-related mortality and are rarely infectious; thus it is unlikely that they are maintenance reservoirs in the absence of infectious domestic dogs (the known disease reservoir). Evidence suggests that infection spills over into foxes from infected sympatric dog populations (Courtenay *et al*. 2001, 2002). Hoary foxes have reportedly been infected with *L. infantum* and the rabies virus in Ceará, Brazil (Deane 1956; Barros *et al*. 1989); however, these animals were probably misidentified crab-eating foxes (Courtenay *et al*. 1996).

In captivity, crab-eating fox deaths have been attributed to infanticide, scabies, echinococcus infection, pulmonary disease, ectoparasites (scabies and fleas), and meningitis (Brady 1978; J. Cartes pers. comm.). Other documented parasites of free-ranging animals include *Hepatozoon canis* (Alencar *et al*. 1997) and various species of fleas (Cerqueira *et al*. 2000) and lice (Hopkins 1949, in Clutton-Brock *et al*. 1976).

Longevity The oldest recorded free-ranging fox was 9.2 years old, captured in Marajó, Brazil (O. Courtenay pers. obs.).

Historical perspective
The crab-eating fox is sometimes tamed as pets by indigenous and rural people (C. Baltzinger pers. comm.); there is limited talisman use, e.g., farmers in Ceará, Brazil, pin fox tails to animal sheds to warn off rabid bats (O. Courtenay pers. obs.).

Conservation status
Threats Potential threat of spill-over pathogenic infection from domestic dogs. In the Serra da Canastra National Park, Brazil, crab-eating foxes raid human refuse dumps in close company with unvaccinated domestic dogs along park boundaries (R. Cunha de Paula pers. comm.).

Commercial use No direct commercial value as furbearer due to the unsuitability of the fur which is coarse and short; however, pelts are sometimes traded as those of the South American grey fox in Argentina, and as those of the latter species and the Pampas fox in Uruguay (Cravino *et al*. 1997; A. Farias pers. comm.). Current illegal trade is small as the probable consequence of low fur prices; in Paraguay, for example, no illegal fox pelts were confiscated from 1995 to 2000 (J. Cartes pers. comm.).

Occurrence in protected areas Occurs in a large number of protected and unprotected areas across its geographical range.

Protection status CITES – Appendix II.
In Argentina, the crab-eating fox was considered "not endangered" by the 1983 Fauna and Flora National Direction (resolution 144), and its exploitation and commercial use was forbidden in 1987 (A. Novaro pers. comm.; A. Farias pers. comm.); currently listed as "potentially vulnerable" in the recent Argentine Red Data Book (Diaz and Ojeda 2000). In Bolivia, it is considered common and is, therefore, excluded from the Bolivian Red Data Book (Ergueta and Morales 1996), as it is from the Brazilian (Biodiversitas 1998) and Colombian (Rodríguez 1998) lists of threatened species.

Current legal protection There is no specific protective legislation for this species in any country, though hunting wildlife is officially forbidden in most countries. Generally, there is no specific pest regulatory legislation for the crab-eating fox, but it is strongly disliked locally as a pest of livestock (poultry and lambs) leading to illegal hunting and consequential sales of pelts. In some countries, pest control is limited by specific quotas (without official bounties), although the system is often ignored, abused, or not reinforced (J. Carvino pers. comm.; A. Soutullo pers. comm.). In Uruguay, hunting permits have not been issued since 1989 on the basis that lamb predation by foxes is negligible (Cravino *et al*. 1997, 2000).

Conservation measures taken Nothing proposed. No protection required.

Occurrence in captivity
Present in many zoos and private collections throughout South America where it generally breeds well and offspring survival rates are high.

Current or planned research projects
R. de Paula (Associação Pró-Carnívoros, São Paulo, Brazil) is studying the interactions between wild and domestic canids in Serra da Canastra National Park, Brazil.

C. Costa and O. Courtenay (Federal University of Piauí, Brazil and University of Warwick, UK) are conducting epidemiological studies on the role of the crab-eating fox in the transmission of zoonotic leishmaniasis.

J. Dalponte, E. Lima and R. Jorge (Serviço Social do Comércio/Fundação Pró-Natureza, Brazil) are investigating the diet and parasites of sympatric carnivores in Reserva Particular do Patrimônio Natural do Serviço Social do Comércio, Pantanal, Mato Grosso, Brazil.

L. Silveira and J. Marinho-Filho (Brasilia University, Brazil) are studying the ecology of sympatric carnivores in Emas National Park, Goias, Brazil.

S. Marques and T. da Santos (Furnas Centrais Elétricas, Brazil) are conducting radio-telemetry studies on the crab-eating fox and hoary fox in Guimarães region of Mato Grosso, Brazil.

Gaps in knowledge
Little is known of population status, particularly in lowland Amazon forest. The significance of infection and disease in population regulation, and behavioural ecology in the context of resource dispersion, are of interest.

Core literature
Berta 1982, 1987; Brady 1978, 1979; Courtenay *et al.* 1994, 1996, 2001, 2002; Macdonald and Courtenay 1996; Maffei and Taber 2003; Montgomery and Lubin 1978; Sunquist *et al.* 1989.

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3.3 Maned wolf
Chrysocyon brachyurus (Illiger, 1815)
Near Threatened (2004)

M. Rodden, F. Rodrigues and S. Bestelmeyer

Other names
French: loup à crinière; **German:** mähnenwolf; **Portuguese:** lobo guará, guará; **Spanish:** aguará guazú (Argentina), lobo de crin, borochi (Bolivia).

Taxonomy
Canis brachyurus Illiger, 1815. Abh. Phys. Klasse K. Pruess. Akad. Wiss., 1804–1811 :121. Type locality: not specified, but later listed by Cabrera (1958) as "los Esteros del Paraguay".

The species was originally placed in the genus *Canis*, but is now widely included in the genus *Chrysocyon* (Langguth 1975; Stains 1975; Van Gelder 1978; Berta 1987; Wozencraft 1993).

Chromosome number is 2n=76, very close to that of *Canis* (2n=78). A comparison of chromosome morphology and banding patterns suggest that the maned wolf and grey wolf (*Canis lupus*) share a common wolf-like ancestor (Wayne *et al.* 1987a).

Description
The maned wolf is hard to confuse with any other canid due to its long, thin legs, long reddish orange fur and large ears. The English common name comes from the mane-like strip of black fur running from the back of the head to the shoulders, averaging 470mm in length. Muzzle black, throat white, inner ears white, forelegs black and most of distal part of hindlegs black. An average of 44% of the tail length is white at the distal end, but the amount varies between individuals (from 17–66% of the tail length). No under fur present. The adult dental formula is 3/3-1/1-4/4-2/3=42. See table 3.3.1 below for body measurements.

Table 3.3.1. Combined body measurements for the maned wolf from Serra da Canastra National Park, Brazil (Dietz 1984), Emas National Park, Brazil (Silveira 1999; Bestelmeyer 2000) and Águas Emendadas Ecological Station, Brazil (F. Rodrigues unpubl.).	
HB	1,058mm (950–1150) n=23
T	446mm (380–500) n=22
E	163mm (135–200) n=23
WT	25.0kg (20.5–30) n=16

Adult female maned wolf. Serra da Canastra National Park, Minas Gerias State, Brazil, 2001.

Rogerio Cunha

Figure 3.3.1. Current distribution of the maned wolf.

Subspecies Monotypic (Dietz 1984).

Similar species Juveniles could possibly be confused with the crab-eating fox (*Cerdocyon thous*) because of their similar black and grey colouring.

Current distribution
The maned wolf inhabits the grasslands and scrub forest of central South America from the mouth of the Parnaiba River in north-eastern Brazil, south through the Chaco of Paraguay into Rio Grande do Sul State, Brazil, and west to the Pampas del Heath in Peru (Dietz 1985) (Figure 3.3.1. Beccaceci (1992a) found evidence of maned wolves in Argentina as far south as the 30th parallel, and a sighting in the province of Santiago del Estero was recently reported (Richard *et al.* 1999). They probably range into northern Uruguay. Their presence in this country was confirmed through a specimen trapped in 1990 (Mones and Olazarri 1990), but there have not been any reports of sightings since that date (S. Gonzalez pers. comm.).

Range countries Argentina, Bolivia, Brazil, Paraguay, Peru, Uruguay (Dietz 1985; Mones and Olazarri 1990; Beccaceci 1992a).

Relative abundance
With their primarily solitary habits and large home ranges (see Social behaviour), maned wolves are found in low densities throughout the range. In some areas of central Brazil, they appear to be more common, but increasing habitat fragmentation may threaten the viability of wild populations (Table 3.3.2).

Estimated populations/relative abundance and population trends

Table 3.3.2. The status of maned wolves in various range countries. (Population trend: D=declining, ?=unknown, Ex=extinct).

Country	Population size	Trend
Argentina	1,000?	D?
Bolivia	>1,000	?
Brazil	?	?
Peru	?	?
Paraguay	?	?
Uruguay	Ex?	?

Habitat
Maned wolves favour tall grasslands, shrub habitats, woodland with an open canopy (cerrado), and wet fields (which may be seasonally flooded). Some evidence indicates that they may prefer areas with low to medium shrub density (Bestelmeyer 2000). Maned wolves are also seen in lands under cultivation for agriculture and pasture. Daytime resting areas include gallery forests (Dietz 1984), cerrado and marshy areas near rivers (Bestelmeyer 2000; F. Rodrigues unpubl.). There is some evidence that they can utilise cultivated land for hunting and resting (A.

Jácomo and L. Silveira unpubl.), but additional studies are essential in order to quantify how well the species tolerates intensive agricultural activity.

Food and foraging behaviour
Food Omnivorous, consuming principally fruits and small- to medium-sized vertebrates. Numerous authors (Dietz 1984; Carvalho and Vasconcellos 1995; Motta-Júnior *et al*. 1996; Azevedo and Gastal 1997; Motta-Júnior 1997; Rodrigues *et al*. 1998; Jácomo 1999; Santos 1999; Silveira 1999; Juarez and Marinho 2002; Rodrigues 2002) have investigated the diet of the maned wolf. These studies have all found a wide variety of plant and animal material in the diet, with about 50% of the diet comprising plant material and 50% animal matter (Table 3.3.3). The fruit *Solanum lycocarpum* grows throughout much of the range and is a primary food source; other important items include small mammals (*Caviidae, Muridae, Echimydae*) and armadillos, other fruits (*Annonaceae, Myrtaceae, Palmae, Bromeliaceae*, and others), birds (*Tinamidae, Emberizidae* and others), reptiles and arthropods. Although the frequency of plant and animal items found in faecal samples is approximately equal (Table 3.2.2), the biomass of animal items is usually greater than that of plant items (Motta-Júnior *et al*. 1996; Santos 1999; Rodrigues 2002). Certain items, such as rodents and *Solanum,* are consumed year round, but the diet varies with food availability. At least occasionally, pampas deer (*Ozotoceros bezoarticus*) are also consumed (Bestelmeyer and Westbrook 1998). In Jácomo's (1999) study, deer appeared in 2.4% of 1,673 samples analysed.

Foraging behaviour Nocturnal and crepuscular, maned wolves may forage for up to eight consecutive hours, feeding on everything they can catch and every ripe fruit they detect (Bestelmeyer 2000; L. Silveira and A. Jácomo unpubl.). Strategies for hunting animal prey include: 1) stalking prey with a final pounce; 2) digging after burrowing animals; 3) leaping into the air to capture flying birds and insects, and 4) sprinting after fleeing deer. Approximately 21% of all hunting attempts end with the successful capture of prey, and the strategies do not differ in their success rates (Bestelmeyer 2000). Beccaceci (1992a) and C. Silva (unpubl.) recorded maned wolves feeding on coypus (*Myocastor coypus*) that were caught in traps set by hunters. L. Silveira and A. Jácomo (unpubl.) observed maned wolves scavenging opportunistically on road-kill carcasses.

Damage to livestock and game The maned wolf has been known to prey on domestic animals, especially chickens (Dietz 1984). However, poultry remains were found in only 0.6–1.4% of analysed scat samples (Dietz 1984; Motta-Júnior *et al*. 1996; Rodrigues 2002).

Adaptations
The maned wolf's long legs, large ears and pacing gait are considered adaptations for standing in and moving above tall grasses to hear small prey below. The long legs also enable maned wolves to run swiftly, at least occasionally tracking down fleeing pampas deer (Bestelmeyer and Westbrook 1998).

Table 3.3.3. Frequency of classes of food items in the maned wolf's diet in 11 places of the Cerrado of Brazil. (1) Juarez and Marinho 2002; (2) Dietz 1984; (3) Motta-Júnior *et al*. 1996; (4) – Motta-Júnior 1997; (5) Azevedo and Gastal 1997; (6) Jácomo 1999; (7) Silveira 1999; (8) Santos 1999; (9) Carvalho and Vasconcellos 1995; (10) Rodrigues 2002.

Items	Faz. Rio Pratudão/ BA (1)	P.N.S. da Canastra/ MG (2)	Faz. Água Limpa/ DF (3)	E.E. de Jataí/ SP (4)	Faz. Salto e Ponte/ MG (4)	Campus da UFSC AR/ SP (4)	APA Gama-Cab Veado/ DF (5)	P.N. Emas/ GO (6, 7)	Faz São Luis/ MG (8)	Santa Bárbara/ SP (9)	Águas Emendadas E.E./ DF (10)
Solanum lycocarpum	31.9	32.6	25.7	15.6	31.0	24.4	23.1	18.0	29.3	32.3	27.4
Miscellaneous fruit	9.4	7.3	9.2	14.7	2.8	10.2	10.7	36.3	7.8	6.3	24.2
Grass	9.4	11.1	11.8	14.3	20.0	12.8	13.8	3.2	17.2	9.4	8.2
Subtotal – vegetable	**50.7**	**51.0**	**46.7**	**44.6**	**53.8**	**47.4**	**47.6**	**57.5**	**54.3**	**48.0**	**59.8**
Arthropods	3.6	5.7	2.0	5.5	2.1	5.1	23.1	1.6	12.1	7.3	5.8
Reptiles	1.6	0.3	2.6	3.4	4.8	1.3	–	3.1	1.8	–	0.1
Birds	8.4	12.0	13.8	8.4	10.4	7.7	10.7	11.1	11.1	12.5	10.1
Eggs	–	–	–	–	–	–	3.1	0.2	–	–	0.4
Rodents & marsupials	33.0	26.6	25.0	32.1	27.5	34.6	15.4	24.0	14.1	29.2	16.7
Armadillos	1.6	3.1	9.2	2.9	–	1.3	–	2.1	6.3	1.0	6.7
Other mammals	1.0	0.7	0.7	2.1	1.4	1.3	–	0.2	0.5	–	0.5
Other vertebrates	–	0.6	–	1.0	–	1.3	–	–	0.3	2.1	–
Subtotal – animal	**49.2**	**49.0**	**53.3**	**55.4**	**46.2**	**52.6**	**52.3**	**42.3**	**46.2**	**52.1**	**40.3**
No. of occurrences	191	2,056	304	237	145	78	65	4,540	396	96	901
No. samples	70	740	104	61	46	21	20	1,673	150	?	328

Social behaviour

Maned wolves appear to be facultatively monogamous. Pairs are not often seen together, although researchers have observed pairs resting, hunting and travelling together.

Dietz (1984) found that home ranges of pairs in Serra da Canastra National Park varied between 21.7 and 30.0km² (average 25.2 ± 4.4km²; n=3 pairs). The home ranges of individuals studied in other areas are larger, ranging from 15.6–104.9km² (average 57.0 ± 34.3km², n=5) in Águas Emendadas Ecological Station (Rodrigues 2002) and 4.7–79.5km² (average 49.0 ± 31.8km², n=5) in Emas National Park (Silveira 1999). Home range boundaries appear stable over time and are defended against adjacent pairs, although there may be overlap at the edge of the home range (Rodrigues 2002). Males and females do not differ in their rates of scent marking. Termite mounds are preferentially used as urine-marking sites, and more marks are placed on the upwind side of objects than on the downwind side (Bestelmeyer 2000). Floater individuals without territories appear to move along territory boundaries (Dietz 1984) and do not scent mark (Bestelmeyer 2000).

The most frequently heard vocalisation is the roar-bark, a loud vocalisation that has been heard during all times of the day and night and at all times of the year (Brady 1981; Bestelmeyer 2000; L. Silveira and A. Jácomo unpubl.).

Reproduction and denning behaviour

Female maned wolves enter oestrus once per year, for approximately five days. Peak breeding season is from April to June. There are numerous published accounts of breeding behaviour in captivity, but little information is available from wild populations (Silveira 1968; Encke 1971; Brady and Ditton 1979; Bartmann and Nordhoff 1984; Dietz 1984; Rodden *et al.* 1996; Bestelmeyer 2000). In captivity, the frequency of vocalisations (roar-bark) and scent marking increases during the weeks prior to mating (Brady 1981), and the amount of time a pair spends in close proximity increases significantly during the oestrous period. Courtship is characterised by frequent approaches, mutual anogenital investigation, and playful interactions. Mounting may occur frequently during oestrus; successful breeding includes a copulatory tie that may last several minutes. In Emas National Park, Brazil, a breeding pair observed at night for approximately 3.5 hours foraged together and vocalised frequently whenever one partner was out of sight. The male marked with urine or faeces wherever the female marked. A breeding display lasting 10 minutes included a two-minute copulatory tie. After copulation, the pair continued to forage together (L. Silveira and A. Jácomo unpubl.).

Gestation length is approximately 65 days, with the majority of births occurring from June to September, during the dry season. One female gave birth to three pups in a bed of tall marsh grass. At 45 days of age the pups had not yet left the den and weighed 2.0kg (female) and 2.25kg (males) (L. Silveira and A. Jácomo unpubl.). All dens found in the wild have been above ground, gaining shelter from natural features such as the canopies of shrubs, rock crevices, gullies, and dry mounds in marshy, tall-grass areas.

In captivity, an analysis of 361 births indicated that parturition peaks in June (winter), and the average litter size is 3 (range=1–7; Maia and Gouveia 2002). Birth weights average 390–456g (n=8). In captive animals, nursing bouts begin to decline after the first month, and weaning is complete by around 15 weeks. Pups begin consuming solids regurgitated by the parents at around four weeks of age; regurgitation has been recorded up to seven months after birth (Brady and Ditton 1979). Females with 7–14-week-old pups have been observed hunting for continuous periods of eight hours over 3km from their den sites and pups (Bestelmeyer 2000; F. Rodrigues unpubl.). Pups stay in the mother's home range for approximately one year, when they begin to disperse. Juveniles attain sexual maturity at around the same time, but usually do not reproduce until the second year.

One of the many unknown aspects of maned wolf behaviour is the role the male plays in rearing pups. Pups have been seen accompanied by two adults (Dietz 1984), and a female with pups was seen accompanied by a male many times (F. Rodrigues unpubl.). In captivity, males increase pup survival rates and are frequently observed regurgitating to pups and grooming pups (Bestelmeyer 2000). Nonetheless, direct confirmation of male parental care in the wild is still lacking.

Competition

No direct competition has been observed with other carnivores sharing maned wolves' primary habitat, including the bush dog (*Speothos venaticus*), crab-eating fox (*Cerdocyon thous*), hoary fox (*Pseudalopex vetulus*), pampas fox (*P. gymnocercus*), puma (*Puma concolor*), jaguar (*Panthera onca*), pampas cat (*Oncifelis colocolo*), jaguarundi (*Herpailurus yaguarondi*), crab-eating raccoon (*Procyon cancrivorus*), hog-nosed skunk (*Conepatus semistriatus*), and grison (*Galictis cuja* and *G. vittata*). The diet of the maned wolf significantly overlaps with that of the crab-eating fox, and to a lesser extent with that of the smaller hoary fox (Silveira 1999; Juarez and Marinho 2002). However, maned wolves can take larger prey than either fox species (Bestelmeyer and Westbrook 1998; Silveira 1999; Juarez and Marinho 2002). Evidence from northern Argentina indicates that the maned wolf and pampas fox may eat many of the same food items (L. Soler pers. comm.). Packs of domestic dogs may also compete for prey with maned wolves.

Mortality and pathogens

Natural sources of mortality Because of its size, other carnivores do not usually prey upon the maned wolf,

although there is a record of predation by a puma (M. Reis pers. comm.). In areas inhabited by humans, domestic dogs have been observed pursuing and killing maned wolves (A. Hass pers. comm.; F. Rodrigues unpubl.; and see also Threats).

Persecution Maned wolves are not viewed as a serious threat to livestock, although they may occasionally be shot when caught raiding chicken pens. Diet studies indicate that domestic chickens have little importance in their diet, but this relationship needs to be studied more thoroughly.

Hunting and trapping for fur The pelt of the maned wolf is of no value to the fur trade.

Road kills Road kills are one of the main causes of mortality of maned wolves, especially for young individuals and sub-adults (Beccaceci 1992a; Vieira 1996; Silveira 1999; Rodrigues 2002; L. Soler pers. comm.). Road kills on highways are responsible for mortality of approximately half of the annual production of pups in some reserves (Rodrigues 2002).

Pathogens and parasites The giant kidney worm, *Dioctophyma renale*, which infects wild and captive maned wolves in South America, is considered a serious health threat (Matera *et al*. 1968; Beccaceci 1990). Beccaceci (1992b) found evidence of tuberculosis in a wild specimen, and hemo-parasites have also been recorded (F. Vinci pers. comm.).

In captivity, maned wolves are susceptible to typical canine viruses, including canine distemper, parvovirus, rabies, and adenovirus. Infectious diseases and digestive disorders are among the main causes of death among pups 31–120 days old (Maia and Gouveia 2002). Ovarian tumours are frequently found in adult females (Munson and Montali 1991). Cystinuria, a metabolic disease of the renal system, is prevalent in both captive and wild maned wolves, although its impact on wild populations is not known (Bush and Bovee 1978; Bovee *et al*. 1981; Mussart and Coppo 1999).

Longevity In captivity, maned wolves may live up to 16 years. To the best of our knowledge, there is no information available for longevity in the wild.

Historical perspective
Throughout its range, attitudes towards the maned wolf range from tolerance to fear and dislike. Native folklore and superstitions contribute to the attitudes of local people. For example, in Brazil certain parts of the maned wolf are used in local medicines to cure bronchitis and kidney disease or as a treatment for snakebite. Other body parts are believed to bring good luck (C. Silva pers. comm.). In

Bolivia, cowboys believe that sitting on the pelt of a maned wolf will protect them from bad luck (L. Sainz pers. comm.).

Although it is one of the largest carnivores in the grasslands, the species is apparently not well known to a large segment of the population. In a study of visitors at Brasilia Zoo, which is surrounded by cerrado, 32% of 30 adults and 30 children surveyed did not recognise the maned wolf when shown a photograph of the animal (Bizerril and Andrade 1999).

Conservation status
Threats The most significant threat to maned wolf populations is the drastic reduction of habitat, especially due to conversion to agricultural land (Fonseca *et al*. 1994). The cerrado has been reduced to about 20% of its preserved original area (Myers *et al*. 2000), and only 1.5% of it is currently protected (Ratter *et al*. 1997). In addition, habitat fragmentation causes isolation of sub-populations. Many maned wolves are killed on the nation's roads. Highways border many of the Conservation Units of the Brazilian cerrado, and drivers often do not respect speed limits. Reserves close to urban areas often have problems with domestic dogs. These dogs pursue and may kill maned wolves and can also be an important source of disease. Domestic dogs also possibly compete with the maned wolf for food. Interactions with humans also pose a threat to the maned wolf. Diseases, such as those mentioned above, can be important causes of mortality in the wild, but there is very little information available about the health of wild populations. In areas where there are domestic dogs, the problem is certainly greater.

Commercial use None. Indications are that the use of maned wolf parts for medicinal purposes does not involve any sort of large-scale commercial transactions and is confined to native folk medicine (see Historical perspective).

Occurrence in protected areas
— *Argentina*: Chaco National Park, Mburucuyá National Park, Iberá Provincial Reserve, San Juan de Poriahú, San Alonso Private Reserves, Río Pilcomayo National Park, El Bagual Private Reserve, Campo Bouvier, La Esmeralda Reserve, and possibly La Loca Provincial Reserve;
— *Bolivia*: Estación Biológica del Beni, Parque Nacional Noel Kempff Mercado, Parque Nacional and Area Natural de Manejo Integrado Otuquis and San Matías, Parque Nacional Madidi. May occur in Parque Nacional Kaa Iya del Gran Chaco and Territorio Indígena & Parque Nacional Isiboro Sécure;
— *Brazil*: occurs in the following National Parks: Brasília, Emas, Chapada dos Veadeiros, Araguaia, Serra da Canastra, Grande Sertão Veredas, Serra do Cipó,

Chapada dos Guimarães, Serra da Bodoquena, Ilha Grande, Aparados da Serra, Serra Geral, São Joaquim, Serra da Bocaina, Itatiaia. Ecological Reserve Roncador, Ecological Stations Águas Emendadas, Uruçuí-Una, Serra das Araras, Pirapitinga and Taiamã. State Parks: Ibitipoca, Itacolomi, Nascentes do Rio Taquari, Caracol, Iatapuã, Turvo, Cerrado, Vila Velha;
— *Paraguay*: Mbaracayu Forest Biosphere Reserve;
— *Peru*: Pampas del Heath?

Protection status CITES – Appendix II.
Protected in Argentina (classified as Endangered on the Red List); and included on the list of threatened animals in Brazil (Bernardes *et al*. 1990).

Current legal protection Hunting is prohibited in Brazil, Paraguay and Bolivia. Maned wolves are protected by law in many parts of their range, but enforcement is frequently problematic. Included in the United States Endangered Species list.

Conservation measures taken We are not aware of any conservation actions specific to the maned wolf. However, they are the beneficiaries of broader attempts to protect the cerrado (for example, recent actions to reduce the impact of road kills in Brasilia).

Occurrence in captivity
Records of captive maned wolves have been kept in an International Studbook, which was maintained by the University of Heidelberg from 1973 to 1978, and since 1979 by Frankfurt Zoo, Germany. As of 31 December 2003, 146 institutions reported a total of 431 maned wolves in captivity, including 208 males and 222 females. Cooperative breeding programmes exist among zoos in Europe, North and South America, and there has been considerable research on reproductive behaviour and physiology, nutrition, diseases and other husbandry issues. There are no known reintroduction projects currently underway. Individuals are sometimes kept as pets or in private collections.

Current or planned research projects
In Brazil, there are several ecological studies underway, investigating aspects such as home range, feeding ecology, behaviour and reproductive behaviour, including studies by: F. Rodrigues, Rogério Cunha and Eduardo Eizirik (Associação Pró-Carnívoros), Adriana Hass (CNPq) and F. Vinci (União de Ensino do Planalto Central) in Serra da Canastra National Park; F. Rodrigues (Associação Pró-Carnívoros) in Distrito Federal; A. Jácomo and L. Silveira (Associação Pró-Carnívoros) in Goiás; J. Carlos Motta-Júnior (Universidade de São Paulo) in São Paulo and Minas Gerais; L. Fernando Silva (Fundação ZooBotânica de Belo Horizonte) in Minas Gerais; J. Eduardo Mantovani

(Instituto Nacional de Pesquisas Espaciais) in São Paulo; C. Silva (Instituto Brasileiro de Meio Ambiente) in Paraná.

Studies of genetic variability are being done by J. Roberto Moreira (Centro Nacional de Recursos Genéticos / Empresa Brasileira de Agropecuária) and M. Nazaré Clautau (Universidade de Brasília). J. Roberto Moreira is also revising the distribution of the species in Brazil.

In Argentina, A. Soria and S. Heinonen Fortabat (Delegación A.P.N.) have been conducting surveys of maned wolves in three National Parks: Pilcomayo, Chaco, and Mburucuyá. L. Soler (HUELLAS, and Grupo de Ecología Comportamental de Mamíferos, GECM) has proposed a study in the Mburucuyá National Park in the province of Corrientes, to examine habitat use and availability and to census the carnivore species utilising the park and surrounding areas. The attitudes of local people will be a major focus of the study. Although HUELLAS and Oikoveva (a French NGO) are providing partial funding, additional support is being sought. S. Gonzalez (División Citogenética, Universidad de la República Oriental del Uruguay) and M. Beccaceci (Universidad del Salvador) have also proposed a study of the genetic variability of wild populations in Argentina.

In Bolivia, additional studies of canid ecology in eastern Bolivia have been proposed (L. Emmons, Smithsonian National Museum of Natural History, and L. Sainz, Museo de Historia Natural Noel Kempff Mercado).

A captive study of maned wolf nutritional requirements (M. Allen and S. Childs), supported by the American Zoo and Aquarium Association's Maned Wolf Species Survival Planâ, the National Zoological Park, and Purina Mills, is underway. A second captive study focusing on the modes of inheritance of cystinuria, is supported by the AZA MWSSP, University of Pennsylvania, and Morris Animal Foundation (J. Kehler and P. Henthorn, University of Pennsylvania).

Gaps in knowledge
Population surveys throughout the species' range are needed. The impact of human encroachment on suitable habitat is not clearly understood, and the suitability of agricultural land as maned wolf habitat needs to be investigated. The impact of disease processes on wild populations is not well understood.

Core literature
Bestelmeyer 2000; Brady and Ditton 1979; Dietz 1984, 1985; Jácomo 1999; Motta-Junior *et al*. 1996; Silveira 1999.

Reviewers: Marcelo Beccaceci, Otávio Borges Maia, James Dietz, Louise Emmons, Anah Jácomo, Leandro Silveira, Lucía Soler. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.

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

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).

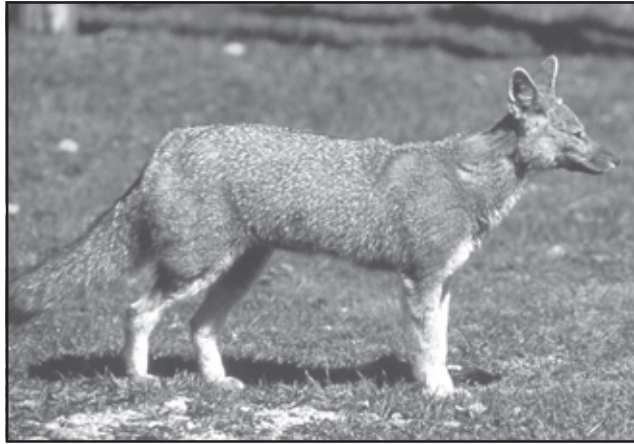Chromosome number: 2n=74 (Vitullo and Zuleta 1992).

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 and neck, as well as legs and flanks are tawny or rufous. The rump is darker, ranging in colour from tawny to dark

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

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

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) (Figure 3.4.1). 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 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

Figure 3.4.1. Current distribution of the culpeo.

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.).

Estimated populations/relative abundance and population trends
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 a.s.l. (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 Argentine 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 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 Silvestre), 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. Lichtschein 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, USA).

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, USA) 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, Argentina), 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.

Reviewers: Elise McMahon, Warren E. Johnson, Fabián M. Jaksic. **Editors:** Claudio Sillero-Zubiri, Michael Hoffmann.

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 congenerics (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

Figure 3.5.1. Current distribution of Darwin's fox.

Known range
? Possible range
Chile
0   50 Km

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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.).

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 Population size	Trend	Other areas Population size	Trend	Total Population size	Trend
Mainland	~78	?	10	D	<100	?
Chiloe 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 (Rhinocryptids).

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 Admistrative 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 guiñas. 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 became 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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3.6 Chilla
Pseudalopex griseus (Gray, 1837)
Least Concern (2004)

R. González del Solar and J. Rau

Other names
English: South American grey fox, Argentinean grey fox, grey zorro; **French:** renard gris; **German:** Patagonischen fuchs; **Spanish**: zorro gris, zorro gris chico, zorro gris Patagónico (Argentina); zorro gris, zorro chico, zorro chilla, zorro de la pampa (Chile); **Indigenous names:** Araucano/Mapuche: ngürü, nuru, n'rú (Argentina/Chile); Puelche: yeshgai (Argentina); Quechua: atój (Argentina/Peru).

Taxonomy
Vulpes griseus Gray, 1837. Mag. Nat. Hist. [Charlesworth's], 1:578. Type locality: "Magellan", listed in Cabrera (1958) as "Costa del Estrecho de Magallanes" [Chile].

The Darwin's fox (*Pseudalopex fulvipes*) was first deemed an island form of *P. griseus* (Osgood 1943; Clutton-Brock *et al.* 1976; Honacki *et al.* 1982). More recently, however, the discovery of sympatric populations of *P. fulvipes* and *P. griseus* on the Chilean mainland (Medel *et al.* 1990), and studies using metachromatic and genetic (see Yahnke *et al.* 1996) analyses support the recognition of *P. fulvipes* as a species. The Pampas fox (*P. gymnocercus*) has recently been suggested to be conspecific with *P. griseus* on the basis of a craniometric and pelage characters analysis (Zunino *et al.* 1995). These authors conclude that *P. gymnocercus* and *P. griseus* are clinal variations of one single species, namely *Lycalopex gymnocercus*.

Chromosome number is 2n=74; fundamental number is FN=76. Somatic karyotype of the female constituted by 36 pairs of acrocentric chromosomes. The X chromosome is metacentric, and the Y chromosome is a micro-chromosome (Gallardo and Formas 1975).

Description
A small fox-like canid with body measurements as shown in Table 3.6.1. Head rufescent, flecked with white. Large ears. Chin with well-marked black spot. Coat brindled grey, made up of agouti guard hairs with pale underfur.

Table 3.6.1. Body measurements for the chilla.

	Tucumán, Argentina (Mares *et al*. 1996).	Parque Nacional Nahuelbuta, Chile (E. McMahon pers. comm.).	Parque Nacional Torres del Paine, Chile (Johnson and Franklin 1994c).	Reserva Nacional Las Chinchillas, Chile (Jiménez 1993, Jiménez *et al*. 1995).
HB male	520mm (501–540) n=2			
HB female	566mm (562–570) n=2	579mm (515–660) n=14		
T male	337mm (328–347) n=2			
T female	319mm (317–322) n=2	283mm (115–330) n=14		
HF male	128mm (125–131) n=2			
HF female	122mm (120–124) n=2	130mm (118–145) n=14		
E male	75mm (70–81) n=2			
E female	81mm (80–82) n=2	84mm (55–169) n=8		
WT male			4.0 ± 0.1 (SE) kg, n=23	
WT female		3.5kg (2.5–5.0) n=14	3.3 ± 0.1 (SE) kg, n=21	2.5 ± 0.9 (SE) kg, n=16

Chilla, age and sex unknown. Parque Nacional Talampaya, La Rioja, Argentina.

Rafael González del Solar

Thighs crossed by a black patch. Legs and feet pale tawny. Underparts pale grey. Tail long and bushy, with dorsal line and tip black. Tail's underside presents a mixed pale tawny and black pattern (Osgood 1943; Clutton-Brock *et al*. 1976).

The cranium is small, lacking an interparietal crest. Teeth widely separated. The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Four subspecies are recognised (Osgood 1943).
— *P. g. domeykoanus* (I Region to IX Region, Chile; southern Peru). Dentition weaker than *P. g. griseus*; pelage paler than *P. g. maullinicus*.
— *P. g. gracilis* (Western Argentina [Monte desert], from Santiago del Estero Province to west Río Negro Province).
— *P. g. maullinicus* (Southern temperate forests of Argentina and Chile, and in the latter from VIII Region to XI Region). Dentition weaker than *P. g. griseus*; pelage darker than *P. g. domeykoanus*.
— *P. g. griseus* (Argentinean and Chilean Patagonia, south from Río Negro to Magellan's Strait in the former, and in the steppes from east XI Region to XII Region in the latter; introduced in Tierra del Fuego).

Similar species Culpeo (*P. culpaeus*): generally larger; chin whitish; cranium with interparietal crest; relatively longer canines and relatively shorter molars. Pampas fox (*P. gymnocercus*): more robust; pelage more uniformly grey (less rufescent). Darwin's fox (*Pseudalopex fulvipes*): smaller; pelage darker brown; deeper and richer shaded rufescent areas on head, ears and legs; tail not bushy.

Current distribution
Widespread in plains and mountains on both sides of the Andes (Figure 3.6.1), from northern Chile (17°S) down to Tierra del Fuego (54°S).

In Argentina, they occur in the western and southern arid and semi-arid regions of the country, from *c.* 23°S (Jujuy and Salta) to Tierra del Fuego, and from the eastern foothills of the Andes mountain range to meridian 66°W, reaching the Atlantic coast (*c.* 63°W) south from Río Negro. Present in the following provinces: Jujuy (Jayat *et al*. 1999), Salta (Mares *et al*. 1996), Tucumán, Catamarca, Santiago del Estero, La Rioja, San Juan, Mendoza, west of San Luis, Neuquén, west of La Pampa, Río Negro, Chubut, Santa Cruz, and Tierra del Fuego (Osgood 1943; Olrog and Lucero 1981).

Widespread in Chile from the I Administrative Region (Atacama Province) in the north, south to the Strait of Magellan (XII Administrative Region, Magallanes Province), and Tierra del Fuego (Medel and Jaksic 1988; Marquet *et al*. 1993), and from the western foothills of the

Figure 3.6.1. Current distribution of the chilla.

Andes mountain range to the Pacific coast (71–73°W). They were introduced to Tierra del Fuego in 1951 in an attempt to control rabbit (*Oryctolagus cuniculus*) infestation (Jaksic and Yáñez 1983).

Other populations have been reported to exist in some of the southern Atlantic islands, including Malvinas/Falkland (Olrog and Lucero 1981), but this requires confirmation. Their presence in Peru is uncertain.

Range countries Argentina, Chile, Peru (?) (Osgood 1943; Olrog and Lucero 1981; Jayat *et al*. 1999).

Relative abundance
In Argentina, Olrog and Lucero (1981) considered chillas to be "locally common". In the latter country, relative abundance of chillas has been evaluated mainly through the scent stations technique. Autumn data collected in Pilcaniyeu (Río Negro) from 1983 to 1989, as well as winter data collected in Patagonia from 1989 to 2000 (A. Novaro and M. Funes unpubl.) and in north-eastern Mendoza from 1993 to 1997 (F. Videla *et al*. unpubl., R. González del Solar *et al*. unpubl.), suggest that populations are essentially stable in the southern half of Argentina where habitat is more favourable. They are reported to have expanded their distribution in Tierra del Fuego since their introduction (A. Novaro pers. comm.). J. Bellati (pers. comm.) estimated in 1996 an ecological density of one chilla/km^2 in Tierra del Fuego. Their status in the northern half of the country is unknown.

Estimated populations/relative abundance and population trends In Chile, chillas are considered frequent in the northernmost and northern regions (1 individual detected weekly); scarce (1 individual detected monthly) in central Chile; frequent-common (common: 1–5 individuals detected daily) in southern Chile; and common-abundant (abundant: >5 individuals detected daily) in southernmost Chile. The species became very abundant around Bahía Inútil (Tierra del Fuego) in the areas where it was first released in 1951 (Jaksic and Yáñez 1983). Despite having been overexploited for their fur in the past, chillas seem not to be decreasing in number (J. Jiménez pers. comm.).

In Chile, a mean ecological density of 3.3 chillas/km^2 was reported for the core area of Parque Nacional Torres del Paine, which is particularly safe and rich in resources for chillas. However, a much lower crude density (1.3 foxes/km^2) resulted when the former figure was extrapolated to the whole park. The density of foxes in Parque Nacional Torres del Paine, however, is likely to be higher than in most other Chilean populations, since the park is located in a particularly productive area. Three different density estimates resulted from the use of three different techniques for a site similar to Parque Nacional Torres del Paine (Durán *et al.* 1985). The most conservative of these estimates is 1.3 foxes/km^2 – a result similar to that of Johnson and Franklin (1994a) – and the highest 2.3 foxes/km^2, a figure that was deemed an overestimation (probably caused by methodological problems) by different authors (see Johnson and Franklin 1994a). In Reserva Nacional Las Chinchillas, the minimum abundance estimate (absolute density) over the entire reserve was 0.43 foxes/km^2, while the ecological density was 2.04 grey foxes/km^2 (Jiménez 1993).

In north-eastern Mendoza (Argentina), visitation indices progressively decrease from summer to winter, suggesting that the population suffers a decline during the cold season (R. González del Solar unpubl.). A similar pattern was found in Chile's Bosque Experimental San Martín (Martínez *et al.* 1993).

Habitat

The chilla occurs in steppes, "pampas" (grasslands), and "matorral" (scrublands) (Olrog and Lucero 1981). They generally inhabit plains and low mountains, but they have been reported to occur as high as 3,500–4,000m a.s.l. (see Marquet *et al.* 1993; Jayat *et al.* 1999). Although chillas occur in a variety of habitats, they prefer shrubby open areas. In central Chile, they hunt more commonly in flat, open patches of low height (1–2m) scrub than in areas with dense vegetation or ravines. Yet, they do visit ravines, apparently in search of fruit (Jaksic *et al.* 1980; Jiménez *et al.* 1996b). In southern Chile (Parque Nacional Nahuelbuta), chillas also prefer open areas to those more dense patches where Darwin's foxes occur (Jaksic *et al.*

1990; Jiménez *et al.* 1990; Medel *et al.* 1990). Durán *et al.* (1985) found that in Chilean Patagonia, their typical habitat was the shrubby steppe composed of "coirón" (*Festuca* spp., *Stipa* spp.) and "ñires" (*Nothofagus antarctica*), and that burning and destruction of forests in order to augment the land for sheep farming seems to have been advantageous for chillas. A similar preference was detected in Parque Nacional Torres del Paine, where 58% of the 12 monitored individuals used matorral shrubland or *Nothofagus* thicket habitat within their home ranges, more than was expected (Johnson and Franklin 1994c). In the north-eastern Mendoza desert (Argentina), these foxes seem to prefer the lower levels of the shrubby sand dunes that characterise the landscape or the valleys among dunes rather than their higher sections (R. González del Solar unpubl.).

Chillas are tolerant to very different climatic regimes from remarkably hot and dry areas, such as the Atacama coastal desert in northern Chile (less than 2mm average annual rainfall, 22°C mean annual temperature), to the humid regions of the temperate Valdivian forest (2,000mm average annual rainfall, 12°C mean annual temperature) and the cold Tierra del Fuego (*c.* 400mm average annual rainfall, 7°C mean annual temperature).

Food and foraging behaviour

Food Chillas are omnivorous generalists, feeding on a variety of food types including mammals, arthropods, birds, reptiles, fruit, and carrion (Medel and Jaksic 1988). Fruits ingested include berries of *Cryptocarya alba* and *Lithraea caustica* in Chile (Yáñez and Jaksic 1978; Jaksic *et al.* 1980), pods of *Prosopis* spp., and the berry-like fruits of *Prosopanche americana* and of several Cactaceae in Argentina (González del Solar *et al.* 1997, unpubl.).

A tendency to carnivory, however, is apparent, since vertebrates, especially rodents, are reported to be the most important prey in most studies. Small mammals were the most important vertebrate prey in most sites in the Chilean matorral (Yáñez and Jaksic 1978; Jaksic *et al.* 1980; Simonetti *et al.* 1984; Marquet *et al.* 1993; Jiménez *et al.* 1996b) and in the temperate rainforests of southern Chile (Martínez *et al.* 1993; Rau *et al.* 1995). Different situations have been found elsewhere. In Reserva Malleco (temperate forest of southern Chile), rodents and insects were similarly represented (R. Figueroa and E. Corales pers. comm.), whereas in Parque Nacional Torres del Paine, the European hare (*Lepus europaeus*) was the most represented vertebrate prey, followed by artiodactyl carrion and akodontine rodents (Johnson and Franklin 1994b). In Argentina's Patagonian steppe (Neuquén), artiodactyl carrion was the most important food item in 42 stomachs collected in winter (representing 62% of biomass ingested), followed by hares and cricetine rodents (Novaro *et al.* 2000). Similar results emerged from Argentina's southern Patagonia (Chubut), where carrion was followed by birds, rodents,

and fruit (S. Saba pers. comm.). Finally, in two studies conducted in Tierra del Fuego, invertebrates were followed by ungulates (reportedly carrion), birds, and rodents (Jaksic *et al.* 1983).

In the harshest habitats of its distribution range, the diet of the chilla includes increasingly higher proportions of non-mammal food as small mammal availability decreases (Yáñez and Jaksic 1978). For example, lizards (44% minimum number of individuals) were the most consumed vertebrate prey in winter, the season of lowest small mammal availability in coastal northern Chile (Simonetti *et al.* 1984). In central Chile, where small mammal availability decreases towards autumn, berries appeared in 52% of the droppings (n=127) collected in that season; while in spring, when small mammal availability is the highest, berries were present in only 18% of the faeces (n=62; Jaksic *et al.* 1980). In north-eastern Mendoza (Argentinean Monte desert), fruit (61% annual mean of weight of remains [MWR]) was represented in 35% of faeces (n=116), followed by small mammals (19% frequency of occurrence [FO], 15% MWR) – mostly the murid (*Eligmodontia typus*). Small mammal consumption decreased from autumn (28% MWR) to summer (8% MWR), while fruit consumption simultaneously increased from 59% to 71% (MWR) (González del Solar *et al.* 1997).

Chillas might favour species richness in terrestrial ecosystems by acting as key predators to competitor rodents (J. Rau unpubl.). Chillas may also have an influence on vegetation structure by restricting the low-scale spatial distribution of rodents (e.g., *Octodon degus*) through predation (Martínez *et al.* 1993), and through seed dispersal (Yáñez and Jaksic 1978; Campos and Ojeda 1997; R. González del Solar unpubl.).

Foraging behaviour Feeding behaviour appears to be rather selective in certain areas (Martínez *et al.* 1993; Novaro *et al.* 2000a) and more or less opportunistic in others (Jaksic *et al.* 1980, 1983; Simonetti *et al.* 1984). Foraging occurs mostly in open areas (Jaksic *et al.* 1980; Jiménez *et al.* 1996b). Although hunting groups of up to 4–5 individuals have been reported, grey foxes mostly hunt solitarily except perhaps at the end of the breeding season, when juveniles may join the parents in the search for food. In Parque Nacional Torres del Paine, the most common foraging behaviour consists of "slow walking, with abrupt, irregular turns through the low (<500 mm) vegetation", while "prey appear to be located by sound, sight, and smell, with the fox's ears often turned forward and back in response to sound and the muzzle turned upward sniffing into the breeze" (Johnson and Franklin 1994a). Mice are captured with a sudden leap or by rapidly digging holes (40–100mm deep, 20–40mm wide). Scavenging is common, as well as defecation on and around guanaco (*Lama guanicoe*) and goat (*Capra hircus*) carcasses (Johnson and Franklin 1994a; R. González del Solar *et al.* unpubl.).

Caching behaviour has also been reported (Johnson and Franklin 1994a).

Direct observation reports suggest that chillas are crepuscular, although they can be commonly seen in daylight (Greer 1965; R. González del Solar pers. obs.). Data from radio-collared individuals showed that they were primarily nocturnal in Parque Nacional Torres del Paine, although having a greater mean daily activity rate in summer and autumn than culpeos (Johnson and Franklin 1994c). Radio-tracking data from Reserva Nacional Las Chinchillas showed that foxes were active day and night (Jiménez 1993). As inferred from their prey, they would be most active in late afternoon and night (Yáñez and Jaksic 1978; Jaksic *et al.* 1980; R. González del Solar *et al.* unpubl.).

Damage to livestock or game The chilla has been considered a voracious predator of livestock, poultry and game (Yáñez and Jaksic 1978). In north-eastern Mendoza (Argentina), local breeders claim important goat losses due to grey fox predation. Despite this, dietary studies suggest that the remains of domestic animals found in faeces (R. González del Solar e*t al.* unpubl.) and stomachs are not only scarce but probably come from carrion, since such remains are often associated with larvae of Diptera (e.g., Calliphoridae) that usually occur in rotten carcasses (Jaksic *et al.* 1983). Furthermore, it is unlikely that one individual of such a small canid would be able to kill a healthy adult goat or sheep. A different situation concerns newly-born livestock. Predation on lambs has been observed in Reserva Nacional Las Chinchillas (Chilean matorral), where an individual fox was seen distracting a ewe while another robbed its lamb (J.E. Jiménez pers. comm.).

Adaptations

The chilla has relatively short canines and relatively long second molars, traits that suggest a tendency to include less meat and more plant and insect food in its diet (Wayne *et al.* 1989).

Social behaviour

The basic component of social organisation in Parque Nacional Torres del Paine is the breeding monogamous pair, accompanied by occasional female helpers, male dispersal, and occasional polygyny (Johnson and Franklin 1994a). Solitary individuals were seen from March to July (94% mean monthly visual observations), while pairs comprised 42% of sightings during August. Male and female of the pair maintained an exclusive home range year-round, which did not overlap with home ranges of neighbouring grey fox pairs. Intraspecific interactions displayed were few and usually aggressive. Individual home range sizes (n=23) varied between $2.0 \pm 0.2\text{km}^2$ (minimum convex polygon) and $2.9 \pm 0.3\text{km}^2$ (95% harmonic mean) (Johnson and Franklin 1994a, b, c).

Reproduction and denning behaviour

Mating occurs in August and September, and the gestation period is 53–58 days (Johnson and Franklin 1994a). In Parque Nacional Torres del Paine, mating takes place mainly in August, and 4–6 pups are born in October. Dens are located in a variety of natural and man-made places such as a hole at the base of a shrub or in culverts under a dirt road, and may be changed to a new location during the nursing period. During the first 3–4 days, the mother rarely leaves the den; during this period the male provisions her with food. Pups are cared for by both parents on an approximately equal time basis. Young foxes start to emerge from the den when they are about one month old, and start to disperse (8–65km) around 5–6 months later, i.e., at 6–7 months of age (Johnson and Franklin 1994a). Therefore, lactation lasts 4–5 months as inferred from the time when radio-tracked adults in Parque Nacional Torres del Paine were last seen with their pups (Johnson and Franklin 1994a). Age of sexual maturity is uncertain but believed to be about one year.

Two interesting phenomena concerning breeding behaviour may occur: combined litters (associated with polygyny) and the presence of female helpers. Both phenomena seem to be related to higher food availability and the possibility to raise larger litters, since an extra female would contribute by bringing more food to the den, increasing anti-predator vigilance, and/or substituting for the other female if she dies during the breeding period (Johnson and Franklin 1994a).

Competition

Interspecific competition has been suggested as a potential mechanism for explaining the distribution patterns of the chilla and the culpeo, since populations of these species coexist in a large section of their geographical distribution, consume similar vertebrate prey items, and have similar activity patterns (Fuentes and Jaksic 1979; Jiménez 1993; Johnson and Franklin 1994b, 1994c; Jiménez *et al.* 1996b). Chillas and culpeos are allopatric in northern Chile and central Argentina, whereas they are sympatric in the southern regions of both countries (Johnson and Franklin 1994b; Jiménez *et al.* 1996b; Novaro *et al.* 2000a), and in north-western Argentina (Jayat *et al.* 1999).

Fuentes and Jaksic (1979) attempted to explain this pattern of distribution in terms of character displacement of body size and altitudinal habitat partitioning (niche complementarity hypothesis). According to these authors, the similar size of both species in central Chile would be due to the chillas tending to use lower and more open habitats, while culpeos would usually occupy higher lands or more densely vegetated areas such as ravines. In the southern part of the country (south of 33°S, Reserva Nacional Las Chinchillas and Parque Nacional Torres del Paine), the rather homogeneous topographic profile would preclude habitat segregation by altitude, causing foxes to diverge in body size (culpeo: 7–12kg, chilla: 3–4kg) and partition food resources in order to lessen interspecific competition.

Other authors (Jiménez 1993; Johnson and Franklin 1994b, c) have suggested that culpeo and chilla distributions are an effect of different energy requirements and interspecific interference. Small size and lower energetic needs would allow chillas to exploit a broader spectrum of less optimal food categories and inhabit poorer habitats, from which culpeos would be excluded because of their higher energetic needs. When in sympatry, chillas would be excluded from the richest patches by culpeos, which are larger and more aggressive.

The Darwin's fox is also thought to be a potential competitor of the chilla, since initial data on the ecology of sympatric populations of these foxes suggest that they exhibit similar activity patterns, a high degree of overlap in home range and habitat use, and considerable overlap in their diets (E. McMahon pers. comm.).

Mortality and pathogens

Natural sources of mortality Little known. A culpeo was reported to attack and kill a chilla at Parque Nacional Nahuelbuta (Jiménez *et al.* 1996b). In Parque Nacional Torres del Paine, five out of 11 radio-tracked individuals lost during the study died from natural causes, and one unmarked individual was killed, but not eaten, by a puma (*Puma concolor*) (Johnson and Franklin 1994a).

Persecution Chillas are hunted on the belief that they are voracious predators of small livestock, poultry and game. The usual means are shooting, dogs, poison, snares, and foothold traps. Hunting occurs despite foxes being protected by legal regulations (Johnson and Franklin 1994a; R. González del Solar pers. obs.). Domestic dogs may also kill chillas. Around 45% of the mortality documented by Johnson and Franklin (1994a) in Parque Nacional Torres del Paine resulted from either poaching or dog attacks.

Hunting and trapping for fur Chillas have been heavily hunted for their pelts in the past (Ojeda and Mares 1982; Iriarte and Jaksic 1986), and are still hunted (though apparently with much less intensity) in Chilean and Argentinean Patagonia.

Ojeda and Mares (1982) report that 5,789,011 pelts were legally exported from Argentina generically labelled as "zorro gris" (grey fox) from 1972 to 1979. In 1979 the total amount of exports reached US$40,877,042, at US$39 per skin. At about the same time (1978), a hunter would receive US$8 for a skin in Salta Province (Ojeda and Mares 1982). From 1976 to 1979, the approximate annual number of pelts reported to have been exported ranged from 700,000 to 1,200,000. However, these extremely high numbers are difficult to interpret, and it is unlikely that the chilla was as heavily hunted as previously thought. Official reports on exports appear to have labelled as "grey fox" pelts

corresponding to three different species, namely the chilla, the crab-eating fox (*Cerdocyon thous*), and, particularly, the Pampas fox (Ojeda and Mares 1982). On the other hand, available data do not include illegal exports or internal commerce. In any case, the legal exports of chilla pelts markedly decreased from 1980 onwards. During the 1980 to 1986 period, annual exports – mostly to Germany – averaged 100,000, reaching 300,000 pelts in some years. The fox-fur market experienced another decline in the late 1980s and early 1990s, plunging from about 100,000 pelts exported in 1987 to approximately 33,000 in 1990. The number of pelts commercialised through the Fine Fur Auctions Office of Río Negro Province also decreased from about 9,000 pelts in 1988 to about 1,000 in 1991, at a rate of roughly one half per year. Whether the cause of this trend was a decline in fox populations, decreased demand for their fur, or simply the failure of the country's administration to cope with the black market is unknown. The continued decline of fox-pelt exports – even when foxes are still heavily hunted in some regions of the country – could also be linked to the particular exchange rate between domestic and foreign currency, which makes exporting goods a barely profitable alternative. In 1996, there was a brief reactivation of the fox-fur market due to commerce with Russia, but during the 1997 to 1999 period the national exports reached an annual average of only 8,000 fox (*Pseudalopex* spp.) pelts (A. Novaro and M. Funes pers. comm.; but see also illegal exports from Chile, below). The current price of a skin at Río Gallegos (Santa Cruz Province) is US$ 2–3 (A. Iriarte pers. comm.).

In Chile, there are official reports on pelt exports since 1910; however, available data correspond to voluntary declaration of legal exports, leaving aside unreported legal exports and illegal trade. Besides, as in the case of Argentina, the significance of the internal commerce is unknown. From 1926 to 1946, fox pelts were the principal native wildlife item being exported from the country, even though no hunting or commercialisation was permitted since 1929. Between 1939 and 1944 the average amount of skins exported was *c.* 24,000 every five years (see details in Iriarte and Jaksic 1986). Chilla pelts, more valuable than those of culpeo, comprised *c.* 90% of the total exports. In 1939, about 1,000 skins, plausibly including a few culpeos, were reported as being brought to market in Punta Arenas, southernmost Chile (Osgood 1943). From 1945 to 1949 (9,692 skins) until 1955 to 1959 (2,845 skins), the exports decreased dramatically, exhibiting a new increase (an average of *c.* 14,000 pelts per five-year period) during the 1960 to 1974 interval, and a final decline from 1975 to 1984 (Iriarte and Jaksic 1986). The numbers of fox skins exported from Chile are consistently lower than those reported from Argentina, even when the area of each country is considered. For the period 1970 to 1979 (see information above for Argentina), a total of 12,846 fox skins (*Pseudalopex* spp.) were exported (see Iriarte and Jaksic 1986). The ban on

chilla hunting was lifted for two years in the mid-1980s, on the basis of density estimates obtained from southernmost Chile (Durán *et al*. 1985). New regulations allowed a limited harvest of 10,000 individuals in Chile, and this was never completed, perhaps due to the difficulty in capturing enough individuals (Johnson and Franklin 1994b, Iriarte 2000). From 1985 to 1995, the chilla was the third most exported Chilean wild mammal (3,630 skins; Iriarte 2000). Illegal exports are estimated at 10,000–15,000 skins/year, especially from Magallanes Region (southernmost Chile) to Río Gallegos (southernmost Argentina). Between 1991 and 1994, a total of 996 chilla pelts or individuals were confiscated by the SAG, the Chilean Bureau of Livestock and Agriculture (Iriarte 2000). In 1996, 8,500 pelts were exported to Argentina (A. Iriarte pers. comm.).

Road kills Little data available, but frequently observed in Mendoza (Argentina), especially in summer (R. González del Solar pers. obs.).

Pathogens and parasites Stein *et al*. (1994) report the presence of nematodes in most of the stomachs (n=22) collected in Neuquén (Argentina) and suggested that the high prevalence of *Physaloptera clausa* (present in 68% of the sample), and the lower prevalence of *Toxascaris leonina* (23%) and *Protospirura numidica criceticola* (9%) may be a result of characteristics of diet and the intermediate vectors of the parasites.

Different gastrointestinal parasites were found in 63% of 22 stomachs obtained in the coastal steppe of Chubut (Argentina), during 1996 (S. Saba pers. comm.). Nematodes were present in 100% of the infected stomachs, cestodes in 14%, and acanthocephalans in 14%. Proglotides of *Echinococcus* spp. were found in the anus and faeces of a chilla captured in Reserva Nacional Las Chinchillas (J.E. Jiménez pers. comm.). Chagas' trypanosomes (*Trypanosoma cruzi*) were absent from the blood samples of two foxes captured at the same site (Jiménez and Lorca 1990).

Longevity Longevity is unknown in the wild. Individuals of undetermined age lived a maximum of five years in the Chilean National Zoo (G. González pers. comm.).

Historical perspective
In ancient times, chillas were used as food by some Argentinean aboriginal groups such as Matacos and Mocovíes, but this was not a common practice among other indigenous groups or among the "criollo" people (the offspring of European immigrants born in Argentinean territory), who only ate fox meat under extreme circumstances. Several aboriginal groups, such as Onas, Yámanas, and Tehuelches, used foxes' pelts to make clothes of different sorts. With the arrival of the Europeans and the emergence of criollos, pelts began to be used as currency. In general, the relation between chillas and human beings

has been conflictive, especially from the settling of small-livestock breeders onwards. Traditionally, Argentinean peasants have deemed foxes to be a nuisance or even a menace for poultry, sheep, goat, and game. Chillas were even considered a pest some 20 years ago in areas of Argentina, where there are still occasional attempts to legalise commerce in fox pelts and their status as a pest. For example, in 1999, small-livestock breeders' pressure led the Office for Natural Resources of Mendoza to partially lift the ban, allowing breeders to kill those individual foxes demonstrably causing trouble to them (González del Solar *et al*. 1997, unpubl.).

Argentinean indigenous folklore regards "Juan" (or "Don Juan") the fox (*Pseudalopex* spp., *Cerdocyon*), as representing shrewdness and generally challenging the authoritarian power of his rich uncle the jaguar (*Panthera onca*). However, far from being the perfect hero, Juan is selfish and never tries to unite with other weak animals. Moreover, Juan sometimes tries to deceive other small animals (e.g., the armadillo *Chaetophractus* spp.), aiming to rob them of their food or females. But, more often than not, the fox ends up fooled by his supposed victims.

Conservation status
Threats The main threat to chilla populations in the past was commercial hunting. However, inferences on the historical rate of chilla extraction are difficult, since official pelt-export reports apparently have conflated data corresponding to different species. Hunting intensity has apparently declined in recent years (see Commercial use). Illegal trapping still occurs in some regions of Chile and Argentina, mainly related to controlling predation on small livestock and apparently not as intensively as in the past (A. Iriarte pers. comm.).

Commercial use Hunted for its pelt in Argentina and Chile (see Hunting and trapping for fur).

Occurrence in protected areas
— *Argentina:* Uncertain. Present in at least six protected areas in central west Argentina: Parque Nacional Talampaya, Parque Nacional Ischigualasto, Reserva Provincial Bosque Telteca, Parque Nacional Las Quijadas, Man and Biosphere Reserve of Ñacuñán, Reserva Porvincial La Payunia;
— *Chile:* present in 30 Wildlife Protected Areas (WPA) from a total of 49 surveyed. However, 40% of those 30 WPAs are smaller than the 115km² needed to sustain a minimum viable population (500 individuals). Estimates of local extinctions in WPAs from central Chile reach 50% (see Simonetti and Mella 1997). The most important Chilean WPAs in which chillas occur include: Parque Nacional Lauca, Parque Nacional Puyehue, Parque Nacional Vicente Pérez Rosales, Parque Nacional Torres del Paine.

Protection status CITES – Appendix II.

Current legal protection Resolution 144/83 of the former National Secretary of Natural Resources and Sustainable Development of Argentina categorises this species as "In Danger". Chillas are totally protected in Mendoza, Catamarca, and San Luis, while in the continental provinces of Patagonia and in Tierra del Fuego, hunting and fur trading are legal (A. Novaro and M. Funes pers. comm.).

In Chile, the passing of the 1972 furbearer's protection law appears to have curtailed the exports of pelts (Iriarte and Jaksic 1986; Iriarte 2000; but see above). Currently, all Chilean populations are protected by law N° 19,473 [1996], except for those from Tierra del Fuego (XII Region), where a maximum of 10 individuals/day/hunter are allowed from May 1 to July 31 (A. Iriarte pers. comm.).

Conservation measures taken Efforts are being made in Argentina to concentrate the relevant biological, legal and commercial information on the species in an attempt to design a plan for sustainable use and conservation (A. Novaro and M. Funes pers. comm.).

Occurrence in captivity
Chillas occur in many zoos of Argentina and Chile, but details of breeding in captivity are not known.

Current or planned research projects
A. Novaro and M. Funes (Centro de Ecología Aplicada del Neuquén, Neuquén, Argentina) have been coordinating an ongoing survey of Patagonian carnivores in Argentina since 1992. The programme includes annual surveys of chilla population trends and periodic meetings attended by specialists, government officials, and pelt-market entrepreneurs.

R. González del Solar, S. Puig and F. Videla (Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina) are conducting a dietary study on the species in the Argentinean central Monte desert.

J. Rau (Universidad de Los Lagos, Osorno, Chile) and A. Muñoz-Pedreros (Universidad Católica de Temuco, Temuco, Chile) are also involved in a dietary study in the Araucania Region (southern Chile), and at the time of writing, were finishing their analysis of a large sample of chilla droppings.

A. Mangione and B. Núñez (Universidad Nacional de San Luis, San Luis, Argentina) are carrying out research on the nutritional ecology of chillas.

F. Jaksic (Universidad Católica de Chile, Santiago, Chile), J. Jiménez. (Universidad de Los Lagos, Osorno, Chile) and collaborators have conducted monitoring of chilla food habits since 1987 in Reserva Nacional Las Chinchillas.

E. McMahon (University of Massachusetts, Amherst, USA) is coordinating a study of niche relationships among

the three Chilean foxes (*P. griseus*, *P. culpaeus* and *P. fulvipes*) at Parque Nacional Nahuelbuta.

Gaps in knowledge
The need for a deeper understanding of the biology of the chilla has been repeatedly emphasised by Argentine as well as by Chilean studies (e.g., Johnson and Franklin 1994b; González del Solar *et al*. 1997). Reliable information is needed especially with regard to those biological aspects required for population management leading to sustainable use and conservation: population-dynamics, incidence of parasites and other diseases, and research on the role of chillas in small-livestock mortality.

Core literature
Campos and Ojeda 1996; Durán *et al*. 1985; González del Solar *et al*. 1997; Jaksic *et al*. 1980; Johnson and Franklin 1994a, b, c; Medel and Jaksic 1988; Rau *et al*. 1995.

Reviewers: Fabián Jaksic, Jaime Jiménez, Mauro Lucherini, Andrés Novaro. **Editors:** Claudio Sillero-Zubiri, Michael Hoffmann.

3.7 Pampas fox
Pseudalopex gymnocercus
(G. Fischer, 1814)
Least Concern (2004)

M. Lucherini, M. Pessino and A.A. Farias

Other names
English: Azara's fox, Azara's zorro; **French:** renard d'Azara; **German:** Pampasfuchs; **Italian:** volpe Azara, volpe grigia delle Pampas; **Portuguese:** graxaim do campo, cachorro do campo, rasposa do mato; **Spanish:** zorro pampeano (Argentina); zorro de patas amarillas (Bolivia); zorro de Azara, zorro Pampa, zorro del país, zorro de campo (Uruguay); **Indigenous names:** Guaraní: aguara cha'I (Argentina, Paraguay); Mapuche: ngürü (Argentina); Quechua: atój (Argentina, Bolivia).

Taxonomy
Procyon gymnocercus G. Fischer, 1814. Zoognosia, 3: xi, 178. Type locality: "Paraguay", restricted by Cabrera (1958) to "a los alrededores de Asunción" [Paraguay, *c*. 25°S, 57°W].

The taxonomic status of the Pampas fox and other related species is controversial. This canid was first included in the genus *Canis* by Linnaeus (1758) and in *Pseudalopex* by Burmeister (1854). However, it was treated as *Dusicyon* by Cabrera (1958) and then by Langguth (1969), who gave *Pseudalopex* subgeneric rank. Later, Langguth (1975) and Van Gelder (1978) placed *Pseudalopex* as a subgenus of *Canis*, excluding *Dusicyon australis*. Clutton-Brock *et al*. (1976) included all these taxa and *Pseudalopex vetulus* in *Dusicyon*. However, Berta (1988) gave full generic recognition to *Pseudalopex*, arguing that the species falling into this genus (*culpaeus*, *griseus, gymnocercus*, *sechurae*, and *vetulus*) share derived features that support a single origin for those taxa, separated from other genera now extinct and more closely related with *Dusicyon australis*. Recently, Zunino *et al*. (1995) proposed that *P. griseus* and *P. gymnocercus* represent clinal variants of *Lycalopex gymnocercus*. They considered *Lycalopex* as the valid genus name because it would have been used by Burmeister two years earlier. Chromosome analyses carried out by Gallardo and Formas (1975), and Vitullo and Zuleta (1992) supported this proposal (see Wozencraft 1993 and Zunino *et al*. 1995 for detailed comments).

Chromosome number: 2n=74 (Wayne *et al*. 1987).

Description
A medium-sized South American fox, smaller than the culpeo (*P. culpaeus*). The head, somewhat triangular in shape, is reddish with a pale grey to white ventral surface.

Adult Pampas fox, thought to be male. Lihuel Calel National Park, La Pampa, Argentina, 2001.

Marcelo Dolsan (via Marcelo Pessino)

Table 3.7.1. Body measurements for the Pampas fox.		
	La Pampa province, Argentina (Crespo 1971)	**Buenos Aires province,** Argentina (E. Luengos Vidal and M. Lucherini unpubl.)	**Colonia Department**, Uruguay (Cravino *et al.* 2000).
HB male HB female	648mm (597–700) n=10 621mm (535–683) n=16	660mm (620–740) n=20 630mm (505–720) n=18	
T male T female	352mm (320–365) n=10 319mm (270–356) n=16	342mm (280–380) n=24 325mm (250–410) n=20	
HF male HF female	140mm (135–155) n=10 128mm (115–145) n=16	145mm (130–160) n=22 135mm (115–170) n=16	
E male E female	86mm (80–90) n=10 84mm (80–90) n=16	74mm (61–90) n=24 73mm (62–83) n=18	
WT male WT female	4.6kg n=116 4.2kg n=163	5.9kg (4–8) n=24 4.7kg (3–5.7) n=20	5.9kg n=11 4.6kg n=8

The ears are triangular, broad and relatively large; they are reddish on the outer surface and white on the inner surface. The rostrum is narrow, ventrally pale, black in the chin and reddish to black dorsally. The eyes, near frontally placed, take an oblique appearance. The body, back and sides are grey, like the outer surface of the hind limbs, which show on the lower rear side a characteristic black spot. A dark band, almost black, runs longitudinally along the trunk and tail dorsum. The tail is relatively long, bushy and grey, being black at the tip (Table 3.7.1). The belly and the inner surface of the limbs are pale grey to white. The outer surface of the front limbs and the distal surface of the hind limbs are reddish. Smaller size and lack of interparietal crest distinguish its skull from that of the culpeo (Zunino *et al.* 1995). Dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Three subspecies have been proposed (Massoia 1982). Their geographic limits are not precise and Massoia (1982) suggested that along their borders they could coexist and interbreed. This author did not clarify the subspecific status of the Pampas foxes from Entre Ríos Province in Argentina, and there is no data regarding the taxonomic position of Bolivian foxes.
— *P. g. gymnocercus* (subtropical grasslands of north-eastern Argentina – southern Misiones, northern Corrientes and eastern Formosa provinces – Uruguay, Paraguay and south-eastern Brazil, from Paraná to Rio Grande do Sul estates).
— *P. g. antiquus (*Pampas grasslands, Monte scrublands and Espinal open woodlands of central Argentina, from Córdoba and San Luis provinces to the Río Negro, and from the Atlantic coast to a poorly defined limit west of the Salado-Chadilevú River).
— *P. g. lordi* (restricted to the Chaco-Mountain Tropical Forest ecotone in Salta and Jujuy provinces of Argentina). The smallest subspecies, with pelage smoother and brighter, denser in the tail, and more contrasting in colour than in the other subspecies.

There are characteristic dark (almost black) spots in the pectoral and axilar regions of the body. Its skull is smaller than in the other subspecies, average length and weight being 924mm and 4.3kg, respectively (Massoia 1982), compared with 960mm and 5.9kg in *P. g. gymoncercus* (Barlow, in Redford and Eisenberg 1992) and 967mm and 4.4kg in *P. g. antiquus* (Crespo 1971).

Similar species Chilla (*Pseudalopex griseus*): overlaps with the south-eastern portion of the range of the Pampas fox; similar in colour and body proportions, but usually smaller and with a more uniformly grey pelage and shorter

Figure 3.7.1. Current distribution of the Pampas fox.

legs (Clutton-Brock *et al.* 1976; Novaro 1997a). Crab-eating fox (*Cerdocyon thous*): occurs in the northern part of the range; similar in size, but with shorter hair and rostrum, and dark-coloured, shorter, legs (Redford and Eisenberg 1992).

Current distribution
The Pampas fox inhabits the Southern Cone of South America (Figure 3.7.1), occupying chiefly the Chaco, Argentine Monte, and Pampas eco-regions. From eastern Bolivia, western Paraguay and east of Salta, Catamarca, San Juan, La Rioja and Mendoza provinces in Argentina, to the Atlantic coast; and from south-eastern Brazil to the Río Negro Province, Argentina, in the south. Information on the limits of its distribution and the extent to which it overlaps with congeneric species is uncertain.

Range countries Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Redford and Eisenberg 1992).

Relative abundance
Little quantitative data are available on the abundance of Pampas fox populations. However, it would be either abundant or common in most areas where the species has been studied.

In the coastal area of central Argentina, a study based on scent-stations found that Pampas fox signs were more frequent than the common hog-nosed skunk (*Conepatus chinga*) and grison (*Galictis cuja*) (García 2001). Similarly, the frequency of observation of Pampas fox was higher than that of skunk, grison, and the Geoffroy's cat (*Oncifelis geoffroyi*) in a Sierra grassland area of Buenos Aires Province (M. Lucherini *et al.* unpubl.). In areas where the Pampas fox is sympatric with the crab-eating fox, the former would be more abundant in open habitats, while the latter would more frequently inhabit woodland areas.

The Pampas fox seems to be tolerant of human disturbance, being common in rural areas, where introduced exotic mammals, such as the European hare (*Lepus europaeus*), could form the bulk of its food intake (Crespo 1971; Farias 2000a; D. Birochio and M. Lucherini unpubl.).

Estimated populations/relative abundance and population trends The highest density has been reported for the Bañados del Izozog in the Bolivian Chaco (1.8 individuals/km²; Ayala and Noss 2000). In an Argentine Pampas area, Crespo (1971) found a density of 1.04 foxes/km², while Brooks (1992) estimated a density of 0.64 fox groups/km² for the Paraguayan Chaco, where fox abundance appeared to be correlated with annual rodent abundance. In La Pampa Province, Argentina, data from scent stations showed a stable tendency in the abundance of this species between 1992 and 1998 (Table 3.7.2) (R. Dosio and M. Pessino unpubl.).

Habitat
The Pampas fox is a typical inhabitant of the Southern Cone Pampas grasslands. It prefers open habitats and tall grass plains and sub-humid to dry habitats, but is also common in ridges, dry scrub lands and open woodlands (Brooks 1992; Redford and Eisenberg 1992). In the driest habitats in the southerly and easterly parts of its range, the species is replaced by the chilla. Where its range overlaps with that of the crab-eating fox, the Pampas fox would select more open areas. Apparently, the Pampas fox has been able to adapt to the alterations caused by extensive cattle breeding and agricultural activities to its natural habitats.

Food and foraging behaviour
Food Like most other medium-sized foxes, the Pampas fox is a generalist and adaptable carnivore. Its diet shows great geographic variation and may include both wild and domestic vertebrates (particularly rodents and birds), fruit, insects, carrion and garbage. Based on stomach contents, wild mammals and sheep appeared to be the two most important food items in Uruguay (Cravino *et al.* 1997), while in La Pampa Province, Argentina, European hares and rodents were the most important food items, followed by birds and carrion (Crespo 1971). Recent studies in Buenos Aires Province, Argentina, using faecal analysis, report high frequencies of occurrence of rodents and birds, but also of insects and fruits (Farias 2000a; D. Birochio and M. Lucherini unpubl.) and crabs (in a coastal

Table 3.7.2. The status of Pampas foxes in various regions (Population: A=abundant, C=common, X=present but abundance unknown; Trend: I=increasing, S=stable). When shown, numeric abundance indicated as rough estimates based on the densities given above.

Region	Protected areas		Other areas		Total	
	Population size	Trend	Population size	Trend	Population size	Trend
La Pampa (Argentina)	150	S/I	150,000	S	>150,000	S/I
Buenos Aires (Argentina)	C	S/I	C	S/I	C	S/I
Uruguay	X	?	C	?	C	?
Rio Grande do Sul (Brazil)	X	?	C	?	C	?
Paraguayan Chaco	X	?	C	?	180,000	?
Bolivian Chaco	X	?	C	?	350,000	?

area; Vuillermoz and Sapoznikow 1998). However, in a study where ingested biomass was estimated, mammal carrion, rodents and hares were the main dietary components (Farias 2000a). Seasonal and local variations in diet are likely connected to variations in food availability (Vuillermoz and Sapoznikow 1998; Farias 2000a; García 2001; D. Birochio and M. Lucherini unpubl.). No sex/age differences in food habits have been reported, but occasional observations of food remains at den sites (M. Lucherini pers. obs.) suggest that cubs feed mostly on small- to medium-sized vertebrate prey.

Foraging behaviour The Pampas fox is a typical solitary and opportunistic carnivore, foraging both during the day and night (E. Luengos Vidal unpubl.), although feeding activity would become mainly nocturnal where heavily hunted. Large, highly concentrated food resources (i.e., large mammal carcasses) may cause several individuals to gather, possibly through movements exceeding the borders of normal home range size (E. Luengos Vidal and M. Lucherini unpubl.). Food caching behaviour has been observed, apparently related to an increase in the availability of a food resource, i.e., rodents (J. Pereira pers. comm.).

Damage to livestock or game Predation on domestic stock traditionally has been one of the main reasons to justify this fox's persecution by rural people. Nevertheless, it is likely that mainly adult sheep are scavenged, while some studies found evidence of predation on newborn lambs, but concluded that foxes were only a secondary factor of lamb mortality (2.9% of total lamb mortality in Uruguay, Cravino *et al.* 1997; 4.1% and 6.9% in Argentina, Bellati 1980 and Olachea *et al.* 1981, respectively), especially when compared to climate (Cravino *et al.* 1997). High levels of predation on poultry have never been supported by observations or dietary studies. Similarly, although Pampas foxes are commonly accused of causing important reductions in game populations, particularly by feeding on eggs and chicks of ground-nesting birds, there is little data to support this view (Vuillermoz and Sapoznikow 1998; Farias 2000a).

Adaptations
Very little is known about the behavioural, morphological and physiological adaptations of this species.

Social behaviour
Pampas foxes are thought to form monogamous pairs. However, they spend most of their time solitarily: in the Paraguayan Chaco (Brooks 1992) and La Pampa Province, Argentina (Branch 1994) 88–93% of observations, respectively, were of single individuals. Pairs are frequently observed from mating until cubs leave the natal den.

In a Sierra grassland area, the home ranges of two adult males have been estimated at 40 and 45ha (E. Luengos Vidal and M. Lucherini unpubl.). In the same area, foxes showed a relatively low frequency of re-use of scat marking sites, and a tendency to mark latrines used by Geoffroy's cats and common hog-nosed skunks (M. Lucherini and C. Manfredi unpubl.). Defecation site features suggest that scats are used in intraspecific communication (M. Lucherini and D. Birochio unpubl.; A.A. Farias pers. obs.).

The long-distance calls of Pampas foxes, which show a peak in frequency during the breeding period, may serve to maintain contact between pair members, as well as in territorial behaviour (Branch 1994). During the breeding season, both pair mates have been observed using a brief and repeated alarm call when detecting potential threats to the young (M. Lucherini pers. obs.).

Reproduction and denning behaviour
In central Argentina, cubs are born in spring, from October to December. Gestation lasts 55–60 days, and litter size ranges from 3–5 (Crespo 1971; M. Lucherini and E. Luengos Vidal unpubl.). Dens may be located in a variety of shelters, e.g., a hole at the base of a tree trunk, in armadillo dens, or among rocks. Cubs are frequently moved to a new location (M. Lucherini and E. Luengos Vidal pers. obs.). Young stay at the den for the first three months. Both pair mates have been observed to guard the den (M. Lucherini pers. obs.) and males provide food to cubs and females at the den. Females may breed at 8–12 months of age. In a Sierra Pampas area, reproductive dens did not appear to be re-used in following years (M. Lucherini pers. obs.).

Competition
In the Lihuel Calel National Park, Argentina, remains of armadillos (*Zaedyus pichy* and *Chaetophractus villosus*), plain viscachas (*Lagostomus maximus*), small rodents (*Ctenomys* spp., *Galea musteloides*) and European hares appeared in the droppings of both the puma (*Puma concolor*) and Pampas fox (M. Pessino unpubl.).

Partial dietary overlap has also been found with the Geoffroy's cat, a similar-sized carnivore whose range widely overlaps that of the Pampas fox. In Buenos Aires Province, most of the food items in the droppings of these two carnivores (e.g., *Cavia, Oligorizomys* and *Akodon* rodents), European hares, small passerines and doves were the same, although their frequency of occurrence was different (Vuillermoz and Sapoznikow 1998, M. Lucherini and C. Manfredi unpubl.). However, signs of presence, suggest that spatial segregation between the Pampas fox and Geoffroy's cat may occur in Mar Chiquita, Atlantic coast of Buenos Aires Province (A.A. Farias unpubl.).

In Uruguay, although temporal segregation has been suggested, a very large food niche overlap was reported between the Pampas fox and crab-eating fox (Cravino *et al.* 2000).

Very little information is available on two other species that share a large proportion of their ranges with the Pampas fox: the Pampas cat (*Oncifelis colocolo*) and the common grison. Some data from scat analysis suggest extensive food niche overlap between the Pampas fox and the grison in a Sierra Pampas area (M. Lucherini *et al.* unpubl.).

Mortality and pathogens

Natural sources of mortality Little is known about natural causes of mortality. Pampas fox remains have been found in puma scats collected in the Lihuel Calel National Park, Argentina (Wander *et al.* unpubl.). Kills by feral dogs have also been reported (A.A. Farías pers. obs., A. Canepuccia and D. Queirolo Morato pers. comm.).

Persecution In Argentina and southern Brazil (Rio Grande do Sul State, C. Indrusiak pers. comm.), the Pampas fox has been considered an important predator of sheep and goats, and consequently has been actively persecuted by livestock ranchers. In the provinces of La Pampa, Buenos Aires, and San Luis, control campaigns were carried out against this species between 1949 and the early 1970s, in order to reduce economic losses caused by predation. As a result, 361,560 individuals were killed using different methods, including leg-hold traps, selective traps with toxic cartridges, shooting, dogs and poisoned baits (Godoy 1963; M. Pessino and R. Sosa unpubl.). Pampas foxes were also hunted by the bounty system in the provinces of San Juan, Catamarca, and Río Negro during 1959 and Córdoba during 1960.

In 2001, the bounty system was used again for the control of this species in La Pampa Province, while fox hunting has been re-opened in Buenos Aires Province. In Brazil, although the fox is protected by law, control measures are regularly taken by sheep breeders with no legal permission (C. Indrusiak pers. comm.). In Uruguay, special hunting authorisation may be easily obtained by the government to control predation on sheep herds (Cravino *et al.* 2000).

Hunting and trapping for fur Rural residents have traditionally hunted the Pampas fox for its fur, and this activity has been an important source of income for them. From 1975 to 1985, *Pseudalopex* fox skins (mostly belonging to *P. gymnocercus*; García Fernández 1991) were among the most numerous to be exported legally from Argentina (Chebez 1994). However, exports have declined from the levels of the early and mid-1980s mainly due to a decline in demand (Novaro and Funes 1994). From 1997 to 1999, national fox pelt exports averaged a

mere 8,000 specimens per annum (M. Elisetoh unpubl.). In Uruguay, because of their relatively high commercial value, illegal trade of *P. gymnocercus* fur is still widespread (D. Queirolo Morato pers. comm.), while in Paraguay no illegal fox pelts were confiscated during 1995 to 2000 (J. Cartes pers. comm.).

Road kills Pampas foxes are frequently struck by cars (N. Fracassi and D. Queirolo Morato pers. comm.). However, no data are available in order to establish the impact of road kills on fox populations.

Pathogens and parasites Animals kept in captivity are susceptible to parvovirus and distemper (F. Baschetto pers. comm.). Ectoparasites in the Pampas fox include ticks (*Amblyomma maculatum, A. auriculare*) and fleas (*Pulex irritans, Ctenocephalides felix, Hectopsylla broscus, Malacopsylla grossiventris, Tiamastus cavicola, Polygenis* spp.). In a sample of 132 foxes, the most common parasites were *A. maculatum*, *M. grossiventris* and *P. irritans* (A. Bischoff de Alzuet unpubl.). Recorded endoparasites include *Taenia pisiformis* (*Taenidae*), *Dipylidium caninum* (*Dilepididae*), *Joyeuxiella* spp. (*Dilepididae*), and many species from the *Cestoda* Class. Nematodes such as *Molineus felineus* (*Trichostrongylidae*), *Toxocara canis* (*Ascariidae*), *Ancylostoma caninum* (*Ancylostomidae*), *Rictularia* spp. (*Rictularidae*), and *Physaloptera* spp. (*Physalopteridae*) (Led *et al.* 1970), as well as *Echinococcus granulosus* and *E. cepanzoi*, have also been noted. Another internal parasite, *Athesmia foxi* (*Trematoda: Dicrocoeliidae*), was found in the small intestine. Cases of *Sarcoptes scabiei* infection have also been reported (S. Deem pers. comm.).

Longevity Few individuals are likely to live more than a few years in the wild, but a captive animal lived nearly 14 years (Jones 1982).

Historical perspective

Fox furs were used by native communities for making shawls. When white traders appeared, fox furs became valued merchandise. Rural people inhabiting La Pampa Province use Pampas fox fat for medicinal purposes (M. Pessino pers. obs.). Among natives and settlers, foxes in general, and particularly the Pampas fox, have been the main characters of numerous stories and proverbs, which have been passed down from generation to generation. Also, these communities have interpreted their presence and behaviour in certain circumstances as omens.

Conservation status

Threats The implementation of control measures (promoted by ranchers) by official organisations, coupled with the use of non-selective methods of capture, represent actual threats for the Pampas fox. Fox control by

government agencies involves the use of bounty systems without any serious studies on population abundance or the real damage that this species may cause. In rural areas, direct persecution is also common, even where hunting is officially illegal.

Most of the species' range has suffered massive habitat alteration. For instance, the Pampas, which represents a large proportion of the species' distribution range, has been affected by extensive cattle breeding and agriculture. Approximately 0.1% of the original 500,000km² range remains unaffected. However, due to the species' adaptability, the Pampas fox seems able to withstand the loss and degradation of its natural habitat, as well as hunting pressure. Since no studies are available on its population dynamics in rural ecosystems, caution is required, since the sum of these threats may eventually promote the depletion of fox populations. Hunting pressure has resulted in diminished populations in the provinces of Tucumán (Barquez *et al.* 1991) and Salta (Cajal 1986) of north-western Argentina.

Commercial use Considering that the Pampas fox trade is banned, no statistical information on the fur harvest is available. Different authors have pointed out that Argentine exports corresponding to the chilla historically included other species, such as the crab-eating fox and the Pampas fox (Ojeda and Mares 1982; García Fernandez 1991).

Occurrence in protected areas
— In Uruguay, the Pampas fox has been reported in many protected areas which are included in a law passed in 2000 establishing the national protected areas system. However, this law has not been implemented yet (R. Rodríguez-Mazzini and D. Queirolo Morato pers. comm.).
— *Argentina:* National Parks Chaco (Chaco), Mburucuyá (Corrientes), Calilegua (Jujuy), El Palmar (Entre Ríos), Lihuel Calel (La Pampa) (Heinonen Fortabat and Chebez 1997), E. Tornquist and Bahía Samborombón Provincial Parks, and Campos del Tuyú Wildlife Reserve (Buenos Aires). The Pampas fox is the least well represented among the *Pseudalopex* species in the National Park system of Argentina (Heinonen Fortabat and Chebez 1997).

Protection status CITES – Appendix II.
The Argentina Red List of Mammals (Diaz and Ojeda 2000) assigned the Pampas fox to the "Least Concern" category.

Current legal protection In Argentina, it was declared not threatened in 1983, and its trade was prohibited in 1987. However, this species continues to be hunted and demand for its fur exists.

In Uruguay, all foxes are protected by law, and the only legal exception is the government's so-called "control hunting permission", which does not allow the taking of animals for the fur trade. The situation is very similar in Paraguay.

Conservation measures taken None.

Occurrence in captivity
In Argentina, the Pampas fox has been successfully bred in captivity and presently is the best represented carnivore species in captivity in the country (Aprile 1999).

Current or planned research projects
In the Argentina Pampas grassland, the GECM (Grupo de Ecología Comportamental de Mamíferos), Universidad Nacional del Sur, Argentina, is presently comparing the abundance, spatial behaviour and social organisation as well as food niche of the Pampas fox in a protected site versus a site affected by farming.

A. Farias and V.B. García (Pontificia Universidad Católica de Chile) have started studies on the trophic ecology of the Pampas fox in two coastal areas of Buenos Aires Province.

S.J. O'Brien and W.E. Johnson (National Cancer Institute, USA) have proposed a DNA-based study on the phylogeny of *Pseudalopex* foxes.

S. González *et al.* (División Citogenética-IIBCE, Unidad Asociada Facultad de Ciencias, Uruguay) initiated a study aimed at determining the genetic variability of *P. gymnocercus* and the crab-eating fox in wooded areas in northern and eastern Uruguay in order to test whether hybridisation occurs.

Gaps in knowledge
Most aspects of the species' ecology remain unknown. Studies on population dynamics in agricultural land, impact and sustainability of hunting, effect of predation on livestock and game species are needed, particularly for an appropriate management of wild populations. In addition, resolution of the species' taxonomic status is essential.

Core literature
Crespo 1971; Massoia 1982; Zunino *et al.* 1995.

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3.8 Sechuran fox
Pseudalopex sechurae (Thomas, 1900)
Data Deficient (2004)

C. Asa and E.D. Cossíos

Other names
English: Sechura desert fox, Peruvian desert fox; **French:** renard de Sechura; **German:** Sechurafuchs, perufuchs; **Spanish:** perro de monte de Sechura, zorra Pampera (Ecuador), zorro costeño, zorro de Sechura, Pacha zorro, Juancito (Peru); **Indigenous names:** Pacha zorro (Cajamarca Department); Moche and Olmo: Pacter, Pacterillo (Peru).

Taxonomy
Canis sechurae Thomas, 1900. Ann. Mag. Nat. Hist., ser. 7, 5:148. Type locality: "Desert of Sechura, N.W. Peru… Sullana".

Simpson (1945) included the Sechuran fox in the genus *Dusicyon*. Langguth (1969) also considered *Pseudalopex* a subgenus of *Dusicyon*, although he subsequently (1975) regarded it as a subgenus of *Canis* (as did Van Gelder 1978). Clutton-Brock *et al*. (1976) also included the species in the genus *Dusicyon*, but did not recognise subgenera. Berta (1987) recognised *Pseudalopex* as a distinct genus including the Sechuran fox. This treatment was followed by Wozencraft (1993) and Nowak (1999).

Chromosome number is not known.

Description
The Sechuran fox is the smallest species of the genus *Pseudalopex* (Huey 1969) (Table 3.8.1). The head is small, with relatively long ears (about 2/3 the length of the

Table 3.8.1. Body measurements for male Sechuran foxes from Coto de Caza El Angolo, Piura (CDC Universidad Nacional Agraria Molina).

HB	670mm (500–780) n=4
T	292mm (270–340) n=4
SH	288mm (220–360) n=4
E	70mm (60–80) n=4
WT	3.6kg (2.6– 4.2) n=4

head) and a short muzzle. Face is grey, and there is a rufous-brown ring around the eyes (Thomas 1900). The ears may be reddish on the back; the dark muzzle may have paler hairs around the lips. The pelage consists of pale underfur with agouti guard hairs, while the underparts are fawn or cream-coloured. There is sometimes a dark stripe down the back. The frontal limbs (up to the elbows) and the back limbs (up to the heels) are usually reddish in colour. The tail is relatively long and densely furred, ending in a dark tip. The dental formula is 3/3-1/1-4/4-2/3=42. The carnassials are slightly smaller, and the grinding teeth larger, than in allied forms (Thomas 1900); the canines are "fox-like" (Clutton-Brock *et al*. 1976).

Subspecies Monotypic.

Similar species Chilla (*Pseudalopex griseus*): usually presents a rufous tinge on the face and muzzle and a black spot on the chin; muzzle slightly narrower. Hoary fox (*P. vetulus*): rufous face and muzzle; well-marked dark stripe along the dorsal line of the tail; general colour normally brighter.

Adult male Sechuran fox. Lambayeque, Peru, 2001.

Daniel Ascensios

Current distribution

The Sechuran fox can be found in the coastal zones of north-western Peru and south-western Ecuador, between 3 and 12°S (Figure 3.8.1). In Peru, it is distributed on the western slope of the Andes between the frontier with Ecuador and Lima. Specimens living further south may be the chilla or another species not yet described (E. Vivar pers. comm.).

Range countries Ecuador, Peru (Eisenberg and Redford 1999).

Relative abundance

Little known. This species was judged by Grimwood (1969) as abundant and not in need of protection. The species is easily observed in rural areas and disturbed environments from Piura department to La Libertad department in Peru. Surveys based on footprints in Coto de Caza El Angolo in Piura, Peru, show an average of 12.6 foxes per km (CDC 1989). The Sechuran fox is uncommon in Ecuador.

Estimated populations/relative abundance and population trends

| Table 3.8.2. The status of Sechuran foxes in various regions (Population: A=abundant, C=common, U=uncommon; X=present but abundance unknown, ?=current presence not confirmed; Trend: S=stable, D=declining, ?=unknown).		
Country	**Population size**	**Trend**
Ecuador	U	D
Peru	A	S
Tumbes Department	C	S
Piura Department	A	S
Lambayeque Department	A	S
La Libertad Department	A	S
Cajamarca Department	C	S
Ancash Department	X	?
Ica Department	?	?
Lima Department	U	?

Habitat

The Sechuran fox occupies habitats ranging from sandy deserts with low plant density to agricultural lands and dry forests (Cabrera 1931; Huey 1969; Langguth 1975).

Food and foraging behaviour

Food A generalist, omnivorous species, the Sechuran fox varies its diet opportunistically, preferentially consuming vertebrate prey or carrion when available, but often depending predominantly on seeds or seed pods. Studies during late winter and early spring in the inland Sechuran desert found droppings containing mainly the remnants of seeds or seed pods of *Prosopis juliflora* (algarrobo), *Capparis scabrida* (zapote) and *C. avicennifolia* (vichayo)
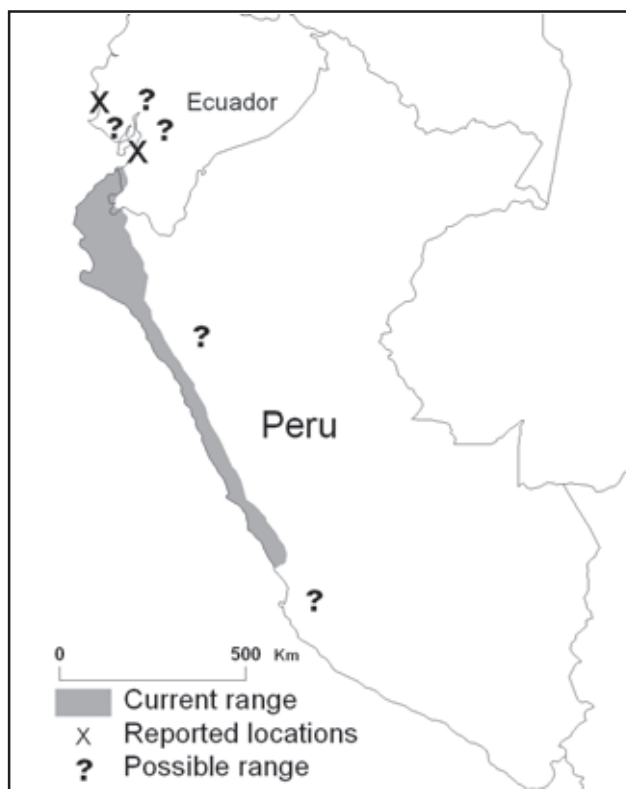
Figure 3.8.1. Current distribution of the Sechuran fox.

(Huey 1969; Asa and Wallace 1990). Seeds in faeces were not digested, indicating that the syrupy matrix surrounding the seeds may be the actual source of nourishment. In a germination study (C. Asa unpubl.), seeds recovered from faeces sprouted earlier than those gathered from the ground, suggesting that the foxes not only act as seed dispersers, but affect the ability of the seeds to germinate rapidly when sporadic rains occur.

Fox droppings along the coast contained crabs and several bird species, probably obtained as carrion that washed ashore (Huey 1969; Asa and Wallace 1990). However, following the El Niño rains of 1983/1984, fox droppings revealed a dramatic dietary shift to grasshoppers and mice (*Phyllotis gerbillus*) as these prey became more abundant (Asa and Wallace 1990). During summer in Reserva Nacional Lachay (coastal loma in central Peru), the main foods were insects, scorpions (*Carica candicans*), fruits and rodents (Asa and Wallace 1990). The lack of standing water in the inland desert habitat suggests that the foxes can survive without drinking. However, foxes may lick condensation from vegetation on foggy mornings.

Foraging behaviour The Sechuran fox is primarily nocturnal. Radio-telemetry data indicated that individuals emerged from daytime sleeping dens in rocky buttes before sunset and remained active through most of the night before re-entering dens at dawn (Asa and Wallace 1990).

The phases of the moon did not influence this activity pattern, perhaps because foxes were consuming seeds and seed pods rather than hunting. Occasionally, foxes can be seen during the day (Huey 1969; C. Asa and M.P. Wallace pers. obs.). No food caching has been recorded.

Damage to livestock or game Damage to poultry and guinea pigs has not been measured, but some rural habitants (principally of Lambayeque, La Libertad and Piura departments, Peru) often report such damage, principally from September to January (D. Cossíos unpubl.). There are no reports of damage to game.

Adaptations
In addition to the species' nocturnal activity, the small size and somewhat large ears of the Sechuran fox may also be adaptation to desert life. The species' ability to exist in areas with no standing water also attests to its adaptation to arid habitats.

Social behaviour
Little is known about the social behaviour of this species. Groups larger than three individuals are rare, and usually only observed in cases where food sources are concentrated. Of four radio-collared foxes, the home range of one adult male adjoined that of one adult female accompanied by two almost full-grown juveniles (one male and one female) (Asa and Wallace 1990). However, each individual foraged separately during the night and occupied separate, though nearby, dens during the day.

Reproduction and denning behaviour
Birdseye (1956) reported births occurring primarily in October and November. Abdominal distension suggested that one adult radio-collared female may have been pregnant when captured in August (Asa and Wallace 1990). If this female was indeed pregnant, it is significant that the adult male in the adjoining territory did not associate with her at that time, as might be expected if he was her mate. The male in her territory appeared to be juvenile, but could possibly have been her mate. However, the other juvenile within her territory was female, suggesting that both juveniles may have been her offspring from the previous breeding season.

Competition
Occasional competition with the culpeo (*P. culpaeus*) may arise when this species moves to the coast. There is probably competition with the chilla at the southern limit of its range.

Mortality and pathogens
Natural sources of mortality According to local reports boa constrictors prey on pups. Predation by other carnivores, like pumas (*Puma concolor*), other felids and culpeo foxes is possible in some areas, but pumas and jaguar (*Panthera onca*) are now uncommon in the Sechuran fox´s habitat. Large raptors in these areas normally prey on smaller animals (e.g., *Geranoetus melanoleucus*, *Sarcorhamphus papa*, *Buteo* spp., and others).

Persecution The Sechuran fox is persecuted in some zones where it is considered a predator of poultry, guinea pigs and other domestic animals.

Hunting and trapping for fur Although the use of this species for fur is not permitted, the illegal practice does exist though on a very small scale. Illegal hunting and trapping for making amulets and dissecting specimens is more extensive.

Road kills Road kills are common in northern Peru, but the number of the road kills is not estimated.

Pathogens and parasites Not known.

Longevity Not known.

Historical perspective
Shamans in northern Peru use dissected specimens or parts of the fox's body (e.g., paws, tails or heads), to perform traditional magic-religious rituals.

Conservation status
Threats The most important threats are from the market for handicrafts and amulets and from persecution because of damage to livestock. In Peru, the rural inhabitant's attitude towards the species is one of persecution (68.3% of correspondents) or indifference (31.7%). The stated reasons for persecution were due to damage on domestic fowl and guinea pigs (65% of correspondents), the consumption of vegetal or stored goods (13.3%), and the belief of goat predation (10%) (D. Cossíos unpubl.). The Sechuran fox also faces some pressure in agricultural zones and from urbanisation and habitat degradation; habitat reduction or loss is considered the principle threat to this species in Ecuador (Tirira 2001).

Commercial use Illegal sale of puppies, of amulets made from body parts, and of handicrafts made from fur occurs principally in the markets of Tumbes, Chiclayo, Piura and Lima city. The most common type of handicraft made with coastal fox parts consists of preserved adult animals in a "sitting" position. This activity is limited almost exclusively to the department of Piura, Peru.

The practice of magic-religious rituals by shamans involving preserved Sechuran fox specimens or parts is the principal human use of this species in Peru. The specimens are used to attract "good spirits" or "positive energies" during premonition rituals or to manufacture amulets,

called seguros, with different purposes. Some shamans use also the Sechuran fox's fat for the treatment of bronchial illness and stomach disorders (D. Cossíos unpubl.).

Occurrence in protected areas
— *Ecuador*: Parque Nacional Machalilla, Manabí; Reserva Ecológica Manglares Churute, Guayas.
— *Perú*: Zona Reservada de Tumbes, Tumbes; Parque Nacional Cerros de Amotape, Tumbes; Coto de Caza el Angolo, Piura; Coto de Caza Sunchubamba, Cajamarca; Santuario Histórico Bosque de Pomac, Lambayeque; Zona Reservada Algarrobal el Moro, Lambayeque; Zona Reservada de Laquipampa, Lambayeque; Reserva Nacional de Calipuy, Ancash; Reserva Nacional de Lachay, Lima.

Protection status CITES – not listed.

Current legal protection Between 1975 and 2000, a governmental authorisation was required to hunt the species in Peru. Since 2000, hunting outside the established areas and trade of the species has been prohibited. The police and the Ministry of Agriculture are responsible for the control of illegal trade. However, it has proven especially difficult to control trade in rural areas and in some cities. Currently, there are no international treaties or conventions regarding this species.

Conservation measures taken The Sechuran fox was not traditionally protected, for cultural reasons, until recently. Now it is protected in Santa Catalina de Chongoyape, a rural community of Lambayeque department, because they are considered important for tourism and as seed dispersers (D. Cossíos unpubl.).

Occurrence in captivity
Some specimens are kept in the following authorised collections: Parque de las Leyendas Zoo, Lima (26 specimens) and Atocongo Zoo, Lima (3 specimens).

Current or planned research projects
E. Vivar (Museum of Natural History, U.N.M.S.M, Lima, Peru) is currently conducting research on the taxonomy and distribution of the Sechuran fox.

Investigations of its relationship with humans, its role in seed dispersal and its diet in Peru are being conducted by D. Cossíos (Instituto Nacional de Recursos Naturales – INRENA, Peru).

Core literature
Asa and Wallace 1990; Birdseye 1956; Cabrera 1931; Huey 1969; Langguth 1975.

Reviewers: Elena Vivar, Michael P. Wallace. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.

3.9 Hoary fox
Pseudalopex vetulus (Lund, 1842)
Data Deficient (2004)

J. Dalponte and O. Courtenay

Other names
English: hoary zorro, small-toothed dog; **French:** renard du Brésil; **German:** Brasilianischer, kampfuchs; **Portuguese:** raposa-do-campo, raposinha (Brazil); **Spanish:** zorro de campo común; **Indigenous names:** Tupy: jaguarapitanga; Xavante: waptsã wa (Brazil).

Taxonomy
Canis vetulus Lund, 1842. K. Dansk. Vid. Selsk. Naturv. Math. Afhandl., 9:4. Type locality: Lagoa Santa, Minas Gerais [Brazil] (Cabrera 1958).

Burmeister (1854) created the genus *Lycalopex* for the hoary fox. Osgood (1934) reduced *Lycalopex* to a subgenus of *Dusicyon*, followed by Simpson (1945), Cabrera (1958) and Clutton-Brock *et al.* (1976). Langguth (1969, 1975) placed the species in *Lycalopex*, and Van Gelder (1978) included it in *Canis* (*Lycalopex*). Berta (1987) placed the species in *Pseudalopex* and was followed by Wozencraft (1993).

Chromosome number: 2n= 37 (Wurster-Hill and Benirschke 1968).

Description
The hoary fox is a slender animal with a relatively short, pointed muzzle, and large ears (Table 3.9.1). Pelage colour is variable: the upper body regions are pale grey, whereas the underparts are generally buff yellow to chestnut including the neck, chest and patch behind the ears. The anterior part of the neck is buff white, but the underside of

Table 3.9.1. Combined body measurements for the hoary fox from Pirapora (Minas Gerais), Franca (São Paulo) (Vieira 1946); Chapada dos Guimarães (Mato Grosso) (Thomas 1903); São Miguel (Minas Gerais) (Courtenay unpubl.); Nova Xavantina, Cuiabá, Chapada dos Guimarães (Mato Grosso), Arinos (Minas Gerais) (J. Dalponte unpubl.); Planaltina (Distrito Federal), São Miguel (Minas Gerais) (J. Marinho-Filho pers. comm.)

HB male	587mm (490–715) n=13
HB female	575mm (510–660) n=6
T male	338mm (270–380) n=13
T female	282mm (250–310) n=5
HF male	129mm (120–135) n=11
HF female	129mm (127–130) n=3
E male	69mm (60–76) n=10
E female	67mm (60–75) n=3
WT male	3.3kg (2.5–4) n=8
WT female	3.4kg (3.0–3.6) n=3

Hoary fox, age and sex unknown. São Paulo State, Brazil, 2003.

Adriano Gambarini

the lower jaw is dark, almost black, as is both the tail base and tail tip; a dark spot on dorsal surface of tail base variably present. Near melanic forms have been described (Cabrera 1931; Vieira 1946; Cabrera and Yepes 1960; J. Dalponte pers. obs.). Dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Monotypic (Stains 1975).

Similar species Crab-eating fox (*Cerdocyon thous*): sympatric throughout the geographical range of the hoary fox; more robust, larger (4.5–8.5kg), and has coarse bristly pelage; colour variation is substantial within and between populations, ranging from dark grey/black (e.g., Amazonia, central Brazil) to grey/yellow rufous (e.g., Ceará, north-east Brazil), with or without a dark dorsal line along the body to tail tip (specimens of the lighter colour type could be confused with the hoary fox); footpad (and footprint) differentiation of the two species is possible by the experienced field worker (Becker and Dalponte 1991). Pampas fox (*P. gymnocercus*): possibly sympatric with the hoary fox in southern São Paulo state; more robust and larger (4–6kg); pelage colour and body proportions are similar. Sechuran fox (*P. sechurae*): not sympatric, occurring in north-west Peru and south-west Ecuador; similar size (4–5kg), and pelage colour, but lacks the dark stripe along the dorsal line of the tail.

Current distribution
The hoary fox is confined to Brazil (Figure 3.9.1), associated with the cerrado habitats (mosaic of grasslands and xerophytic vegetation) of the central Brazilian plateau, and peripheral transitional zones including dry open habitats of the Pantanal (Mato Grosso state). Confirmed in the

states of Minas Gerais, São Paulo, Mato Grosso do Sul, Mato Grosso, Tocantins and Goiás (J. Dalponte unpubl.), southern and western Bahia (Juarez and Marinho-Filho 2002; J. Dalponte pers. obs.), and western Piauí in Parque Nacional Serra da Capivara (F. Olmos pers. comm.). Capture records of an extant specimen held in Teresina Zoological Park indicate its northerly geographical limit is probably in north Piauí (Costa and Courtenay 2003). A previous report of its occurrence in Ceará (north-east Brazil) (Deane 1956) was contested by Courtenay *et al.* (1996). Records along the Brazil-Bolivian border in Mato Grosso (Anderson 1997) are unsubstantiated; the nearest record is 70km to the south in the Pantanal (Mato Grosso do Sul) (J. Dalponte unpubl.).

Figure 3.9.1. Current distribution of the hoary fox.

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Historical distribution A single fossil record exists from Vila de Lujan, Província de Buenos Aires, Argentina, dating back to the Lujanian period, late Pleistocene (Berta 1987). In Brazil, fossil records are those of Lund's expeditions in Lagoa Santa caves, Minas Gerais, south-east Brazil (Lund 1842).

Range countries Brazil (Cabrera 1958).

Relative abundance
There are no reliable data available. Locally abundant in the central highland cerrado biome, but populations appear smaller than those of the sympatric Crab-eating fox for which population estimates are similarly lacking.

Habitat
Occurs in open cerrado habitats, but readily adapts to insect-rich livestock pastures and areas of agriculture (soybean, rice, corn, eucalyptus plantation). Rarely observed in densely wooded cerrado, floodplains, dry or gallery forests.

Food and foraging behaviour
Food Omnivorous, though diet mainly of insects, particularly ground-dwelling harvester termites (*Synthermes* spp. and *Cornitermes* spp.), recorded in 87% of faeces collected in six localities across its geographical range (Dalponte 1997; Silveira 1999; Juarez and Marinho-Filho 2002; O. Courtenay unpubl.; J. Dalponte unpubl.). Dung beetles are consumed in great quantities when seasonally abundant. Other dietary items include small mammals, grasshoppers, birds and reptiles. Seasonal variation in most diet components has been noted (Dalponte 1997; Silveira 1999; Juarez and Marinho-Filho 2002; O. Courtenay unpubl.).

Foraging behaviour Hoary foxes are predominantly nocturnal and tend to hunt as individuals, or in loosely-knit pairs, with or without their juvenile offspring. Foraging group sizes of 3–5 were most common during periods of insect swarming (O. Courtenay unpubl.). They consume termites directly from the ground surface, or from the underside of dried disks of cattle dung which they flip over by pushing the dried disks along the ground at speed. Hoary fox cubs consume insects from the age of at least two months (O. Courtenay unpubl.). During the early rainy season, adult and young foxes catch swarming winged ant and termite elates, and dung beetles, on the wing by acoustic and visual location.

Damage to livestock or game There is no evidence that hoary foxes prey upon livestock or domestic fowl, despite their frequent close proximity to human dwellings (Dalponte 1997; Silveira 1999; Juarez and Marinho-Filho 2002; O. Courtenay unpubl.).

Adaptations
Small carnassials and wide crushing molars and the exceptionally large auditory bullae (Clutton-Brock *et al*. 1976) suggest adaptations to a predominantly insectivorous rather than larger prey-based diet. However, their cranio-dental morphology is not dissimilar to members of the *Dusicyon* [*Pseudalopex*] group (Clutton-Brock *et al*. 1976), which are not insectivorous. Whether their small size and slender build is an adaptation to, or consequence of, a small prey-base and/or hunting in grasslands is not known. Their preference for insects allows them to partition food resources and coexist with other sympatric canids such as the crab-eating fox and maned wolf (*Chrysocyon brachyurus*) (Juarez and Marinho-Filho 2002).

Social behaviour
Monogamous. One study group living in pasture comprised an adult breeding pair and five (3M:2F) juvenile offspring that shared largely overlapping home ranges of 4.6km² (range = 4.5–4.6km²) (O. Courtenay unpubl.). In Bahia, an adult female occupied a home range of 3.8km² (Juarez and Marinho-Filho 2002). Contact rates of a single breeding pair estimated by radio-telemetry indicated that they spend up to 35% of their activity period in close proximity, with substantial variation during offspring rearing (October to May) (O. Courtenay unpubl.). Spot sightings in different habitats and localities revealed that groups were composed of single animals on 75% of occasions, followed by pairs (30%), and groups larger than two (4%) (J. Dalponte and E. Lima unpubl.).

Vocalisations include a roar and threat bark; vocalisations are most common during the mating season (J. Dalponte unpubl.). Hoary foxes urinate using a raised leg urination position; frequent urination in small quantities is typical of territory marking behaviour (J. Dalponte unpubl.).

Reproduction and denning behaviour
In the wild, females produce litters of 4–5 offspring once a year during July and August, at observed male:female sex ratios of 4:2 (O. Courtenay unpubl.), and 2:2 (J. Dalponte and E. Lima unpubl.). A similar parturition season (September/mid-October) occurs in captive animals, with litter sizes of 3–4 (n=2) (Coimbra-Filho 1966, J. Dalponte pers. obs.). The precise length of the gestation period is not known, but mating occurs in late May/early June suggesting that it falls within the range of other members of the *Pseudalopex* group (53–60 days).

Pups are born in dens in disused armadillo holes, particularly that of the yellow armadillo (*Euphractus sexcinctus*) (n=5 social groups, J. Dalponte and E. Lima unpubl., O. Courtenay unpubl.). Offspring are cared for by the breeding male and female; there is currently no evidence of helpers. In one case, a lone breeding female was observed to successfully nurse and rear four cubs to

six months of age (J. Dalponte and E. Lima unpubl.). During late lactation, the female visits the den perhaps a couple of times per night to nurse; in her absence, the male baby-sits, grooms and guards the cubs against potential predators (O. Courtenay unpubl.). Post-weaning, adult gender roles change: female contact declines substantially, whereas the male stays with the cubs as chaperone during hunting expeditions to insect patches close to the den (O. Courtenay unpubl.). The estimated lactation period in the wild is three months indicated by the cessation of nursing in mid-November (O. Courtenay unpubl.). Juveniles of both sexes disperse in May when 9–10 months old and may establish home-ranges adjacent to their natal territory (J. Dalponte and E. Lima unpubl., O. Courtenay unpubl.).

Competition
The main competitors are likely to be the similarly sized crab-eating fox (4.5–8.5kg) and the larger-sized maned wolf (23kg) which often occur in sympatry. Inter-specific divergence in diet composition appears to allow these three canid species to coexist (Juarez and Marinho-Filho 2002). Adult hoary foxes with their young have been observed to tolerate the presence of crab-eating foxes at insect foraging grounds (Courtenay *et al.* unpubl.). Due to its predominantly insectivorous diet, the hoary fox potentially competes also with the large guild of myrmecophagous predators of the cerrado biome. However, the latter group tend to forage termite species that are mound builders and produce chemical secretions, making them largely inaccessible to the hoary fox.

Mortality and pathogens
Natural sources of mortality Hoary fox remains (hairs, teeth and bone fragments) have been identified in 0.3–4% of maned wolf faeces from three different sites in Central Brazil: Parque Nacional de Chapada dos Guimarães (J. Dalponte and E. Gomes da Silva unpubl.), Parque Nacional de Emas (Silveira 1999; A.T. Jácomo pers. comm.), and Parque Nacional Grande Sertão Veredas (J. Dalponte unpubl.), suggesting that maned wolves are opportunist consumers of hoary foxes, presumably as scavengers. It is debatable that maned wolves actively hunt live adult foxes. Hoary foxes are not represented in stomach contents or faeces of large predatory birds or large felines, though Xavante hunters in the Rio das Mortes Indigenous Reserve, Mato Grosso state, reported at least one fox being killed and eaten by a puma (*Puma concolor*) (E. Lima pers. comm.).

Persecution Hoary foxes are killed indiscriminately as predators of domestic fowl, although they probably earn this reputation from crab-eating foxes which are formidable thieves (Courtenay and Maffei chapter 3.2 this volume). Young foxes are often taken as pets, and domestic dogs are responsible for cub deaths when dens are located in peri-urban areas.

Hunting and trapping for fur Occasional hunting occurs as a predator control measure, but populations are not trapped for fur.

Road kills In north-east São Paulo state, seven hoary fox deaths were recorded along 13,500km of road between January 1981 and December 1983, with a ratio of crab-eating to hoary foxes of about 10:1 (J. Dalponte and J.A. Tavares-Filho unpubl.). The proportion of male to female hoary foxes in an additional sample of 19 road-killed foxes in central Brazil was approximately 2:1 (J. Dalponte unpubl.).

Pathogens and parasites Population declines due to pathogen infection have not been documented; however, at least one death due to sarcoptic mange is thought to have occurred in the Serra da Canastra (J. Dietz pers. comm.). Two other individuals, a female and her infant, which had been radio-tracked in the Rio Pratudão ranch, Posse, W Bahia, seemingly died following a sarcoptic mange infection that was also seen to infect at least one maned wolf (J. Marinho-Filho pers. comm.). Reports of hoary fox infection with the rabies virus and the protozoan parasite *Leishmania infantum* in the state of Ceará (Deane 1956; Barros *et al.* 1989) almost certainly refer to crab-eating fox and not hoary fox (Courtenay *et al.* 1996). Disease outbreaks due to other common canid pathogens (e.g., canine distemper virus and canine parvovirus) have not been reported in the wild. Other documented parasites of hoary foxes include *Trypanosoma cruzi* (Albuquerque and Barretto 1970), and *Angiostrongylus vasorum* found in eight animals captured in Minas Gerais (Lima *et al.* 1994).

Longevity No information available, however an eight-year-old captive female (in August 2002) was observed in Teresina Zoological Park (Costa and Courtenay 2003).

Historical perspective
Unknown.

Conservation status
Threats The principal biome where hoary foxes occur is the cerrado which is being destroyed at a rate of 3% each year, largely in the interests of agriculture (livestock and soybean) (MMA-BRASIL 1998). It appears that hoary foxes adapt to livestock pasture rich in termites and dung beetles. Breeding hoary foxes are found in deforested wooded areas (J. Dalponte pers. obs.), thus it is possible that deforestation may not have a negative impact on the species. Areas of high human population density are unlikely to be suitable. There are no population estimates available.

Commercial use Not exploited for fur or any other products.

Occurrence in protected areas *Brazil:* Parque Nacional de Chapada dos Guimarães, Parque Nacional da Serra da Capivara, Parque Nacional da Serra da Canastra, Parque Nacional de Emas, Parque Nacional Grande Sertão Veredas, Estação Ecológica de Águas Emendadas, Parque Nacional de Brasília, Refúgio de Vida Silvestre da Fazenda Nhumirim e RPPN do Rio Negro, Parque Estadual da Serra do Lageado, Parque Estadual de Santa Bárbara, Santuário de Vida Silvestre do São Miguel, Fazenda São Miguel.

Protection status CITES – not listed.
Listed as "Vulnerable" by the Canid Conservation Assessment and Management Plan (CAMP) 1993 meeting in São Paulo; "Vulnerable" in individual state faunal status accounts, but not listed in the Brazilian official list of threatened mammals (Fonseca *et al*. 1994).

Current legal protection Hunting and trade in wildlife is generally forbidden in Brazil. There is no specific hunting legislation for hoary foxes.

Conservation measures taken Nothing proposed. No cultural protection reported.

Occurrence in captivity
Specimens in Brazilian zoos at the time of writing include: Brasilia (1); São Paulo (1); Ribeirão Preto (1); Belo Horizonte (5); Teresina (1). High mortality rates due to starvation amongst captive cubs are reported. There are no current plans to reintroduce hoary foxes into the wild.

Current or planned research projects
J. Dalponte (Universidade de Brasília, Brazil) is currently studying the ecology and behaviour of the hoary fox in Mato Grosso, Brazil.

Gaps in knowledge
Areas for further research include focusing on aspects of behavioural ecology, population status, geographical range, the potential role of disease in population regulation, and their status as potential reservoirs of veterinary (e.g., scabies, distemper) and public health (e.g., leishmaniasis, rabies) pathogens.

Core literature
Costa and Courtenay 2003; Dalponte 1997, 2003; Juarez and Marinho-Filho 2002; Silveira 1999.

Reviewers: Louise Emmons, Jader Soares Marinho-Filho.
Editors: Claudio Sillero-Zubiri, Michael Hoffmann.

3.10 Bush dog
Speothos venaticus (Lund, 1842)
Vulnerable – VU: C2a(i) (2004)

G.L. Zuercher, M. Swarner, L. Silveira
and O. Carrillo

Other names
English: vinegar dog, savannah dog; **Dutch:** boshond, busdagoe (Suriname); **French**: chiens des buissons, zorro; **German**: waldhund, **Italian:** speoto, itticione; **Portuguese:** cachorro-do-mata, cachorro-do-mato-vinagre, cachorro-do-mato-cotó, cachorro-pitoco (Brazil); **Spanish:** zorrito vinagre (Argentina); zorro/perro vinagre, perro/perrito de monte (Bolivia/Ecuador/Venezuela); perrito venadero, umba (Colombia); perro de la selva, pero selvático, perro de agua, Guanfando (Ecuador – origin undeterminado); **Indigenous languages:** Cubeo: maca tawimi, Huitoto: itón+maido, Shuku: puinave, Yucuna: huerateyaniminami (Colombia); Achuar: tuwen'k, patukam yawa, Chachi: pikucha, Huaorani: babeguinta, Quichua: sacha alcu, Secoya: airo jo'ya, masi̲oco yai (Ecuador); Aché: mbetapa, Guarani: jagua yvyguy (Paraguay); Amarakaeri: dumba cuhua, cuan cuan, Shibipo: hueshes (Peru).

Taxonomy
Cynogale venatica Lund, 1842. K. Dansk. Vid. Selsk. Naturv. Math. Afhandl. 9:67. Type locality: "Lagoa Santa" [Minas Gerais, Brazil, *c.* 19°39'S, 43°44'W].

The bush dog is accepted as the sole extant representative of the monotypic genus *Speothos*. *Speothos pacivorus* Lund, 1839, an extinct species, is known only from fossil deposits discovered at the Lagoa Santa caves in Minas Gerais, Brazil, and may not have existed past the Holocene (Berta 1984). This is the same site for the type locality specimen of *S. venaticus*. The two species are distinguished by several dental features, including the presence of a metaconule and hypocone on M_1 a large, double-rooted M_2, as well as the larger size of *S. pacivorus* (Berta 1987). A third species, *S. major* (Lund 1843), is now considered synonymous with *S. venaticus* (Berta 1984).

The taxonomic relationship of bush dogs to other canids remains debatable. The presence of a unicuspid M_1 talonid led to the inclusion of the bush dog in the subfamily Simocyoninae, along with two other species that share this characteristic, the African wild dog (*Lycaon pictus*), and dhole (*Cuon alpinus*). Berta (1984, 1987) suggested bush dogs are most closely related to small-eared dogs (*Atelocynus microtis*), and members of the *Cerdocyon* clade (one of four monophyletic groups of South American canids). This group includes the raccoon dog (*Nyctereutes procyonoides*). Berta (1987) suggests a single ancestor for this group, ranging over Eurasia and North America, with isolation of the raccoon dog occurring when the Bering Land Bridge disappeared. Recent molecular analyses,

Adult male (front) and female (behind) bush dog. Oklahoma City Zoo, USA.

based on mitochondrial DNA, suggest bush dogs and maned wolves (*Chrysocyon brachyurus*) constitute a monophyletic group distinct from other South American canids (Wayne *et al.* 1997).

Chromosome number: 2n=74 (Schreiber and Dmoch 1994).

Description

The bush dog is characterised by an elongate body, a short and sometimes stubby tail, broad face with short muzzle, small rounded ears, brown eyes, and short legs (Table 3.10.1). Head and neck are generally reddish/tan or tawny, gradually darkening to black or dark brown hindquarters and legs. The underside is also dark and some individuals may show a pale white throat (i.e., Bolivia) or chest patch. Coat patterns can, however, be highly variable, ranging from almost all black to very light blonde. Feet are partially webbed and tracks are nearly identical to those of the domestic dog. Bush dogs are one of three canid species with trenchant heel dentition, a unicuspid talonid on the lower carnassial molar that increases the cutting blade length. Dental formula is 3/3-1/1-4/4-2/2=40.

Table 3.10.1. Body measurements for the bush dog from Paraguay (Van Humbeck and Perez 1998; Nowak 1999).

HB	630mm (575–750)
T	140mm (125–150)
E	30mm
SH	200mm (200–300)
WT	5–8kg

Subspecies Three subspecies are recognised (Cabrera 1961).
— *S. v. panamensis* (Panama)
— *S. v. venaticus* (Argentina, Bolivia, northern and central Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, Venezuela).
— *S. v. wingei* (south-eastern Brazil).

Similar species Short-eared fox (*Atelocynus microtis*): distinguished by a grizzled, blackish/grey coat, erect pointed ears, longer legs, and a bushy tail long enough to touch the ground. Tayra (*Eira barbara*): longer bushy tail and a yellow throat and head patch.

Current distribution

This species occurs from extreme eastern Central America and northern South America, south to Paraguay and north-eastern Argentina (Figure 3.10.1). Isolated populations may also still occur in Ecuador (Tirira 2001) and Colombia, west of the Andes. However, historical distribution may have extended as far north as Costa Rica (De la Rosa and Nocke 2000), where the species may still survive in suitable habitat.

Range countries Argentina, Bolivia, Brazil, Colombia, Costa Rica (?), Ecuador, French Guiana, Guyana, Panama, Paraguay, Peru, Suriname, Venezuela (Fonseca and Redford 1984; Defler 1986; Strahl *et al.* 1992; Aquino and Puertas 1997; Silveira *et al.* 1998; De la Rosa and Nocke 2000; Barnett *et al.* 2001; Tirira 2001; Zuercher and Villalba 2002).

Figure 3.10.1. Current distribution of the bush dog.

Relative abundance

Although there is currently no information available regarding the species' density, it is important to note that, despite its large distributional range and occurrence in a variety of habitats (i.e., cerrado and rainforest), the species has never been reported as abundant. Thus, it seems to be naturally rare throughout its range, independent of human disturbance.

Habitat

Bush dogs are reported to be a habitat generalist by indigenous peoples, within the context of occurring generally near water sources, particularly small streams, and near available prey populations, especially *Agouti paca* (O. Carrillo and M. Swarner pers. obs.). Bush dogs have been observed in lowland (below 1,500m a.s.l.) forested habitats including primary and gallery forest (Defler 1986), semi-deciduous forest, and seasonally flooded forest (Aquino and Puertas 1997). Observations have also been recorded from cerrado habitat in Brazil (Silveira *et al.* 1998; C. Brady pers. comm.) and Paraguay (Zuercher and Villalba 2002) and pampas (wet savannah) edge/riparian areas (Strahl *et al.* 1992; Emmons 1998). In some cases, they have been observed as far as 5,700m from forest habitat (Silveira *et al.* 1998). The species is also occasionally reported from secondary forest, ranchland (M. Swarner pers. obs.) and fragmented cerrado ranchland (L. Silveira and A. Jácomo pers. comm.).

Food and foraging behaviour

Food Primarily carnivorous, bush dogs are most commonly observed hunting large rodents such as paca (*Agouti paca*) and agouti (*Dasyprocta* spp.) (53.1% and 28.1%, respectively, of reported sightings in central western Amazonia; Peres 1991). Their diet may also include small mammals (i.e., rats, *Oryzomys* spp. and *Proechimys* spp., rabbits, *Sylvilagus brasiliensis*, opossums, *Didelphis* spp. and nine-banded armadillo *Dasypus novemcinctus*; Van Humbeck and Perez 1998; Zuercher and Villalba 2002). Other prey items include teju lizards (M. Swarner pers. obs.), snakes, and possibly ground-nesting birds. Local people report that bush dogs can take prey considerably larger than themselves such as capybaras (*Hydrochaeris hydrochaeris*), and rheas (*Rhea americana*), as well as deer (*Mazama* spp.)*,* and possibly even tapir (*Tapirus terrestris*) (R. Wallace pers. comm.) by hunting in packs (Deutsch 1983; Peres 1991; Strahl *et al.* 1992). Their diet is reported to vary seasonally.

Foraging behaviour Peres (1991) reported 92% of observed bush dog hunting parties consisted of at least two individuals (mean=4.5; range=2–8). Local people describe a variety of cooperative hunting strategies employed by bush dogs (M. Swarner unpubl.). For example, in Bolivia, they are commonly reported to hunt *Mazama*

deer by attacking the legs until the animal tires and falls. Olfaction may play a large role when foraging. When hunting burrowing animals, some individuals reportedly enter the prey's burrow while other pack members wait at possible escape routes. Once flushed, prey is pursued with seemingly relentless endurance by the pack, even into deep water. Solitary hunting has been observed (Deutsch 1983).

Damage to livestock or game In Bolivia and Ecuador, bush dogs are considered predators of chickens (M. Swarner pers. obs.).

Adaptations

Modified carnassial teeth suggest an exclusively carnivorous diet. Webbed feet suggest swimming capability and imply that large rivers do not represent barriers to distribution (Strahl *et al.* 1992). Small compact body may be an adaptation to pursue burrowing prey and navigate through dense forest. Stocky, muscular neck may aid in prey capture or extraction from burrows. Dark coat colour is a reported general adaptation to humid, forest environments. Nomadic behaviour may reflect responses to changing densities of favoured prey species as well as avoidance of competitors and/or predators.

Social behaviour

Although solitary individuals have been observed, the bush dog is considered the most social of the small canids (Ginsberg and Macdonald 1990; Sheldon 1992), reportedly living in groups ranging from 2–12 individuals with most observed groups comprising 2–6 members (M. Swarner unpubl.; L. Silveira pers. obs.). Captive bush dogs, too, are compulsively social, rarely spending more than a few minutes from companions (Macdonald 1996). Strahl *et al.* (1992) state that the bush dog is probably a cooperative species, and report observations by indigenous hunters and colonists in Venezuela of bush dogs hunting in groups of up to six individuals. The ability of a pack to subdue larger prey appears to be a primary benefit of sociality for bush dogs (Kleiman 1972; Drüwa 1983).

Drüwa (1983) suggests a monogamous pair-bond is likely with multiple years' offspring living with the pair at any given time. A mostly diurnal species, the pair and any family members spend the night in a den (Kleiman 1972; I. Porton pers. comm.). Males exhibit a high degree of parental care that includes food supplementation to females prior to birth and throughout nursing (I. Porton pers. comm.). Silveira *et al.* (1998) estimate the home range as between 4.56 and 4.72km²; this estimate is derived from a canid home range regression based on body mass by Gittleman and Harvey (1982).

Porton (1983) suggests urine marking is important in formation and maintenance of pair-bonds. Indigenous people report a strong smell associated with bush dogs (Swarner unpubl.), lending further evidence that urine is

a particularly effective communication medium for this species. Sex-specific urine-marking behaviour characterises bush dogs. Males extrude the penis and move laterally, creating a spray rather than a stream (Kleiman 1972). Females drag the ano-genital region over a surface or display either a forelimb handstand or a squat. The raised posture of the female allows urine to be deposited approximately 150mm higher than the spray of the male (Kleiman 1972).

Adult bush dog vocalisations have been classified into six categories: (1) whines; (2) repetitive whines; (3) pulsed vocalisation; (4) screams; (5) barks; and (6) growls (Brady 1981). Infant vocalisations include whines, grunts, growls, and barks and are thought to either elicit care or reduce aggression. Habitat and social organisation are thought to influence the physical structure of bush dog vocalisations. The elaborate set of close-range vocalisations assists in communicating subtle changes in mood as well as changes in location (Kleiman 1972; Brady 1981). The use of this close-contact call has been noted in a bush dog group travelling through tall grass during the day in Colombia (Defler 1986). Bush dogs also have a vocalisation similar to the short-distance vocalisation (Brady 1981) but at a different frequency. This particular vocalisation has been reported from Paraguay during the early morning (K. DeMatteo pers. comm.) and night (Beccaceci 1994).

Reproduction and denning behaviour

Free-ranging bush dogs have an unknown mating season, although pups have been found in the wet season (M. Swarner pers. obs.). The majority of information regarding bush dog reproduction comes from captive studies. Captive females have two oestrous cycles per year (Kleiman 1972), demonstrating the species' physiological potential. Oestrus is aseasonal and likely influenced by social factors (Porton *et al*. 1987). Dominant females appear to suppress the oestrus of daughters (Porton *et al*. 1987; Macdonald 1996). Gestation is 67 days, and mean litter size is 3.8 (range=1–6). Lactation lasts approximately eight weeks. Bush dogs are believed to be sexually mature by one year.

Competition

No direct measures of competition are available. However, there is a high degree of overlap in the reported diets of bush dogs and many other Neotropical carnivore species and humans. This potential competition with humans for food resources may partially explain the absence of bush dogs near human settlements. Den-site competition is unlikely as the species is considered very nomadic and often reported to use pre-existing burrows of paca or armadillos. Direct interactions with sympatric carnivore species are unknown.

Mortality and pathogens

Natural sources of mortality Indigenous peoples in Paraguay, Bolivia, and Ecuador report finding bush dogs killed by jaguars and puma.

Persecution Bush dogs are occasionally killed in Bolivia and Ecuador for depredation of chickens (M. Swarner pers. obs.).

Road kills No substantial data exist to quantify bush dog susceptibility to automobile collisions. However, in Brazil, bush dogs have been found as road kills (L. Silveira, pers. obs.).

Hunting and trapping for fur The bush dog is not currently, nor was it historically, valued for its pelt. Local people report that they were an extremely rare by-catch during the pre-1978 spotted-cat skin trade.

Pathogens and parasites Known disease-causing organisms and parasites of bush dogs include bacteria (*Escherichia coli, Proteus vulgaris, Staphylococcus aureus, S. epidermis, Klebsiella* sp*., Shigella* sp*.*), protozoans (*Giardia* sp*.*), fungi (*Candida* sp*.*) (Van Humbeck and Perez 1998), nematodes (*Lagochilascaris* sp*.*) and cestodes (*Echinococcus* sp*.*) (Volcán and Medrano 1991). Captive individuals also have shown susceptibility to parvovirus (Janssen *et al*. 1982) and vaccine-induced canine distemper virus (McInnes *et al*. 1992).

Longevity A captive bush dog reportedly lived for more than 13 years (Jones, in Nowak 1999), but is likely to be around 10 years in the wild.

Historical perspective

Indigenous people have occasionally kept bush dogs as pets and hunting dogs, emphasising their superior hunting abilities when pursuing burrowing prey, especially paca and armadillos (M. Swarner unpubl.). However, other informants report that bush dogs are difficult or impossible to domesticate because of the fierceness, all-meat diet, or susceptibility to domestic dog diseases.

Some lowland Quichua of eastern Ecuador report that bush dogs have owners like any domestic dog (M. Swarner pers. obs.). The "owners" are referred to as *sacha runa* (forest people or spirits) and use them as hunting dogs. Due to this belief, some Quichua are reluctant to capture or kill bush dogs because it would be equivalent to stealing or killing a neighbour's hunting dog.

Many indigenous peoples consider the bush dog to be one of the best hunters in the forest, sometimes singing songs to their own dogs in hopes of passing on the bush dog's skills (Descola 1996). Human hunters often report killing prey pursued by bush dogs whenever encountered and taking it for themselves, even following the bush dog's high-pitched hunting barks in the hope of a stealing opportunity (M. Swarner unpubl.).

Conservation status

Threats Only serious perceived threat is from habitat conversion and human encroachment.

Commercial use None known.

Occurrence in protected areas
— *Argentina:* Iguazu National Park and Urugua-í Provincial Park;
— *Bolivia:* Carrasco National Park, Amboro National Park, Rios Blancos and Negros Reserve, Beni Biosphere Biological Station and Reserve and Madidi National Park, and Noel-Kempff Mercado National Park;
— *Brazil:* Emas National Park, Iguaçu National Park, Cantão State Park, Tocantins State and Serra das Araras State Park, Mato Grosso, IGBE's Ecological Reserve, Gurupi Biological Reserve, Amazonia National Park, Rio Trombetas Biological Reserve, Tapirapé Biological/Tapirapé-Aquiri National Forest, and Mirador State Park; *Colombia:* Tuparro National Park;
— *Ecuador:* Sumaco-Napo Galeras National Park (Centro de Datos para la Conservación del Ecuador), Yasuni National Park, Cotocachi-Cayapas Ecological Reserve, and Cuyabeno Faunistic Reserve;
— *Guyana:* Kaieteur National Park;
— *Paraguay:* Reserva Biosfera del Bosque Mbaracayú, San Rafael National Park, Reserva Privada Golondrina, Reserva Natural Privada Morombi, Reserva Natural Privada Ypeti, and Reserva Natural Privada Ka'I rague;
— *Peru:* Tamshiyacu-Tahuayo Communal Reserve, and National Reserve of Pacaya-Samiria, Biabo Cordillera Azul Reserve, Centro Río Amigos, and Bahauja-Sonene National Park and Tambopata Candamo Reserve;
— *Venezuela:* Canaima National Park.

Protection status CITES – Appendix I (2000). Declared "Vulnerable" in Argentina (Beccaceci, in Ginsberg and Macdonald 1990).

Current legal protection Hunting is prohibited in Colombia (Law Number 848:1973), Ecuador (Law Number 74:1981), French Guiana (Law Number JO19860625:1986), Panama (Law Number 2-80:1980), Paraguay (Law Number 18796:1975) and Peru (Law Number 5056:1970). Hunting and trade is regulated in Argentina (Law Number 22.421:1981), Bolivia (Law Number 12301:1975), Brazil (Law Number 5197:191967), and Venezuela (Law Number 276:1970). There is no Information for Guyana and Suriname.

Conservation measures taken None known.

Occurrence in captivity

Bush dogs do occur in captivity and are breeding successfully. No known attempts at reintroduction.

Current or planned research projects

G. Zuercher (Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University and Sunset Zoological Park, Manhattan, Kansas, USA), with additional support by Sedgwick County Zoo (Wichita, Kansas), and the American Zoo and Aquarium Association, is investigating the ecological role of the bush dog as part of a greater mammalian carnivore community within the Interior Atlantic Forest of eastern Paraguay.

L. Silveira (Pró Carnívoros, São Paulo, Brazil), A. Jácomo (Pró Carnívoros), and C. Brady (Memphis Zoo, Memphis, Tennessee, USA) are exploring the distribution and conservation of bush dogs within the Brazilian cerrado biome, where conservation units of confirmed bush dog presence are being examined, and potential corridor sites are being identified. The project is sponsored by Pró Carnívoros and Memphis Zoo (Memphis, Tennessee, USA).

M. Swarner (University of Maryland, College Park, Maryland, USA) undertook an inventory of indigenous knowledge of bush dogs throughout western Amazonia between July 2000 and August 2001 (a study supported by the Thomas J. Watson Foundation).

K. DeMatteo (St. Louis Zoo and St. Louis University, St. Louis, Missouri, USA) is continuing an ongoing captive study to investigate the reproductive physiology of female bush dogs and the role of social stimulation in ovulation.

Gaps in knowledge

The distribution of bush dogs should be re-evaluated. There are no population estimates or demographic data for bush dogs in any of their range countries. Our understanding of dietary habits is based mostly on anecdotal information and does not address seasonal or geographic variation. Habitat associations are not clearly understood – the species was once thought to be dependent on forests but is now regularly observed in open habitats. The impact of disease, both historically and currently, is unclear (this is especially true for diseases introduced by domestic animals). Accepted ideas of behaviour and social structure, obtained from captive animals, have not yet been verified in wild populations. Interspecific relationships with sympatric carnivores need to be further evaluated.

Core literature

Aquino and Puertas 1997; Brady 1981; Drüwa 1983; Kleiman 1972; Macdonald 1996; Porton 1983; Silveira *et al.* 1998; Strahl *et al.* 1992; Van Humbeck and Perez 1998.

Reviewers: Melissa Rodden; Karen DeMatteo. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.