Ecology of a coastal population of the critically endangered Darwin's fox (*Pseudalopex fulvipes*) on Chiloé Island, southern Chile

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Abstract

The behavioral ecology of the critically endangered Darwin's fox *Pseudalopex fulvipes* was examined during the reproductive season of 2001/2002 on a coastal population, on Chiloé Island in southern Chile. Foxes were radio-tracked and their diet and feeding behavior, activity patterns, home range sizes and spatial organization, habitat use and selection, social organization and abundance were studied. Foxes were solitary hunters and showed a generalist and opportunistic feeding behavior. Insects were the most abundant prey, followed by crustaceans, rodents, birds, amphibians, ungulates, reptiles, and marsupials. As marine organisms were frequently eaten, the ocean subsidy was important. Plant seeds were dispersed up to +650 m from their sources. Prey were hunted in all habitat types recognized, throughout the daily cycle, and were consumed as they were available along the season. All foxes were active throughout the day, but more so at night. Morphologically, aside from males having broader muzzles, they did not show external sexual dimorphism or differences in weight. The tail and feet of Darwin's foxes were relatively shorter than in other congeneric species. Individual home ranges and core areas ranged from 103 to 488 ha and from 30 to 130 ha, respectively, were similar between males and females, and larger than expected for foxes of that size. All home ranges were elongated (2930 m on average) following the shoreline. Foxes overlapped their home ranges extensively – and core areas less so – with individuals of the same or different gender, showing no apparent territorial behavior. They appear to be monogamous, allowing subordinates in their home ranges. The ecological density was 0.92 foxes km^{-2}, which may be higher than in inland populations. Old-growth forest was consistently avoided by all individuals, second-growth forest and shrubland were used as available, and the use of dunes and other lands (mainly shores) was mixed.

Introduction

The Darwin's fox *Pseudalopex fulvipes* (Martin 1837) is perhaps one of the rarest, least known and world's most threatened canid (Macdonald & Sillero-Zubiri, 2004). Its conservation status is Critically Endangered [CR C2a(ii) IUCN code] because of its restricted distribution, small population size and few known populations. It is Critically Endangered also because its main population occurs in only one island and its habitat is facing dramatic declines and changes due to human impact. Thus, its conservation is urgent and recommended (Jiménez & McMahon, 2004; Macdonald & Sillero-Zubiri, 2004).

Until recently, the Darwin's fox distribution was only known from the 8090-km^2 Chiloé Island, in southern Chile. However, in the 1990s a small and isolated population was discovered on the mainland *c*. 600 km north in the 68-km^2 Nahuelbuta National Park (Medel *et al*., 1990). Hence, this

Chilean endemic fox has the smallest distribution of any known canid (Wayne, Geffen & Vilá, 2004). The Darwin's fox was recognized as a legitimate species only very recently; it was considered as an island subspecies of the larger gray fox or chilla *Pseudalopex griseus* until the mainland population was found in sympatry with the chilla and also with the culpeo fox *Pseudalopex culpaeus*, the largest of the three Chilean foxes (Jiménez & McMahon, 2004). In addition, genetic analysis confirmed its specific status and showed that the small mainland population was distinct from that of Chiloé and not a released stock from the island population (Yahnke *et al*., 1996). The genetic study further hypothesized that the Darwin's fox was a relict of an ancestral phylogenetic line that was more broadly distributed in the past in the southern temperate forests. The reason for its current restricted distribution, however, remains a mystery.

Although the fox population size is unknown, educated guesses estimate it as less than 500 individuals (Yahnke

et al., 1996). However, an effective population size of less than 250 reproductive individuals might be a more realistic number (IUCN, 2004). Its small population size, along with the rapid destruction due to cutting and burning of its putative habitat, the Valdivian rainforest (Lara, Donoso & Aravena, 1996), and its naiveness to potential diseases transmitted by the abundant and unleashed dog populations make this species at high extinction risk.

Thus far, ecological studies on the Darwin's fox have been limited mainly to descriptions of its habitat and diet on the mainland and its comparison with that of the chilla (Jaksic *et al.*, 1990) and to a comparative study of the island and mainland foxes abundances, diets, and habitat use (Jiménez *et al.*, 1990). Morphological data are also scant given that there are no animals in zoos (Jiménez & McMahon, 2004) and only seven skins are known to exist in museums: four in Chile's National Museum of Natural History, two in the Field Museum in Chicago and the one that Darwin collected in 1834 in London (Osgood, 1943; Medel *et al.*, 1990). Darwin described the collection of the fox as follows: 'A fox (Canis fulvipes), of a kind said to be peculiar to the island, and very rare in it, and which is a new species, was sitting on the rocks. He was so intently absorbed in watching the work of the officers, that I was able, by quietly walking up behind, to knock him on the head with my geological hammer. This fox, more curious or more scientific, but less wise, than the generality of his brethren, is now mounted in the museum of the Zoological Society' (Darwin, 1962). Its basic ecology and many population parameters such as density, home range size, habitat use patterns and selection, spatial and social structure, as well as activity patterns are not known. Such knowledge is critical for proposing science-based guidelines for the conservation of this unique fox. In this paper I quantify the above parameters for the first time on the species and analyze its spatial ecology by studying a coastal population of the Darwin's fox on Chiloé Island, in southern Chile.

Study area

The study was conducted at Ahuenco mainly between November 2001 (late spring) and April 2002 (mid-autumn). A preliminary collection of fox feces was carried out during October 2000 and no feces were collected in December 2001. Ahuenco is an 800-ha private property owned by a conservation non-governmental organization and is located along the Pacific shore of the Island of Chiloé, *c.* 45 km south-west from the city of Ancud (74°03′W, 42°06′S, Fig. 1). Temperatures were gentle and precipitation records on a nearby site reached 7300 mm annually (Pérez, Hedin & Armesto, 1998). The topography is of rolling hills, with elevations that range from sea level up to 55 m in height. There is a conspicuous dune system in the southern portion of Ahuenco that reaches up to 1000 m inland. The dunes are surrounded by two wetlands. Shores are sandy alternated with rock outcrops.

The vegetation – described below – corresponds to the broad-leaved Valdivian temperate rainforests of North Patagonian type (Veblen, Schlegel & Oltremari, 1983). This is one with the highest conservation priority forest worldwide (Olson & Dinerstein, 2000). The area is mildly impacted by limited clearings and cattle activity during the past 40 years, chiefly along the coast. Currently, aside from the ranger family, which had a free-living cat that stood around the house, no other people live in the area. A few people visit Ahuenco as trekkers during summer. Two oxen and three horses that grazed freely constitute the exotic herbivores.

The physiognomy of the landscape is heterogeneous, generating a rich and diverse environment for the foxes ranging from sandy and rocky shores, large dunes, creeks, wetlands, and a mix of shrublands and forests of different composition and heights (Fig. 1, see below).

Materials and methods

Diet analysis

The diet of the Darwin's fox was studied by examining the contents of the prey remains found in the feces. Feces were collected in the field whenever possible along trails and throughout the area in a non-systematic way. Generally, each feces location was recorded with a Garmin 12X global positioning system (GPS) unit. Feces were placed in labeled paper bags and taken to the laboratory to be dried and later teased apart under a dissecting microscope. The remains of mammals were determined by using keys for molars and hairs (Chehébar & Martín, 1989; Pearson, 1995), whereas birds were determined through the morphology of the feather nodules (Reyes, 1992). Scales and bones aided in the identification of reptiles and frogs and exoskeleton fragments for invertebrates. Seeds found in feces were used for the estimation of fruit consumed. The remains found were also compared with voucher specimens for identification. Prey were identified to the highest taxonomic level possible.

Diet composition was estimated by counting the number of each prey type in each feces and then tallying the percent frequency of each prey item out of the total prey identified in the feces each month. In addition, the percent frequency of occurrence, as the frequency of feces that had each prey type, was computed. No correction for potential differential digestibility was applied to the remains found (Reynolds & Aebischer, 1991).

Radio-telemetry and activity patterns

Foxes were captured with mackerel-baited wire mesh traps set throughout the study area. Traps were checked at least twice daily. Animals were manipulated under sedation with ketamine hydrochloride ($10 \, \text{mg} \, \text{kg}^{-1}$) and xylacine ($1 \, \text{mg} \, \text{kg}^{-1}$), weighed, measured, fitted with a numbered ear tag and 30–38 g activity mode 148–150 MHz Wildlife Materials and ATS transmitters (Isanti, MN, USA), and released at the capture site after recovering from the drug. Relative age was estimated by molar wear.
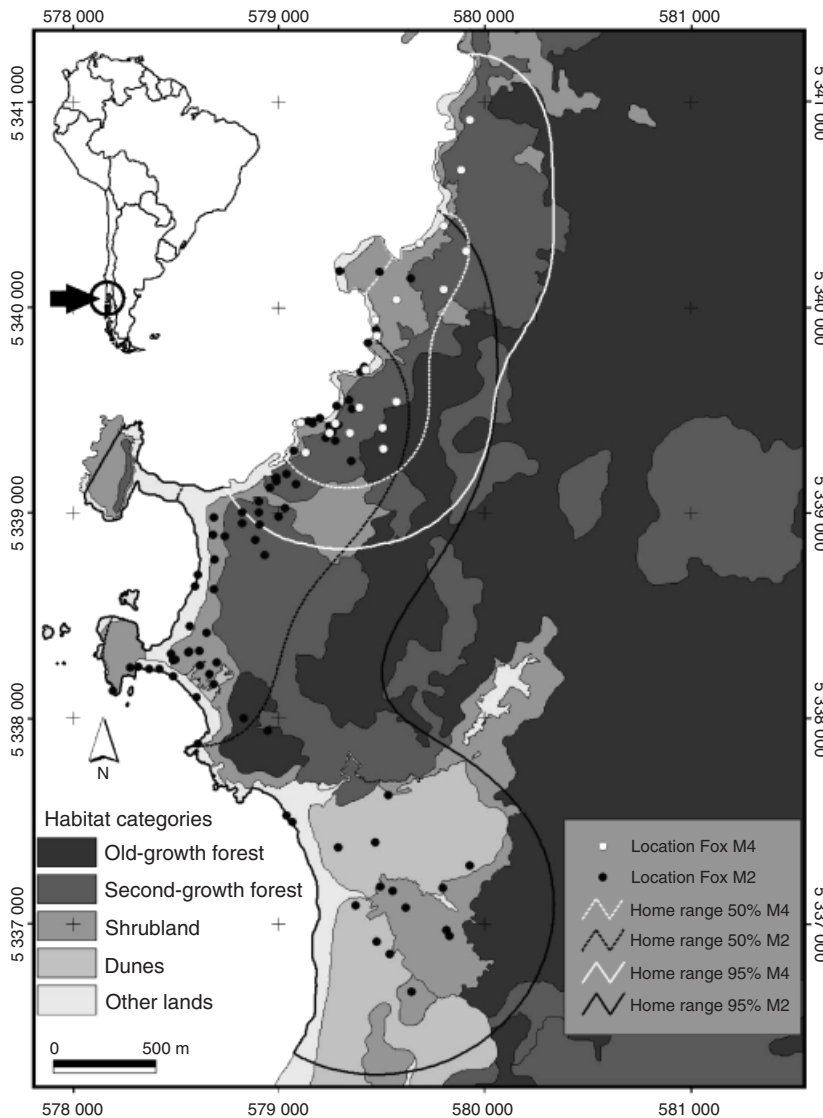
Figure 1 Ahuenco study site showing the habitat types and the fixed kernel home ranges and estimated locations of two male foxes.

Animal locations were estimated from triangulations (mainly two azimuth readings per fix) obtained with three-element hand-held Yagi (Colfax, CA, USA) antennas and AVM LA12-Q (Colfax, CA, USA) and Telonics (Mesa, AZ, USA) RT-2 receivers from many GPS-known points across the study site at random times during entire daily cycles. Azimuths were obtained with a compass and the animal activity status was determined through the activity mode of the transmitter and/or changes in the signal strength (White & Garrott, 1990). To minimize errors due to animal movements, only fixes taken from different points that were within 15 min were used, and most bearings used that resulted in locations were between 45 and 135° of each other. To account for temporal independence of the data (Swihart & Slade, 1985), locations were generally separated by more than 3 h from each other. However, for a hunting mammal of this size the time to independence should have

been 5.6 h (Swihart, Slade & Bergstrom, 1988). Individual activity patterns were estimated by computing the percent of active fixes grouped at intervals of 3 h throughout the daily cycle. Formal assessment of telemetry accuracy was not made. However, on several occasions animals were observed when determining azimuths, and, given the small angle of error and the short distance between the receiver and the animals, it is believed that location error was much smaller than the minimum mapping unit.

Home range size, habitat use and selection, and spatial overlaps

Locations were estimated with LOAS (3.02) and home ranges with BIOTAS (1.03) (Ecological Software Solutions). For each animal the 95% fixed kernel (FK) estimator was used to estimate home range size, and 50% of the locations

were used to determine areas of more intensive use or core areas (Samuel, Price & Garton, 1985; Crooks & Van Vuren, 1996). Although FK estimators were used given their desirable properties compared with other home range estimators (Seaman & Powel, 1996; Kernohan, Gitzen & Millspaugh, 2001), for comparative purposes (Harris *et al.*, 1990) the 95% minimum convex polygon (MCP) was also computed.

Habitat use was determined as the area of each fox home range (95% FK) that intercepted each of the habitat types recognized in the area. Habitat selection was computed as the proportion of locations for each fox in each habitat type (i.e. used) compared with the proportion of area of each of these habitat types available. For each fox, availability of habitat types was estimated at two scales: (1) at the individual level (i.e. third-order selection *sensu* Johnson, 1980), as the proportion of each habitat type within the fox home range plus a buffer of a width equal to the radius of a circle of the same area as the 95% FK home range, and (2) at the population level (i.e. second-order selection *sensu* Johnson, 1980), as the proportion of each habitat type within the composite area covered by all fox home ranges combined plus a buffer equal to the mean radius of a circle of area equal to the mean fox home range. The incremental buffer was used assuming that foxes have a cognitive map of the area (*sensu* Fabrigoule & Maurel, 1982) so that the available area extended beyond the home range border. Preference, avoidance or use as available was determined for each fox by using the 95, 99, and 99.9% Bonferroni confidence intervals as explained by Neu, Byers & Peek (1974). See Garshelis (2000) for a critical review of this terminology and interpretation of results. For all analyses, the estimated areas that fell on the sea were eliminated from the computations.

Areas of exclusive use for each fox as well as the spatial overlap for all pairwise combinations of foxes – of the same and of different gender – were computed to examine their spatial organization, level of territoriality – if any – and social interactions. Static animal interactions between foxes were calculated (Doncaster, 1990) and mean overlap was estimated using Minta's (1992) procedure as applied by Crooks & Van Vuren (1996). Minta's mean overlap estimate can range from 0 to 1, implying lowest to highest overlap, respectively. All the above spatial analyses were conducted using the home range and the core areas as defined above.

Habitat diversity was calculated using the H' index of Shannon–Wiener (Brower, Zar & von Ende, 1998) and was regressed on home range size to test the effect of habitat diversity on home range size (Lucherini & Lovari, 1996). To examine the effect of each habitat type on fox home range size, the percent of each habitat type within each fox range was correlated with home range size (Macdonald, 1981; Geffen *et al.*, 1992).

Habitat types

For the purpose of the analyses, according to the interpretation of a rectified and georeferenced aerial photograph taken in 1996 (1:24.000), and using ArcView 3.2, five habitat types were recognized in Ahuenco (Fig. 1). The untouched

forest was considered old-growth forest (OGF). This forest along the coast was made up mainly of wind-beaten olivillos *Aextoxicon punctatum* mixed with luma *Amomyrtus luma* trees with a dense understory. In the upland areas the OGF was composed of large tineos *Weinnmania trichosperma*, ulmos *Eucryphia cordifolia*, tepas *Laureliopsis philippinana*, maníos *Podocarpus nubigena*, arrayanes *Luma apiculata*, meli *Amomyrtus meli*, canelos *Drimys winteri*, avellanos *Gevuina avellana*, and coigües *Nothofagus nitida* trees with several strata in the understory. OGF, with a high moisture content, is rich in vines and epiphytes and the floor is almost completely vegetated. For further details on this type of forest and general features of the site, refer to Donoso *et al.* (1984). The forest in a process of regeneration, 5 m or taller, was classified as second-growth forest (SGF). Tree species of SGF were dominated by canelos, lumas, ciruelillos *Embothrium coccineum*, and pillo-pillos *Ovidia pillopillo*. Their understory was often made up of dense bamboo thickets *Chusquea quila*. Areas with scrubby vegetation were considered shrublands (SHR). These more open spaces had several species of *Berberis* spp., bamboos, murtas *Ugni molinae*, chauras *Pernettya pumila*, ñipas *Escalonia rubra*, wind-beaten olivillos and upland bromeliads *Greigia sphacelata*, and in moist sandy soils nalcas *Gunnera tinctoria* dominated. Dunes, covered by graminids *Ammophila arenaria* and wild strawberries *Fragaria chiloensis*, were classified as dunes (DUN). Everything else, including sandy and rocky shores as well as wetlands, was considered as other lands (OTL). For our analysis, it is noticeable that OTL were composed mainly (83–93%) of shores and beaches.

Data analysis

For categorical data, *G* log-likelihood-ratio goodness-of-fit tests were used (Sokal & Rohlf, 1981). To compare the frequency distributions of two data sets, two-sample Kolmogorov–Smirnov (KS) tests were used. Paired *t*-tests were used to compare the means of non-independent data sets. Other parametric tests were used when assumptions were met. Otherwise, their corresponding non-parametric counterparts were used (Siegel & Castellan, 1989). Tests were all two-tailed and the significance level was 0.05. Analyses were performed using SAS version 6.03 (SAS Institute Inc., 1989). Unless otherwise indicated, values are shown as mean $\pm$ 1 SE, sample size (*n*).

Results

Diet

In total, between October 2000 and April 2002, 179 feces that rendered 404 animal prey of 52 taxa and 20 242 seeds of three plant species were collected. By number, insects were the most abundant prey (34.7%, 22 prey types, mainly crickets and beetles), followed by crustaceans (22.5%, two shore species only), rodents (20.0%, nine species, mainly sigmodontine rodents), birds (11.9%, nine species, mainly passerines), amphibians (5.9%), ungulates (3.5%, one

species), and equal numbers of reptiles and marsupials (0.7%, one species each; Supplementary Material Appendix S1). However, given their relatively larger sizes, mammals and birds contributed to most of the foxes' diet biomass. The most frequent single animal prey consumed both in number out of all animal prey and as occurrence in the feces were the large red and nocturnal cricket *Cratomelus armatus* and the nocturnal sand-digging crab *Emerita analoga* (Supplementary Material Appendix S1). The former is a ground forest dweller and the latter lives in the sandy beaches where the waves wash the shore.

Foxes fed abundantly on the fleshy fruits of two terrestrial bromeliads. Only two seeds of the Myrtaceae tree *A. luma* were found in one fecal pellet. We found 3756 seeds of the rock bromeliad *Fascicularia* sp. and 16 080 seeds of the larger upland bromeliad *G. sphacelata* in the feces. That is an average of 21 and 90 seeds per feces, respectively. Over 19 and 57% of the feces had seeds from these two plants, respectively (Supplementary Material Appendix S1). The rock bromeliad grows on the rocks on wind-beaten and moist rocky shores, whereas the other species lives in more upland scrubby and disturbed environments.

Foxes preyed on different proportions of animal prey classes throughout the months ($G = 78.4$, d.f. $= 16$, $P < 0.001$). However, with the exception of amphibians, there were no discernible patterns in the occurrence of prey classes in the diet over time. Amphibians were eaten only during January, February, and March (Fig. 2). The consumption of fruits also showed a marked temporal pattern in the fox diet. The rock bromeliad was eaten only during November, January, and February, whereas the upland bromeliad increased in the diet over time.

Given that the availability of some dietary items is spatially very localized, and that these items were found in the feces away from their sources, foxes appeared to feed at one place and defecate at another. Even though the searching effort for feces was relatively even throughout the study site, a large fraction of the feces with marine crustaceans was found inland and up to 743 m from the nearest sandy shore (Fig. 3). Similarly, feces containing rock bromeliad and upland bromeliad seeds were found at long distances from their sources (i.e. rocky shore and shrublands, respectively). The frequency distributions of the location of feces with the two bromeliad seeds and with crustaceans were not different among themselves (all Kolmogorov–Smirnov two-sample tests, KS < 0.13, D < 0.27, KSa < 1.30, P > 0.07; Fig. 3).

Activity patterns, morphometry and weight

A total of 317 trap nights from mid-December 2000 to mid-January 2001 resulted in the capture of four male and three female Darwin's foxes. One fox was trap happy and was caught 16 times, whereas three foxes were caught only once.

Overall, out of 1291 fixes, males were similarly active as females (Wilcoxon two-sample test, $Z = -0.177$, $P > 0.860$; $42.9 \pm 10.1\%$ 4 and $43.0 \pm 8.2\%$ 3, respectively). Although there were differences in the daily activity patterns among individuals, all foxes were active throughout the day and
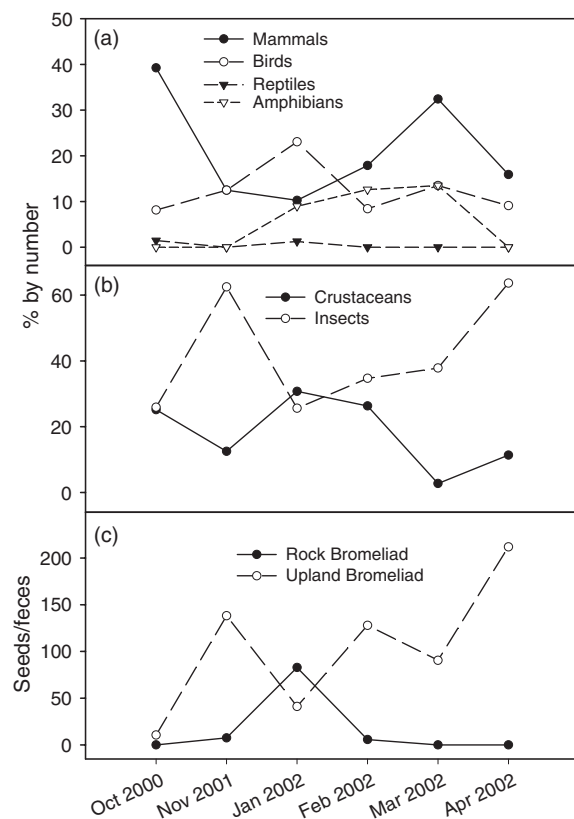

Figure 2 Numerical contribution of prey classes to the diet of the Darwin's fox *Pseudalopex fulvipes* at Ahuenco, Chiloé, and frequency of seeds in fox feces over time.

night, but males and females were more active at night ($53.2 \pm 12.4\%$ 4 and $52.9 \pm 10.1\%$ 3, respectively) than during the day ($32.8 \pm 8.2\%$ 4 and $33.1 \pm 6.4\%$ 3, respectively; paired *t*-test $t = 5.54$, $P = 0.0015$, $n = 7$; Fig. 4). Daily activity patterns did not show a distinctive peak and it did not differ between males and females (Kolmorogov–Smirnov two-sample tests, KS $= 0.0625$, $D = 0.1250$, KSa $= 0.2500$, $P = 1.0$).

Foxes did not show preferences for being active or inactive in the different habitat types. Overall, they were active or inactive in the different habitat types in proportion to their availabilities ($G = 2.850$, d.f. $= 4$, $P > 0.5$). Although variability was high among individuals, they did not show a preference for the active use of these habitats during either the day or the night ($G = 3.367$, d.f. $= 4$, $P > 0.1$; Fig. 5). That is, foxes were active or inactive during either the day or the night, irrespective of the type of habitat they were in.

Although, on average, males were heavier and showed larger total length, hind foot length, ear length, lower canine length, lower intercanine distances and carnassial length than females, these differences were not significant (Table 1). Only in the separation of the upper canines, males were larger than females (Kruskal–Wallis $\chi^2 = 4.5$, d.f. $= 1$, $P = 0.034$), which gave them an appearance of having broader muzzles in the
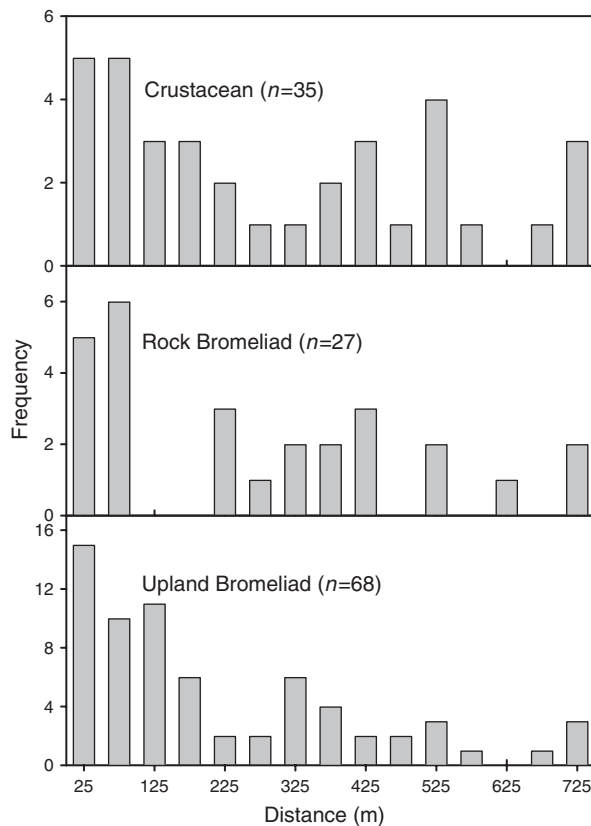
Figure 3 Frequency distribution of minimum distances to the sources of feces that contained crustaceans, rock and upland bromeliads seeds. Assumed sources were the closest sandy shore, rocky shore, and shrubland, respectively. Number of feces in parentheses.

Figure 4 Activity patterns of male and female Darwin's foxes *Pseudalopex fulvipes* during the daily cycle. Sample sizes are shown.

wild. Females appeared to have longer tails than males, but not significantly so (Table 1).

Home range size, social structure, overlaps and density

Fox home ranges varied widely in size [coefficient of variation (CV) = 51.9–74.5%] and shape among individuals (Table 2). Kernel 95% home ranges ranged from 103.2 to 487.8 ha and were always larger (1.8 times on average) than those calculated as MCPs (range 24.9–284.7 ha), but correlated well with them (r_s = 0.857, n = 7, P = 0.014). Core areas were also variable in size (CV = 53.2%) and ranged from 29.5 to 130.4 ha among foxes. Foxes spatially concentrated their activities by using on average 28.1% of their home range areas as their core areas. These were similar in size between males and females (Kruskal–Wallis χ^2 = 0, d.f. = 1, P = 1.000). Neither kernel home range nor core area sizes among individuals were correlated to the number of locations used to compute the estimator (r_s = 0.643, n = 7, P = 0.119; r_s = 0.571, n = 7, P = 0.180, respectively).

Variability in size of ranges was not due to fox gender, and it was also high within each gender (Table 2). Home range and core area sizes of males (272.5 ± 79.0 ha 4,
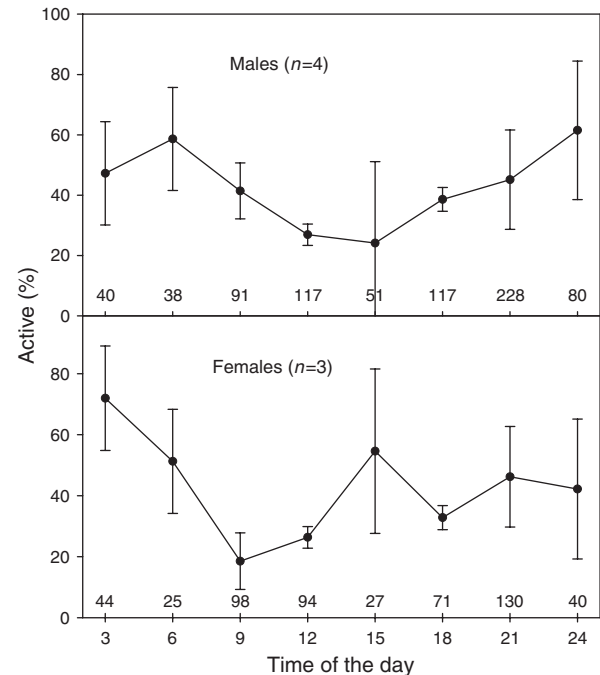
81.0 ± 23.8 ha 4) and females (306.2 ± 96.7 ha 3, 80.2 ± 25.3 ha 3) were similar (Kruskal–Wallis χ^2 = 0.125, d.f. = 1, P = 0.723; χ^2 = 0, d.f. = 1, P = 1.000, respectively).

The shape of home ranges was elongated, followed the south–north shoreline and was less variable (CV for lengths and widths 28.1 and 27.2%, respectively; Fig. 6) than home range sizes among foxes (Table 2). All fox home ranges were sandwiched between the ocean on the west and the fragmented OGF on the east (Figs 1 and 6). Home ranges were on average 2.1 times longer (2933.4 ± 311.2 m 7) than wider (1384.7 ± 142.5 m 7, Kruskal–Wallis χ^2 = 9.016, d.f. = 1, P = 0.0027). Again, although lengths and widths varied within gender, home range shapes were similar between male and female foxes (lengths: 2942.3 ± 520.9 m 4 vs. 2921.7 ± 367.7 m 3, Kruskal–Wallis χ^2 = 0, d.f. = 1, P = 1.000; widths: 1361.8 ± 164.6 m 4 vs. 1415.3 ± 295.3 m 3, Kruskal–Wallis χ^2 = 0, d.f. = 1, P = 1.000, respectively; Table 2).

Although I could distinguish that foxes M4 and F6 (M stands for male and F for female) used the northern area, M0, F1 and F5 used the southern area, M3 used the center and M2 used all areas (Fig. 6), I could not determine with certainty whether or not foxes were paired or reproductive beyond the interpretation explained below. The following social structure was inferred from the general use of space, range overlaps, interaction among foxes, age and their reproductive condition. F5 and F6 were young adult females with no previous or current breeding activity (i.e. small nipples). F1 was an older female that was lactating (dark and elongated nipples with milk) and likely paired
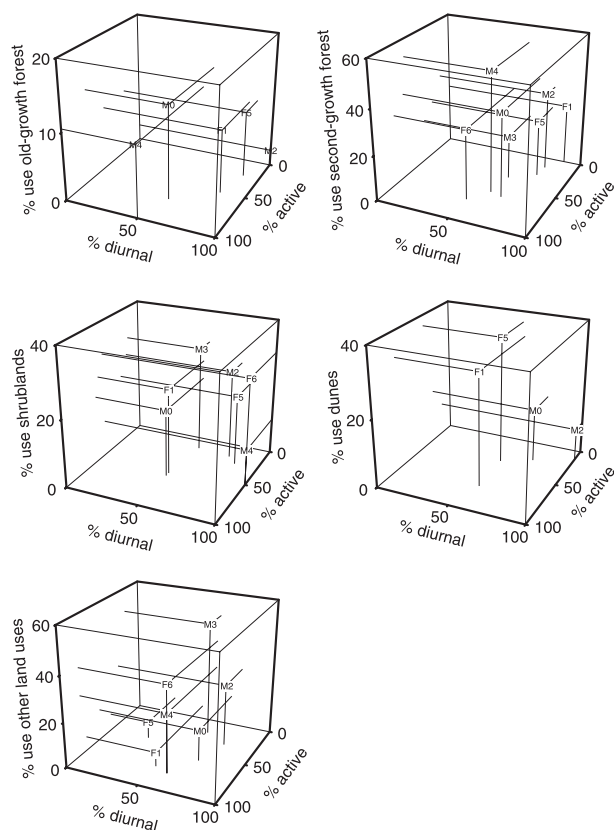
Figure 5 Active and diurnal behavior by habitat type for each individual Darwin's fox *Pseudalopex fulvipes*. M, male; F, female.

feeding from the ranger's cat pot with the pet cat. M4 might have been paired with F6 (they had very similar ranges), but she was not breeding when caught. M3 was likely not paired as he stayed on Penguin Island (or the peninsula when connected during the lowest tides) by himself for various periods of time.

Locations of foxes were never detected close (i.e. < 80 m) to each other simultaneously, nor were foxes resting together when tracked. However, foxes overlapped their home ranges and core areas extensively with individuals of the same or of different gender (Fig. 7) and appear to use the same areas at different times. For instance, the areas of exclusive use by each fox were small and varied between 0 and only 17% of their respective home ranges. Some fox home ranges were contained almost completely within other home ranges (e.g. F5 within F1), and one fox range (M0, with no area of exclusive use) was completely included into the other's space. With the exception of females F5 and F6 that did not overlap ranges, each of the other five foxes co-used at least a portion of their home range with the other six foxes. On average, 20.1–76.4% of each fox home range was shared with other foxes (Fig. 6). In pairwise comparisons of foxes of the same or of different gender, their mean home range overlap did not differ among dyads (Minta's proportions, male–female 0.45 ± 0.09 12, male–male 0.46 ± 0.07 6, female–female 0.28 ± 0.23 3, Kruskal–Wallis $\chi^2 = 1.883$, d.f. = 2, $P = 0.390$; Fig. 8).

When analyzing the overlaps of core areas among dyads of foxes, same-gender foxes showed a tendency to have larger Minta overlap values (female–female 0.23 ± 0.23 3, male–male 0.30 ± 0.08 6) than different-gender individuals (male–female 0.12 ± 0.06 12), but differences were not significant (Kruskal–Wallis $\chi^2 = 3.561$, d.f. = 2, $P = 0.1585$; Fig. 8). Although fewer foxes overlapped their core areas with neighbors and core area overlaps were smaller (0.19 ± 0.05 21) than overlap for their 95% home ranges (0.43 ± 0.06 21, t-test $t = -3.031$, d.f. = 40, $P = 0.0043$), no clear social structure or territorial behavior was evident.

The interpretation of the results is that foxes appear to be monogamous – at the most only one female per group bred –

with M0 (they had large range overlaps). F5 was probably F1's daughter from the previous season and may have helped her to raise their siblings. M2 was the oldest fox and appeared to be subordinated to the younger M0, and moved across M0 and M4 ranges. M2 was found wounded twice (he had an open wound on the shoulder and his left ear was dropped) in M0 range, whom he avoided. M2 was fed by fishermen on the shore, and on one occasion was seen

Table 1 Morphometry of Darwin's foxes *Pseudalopex fulvipes* at Ahuenco

Variable	Males		Females		χ^2	P
	Mean	SE	Mean	SE		
Weight	3238.75	109.74	2993.33	121.29	2.000	0.1573
Total length	765.00	13.39	742.33	6.23	0.500	0.4795
Tail length	228.75	4.89	235.33	8.67	0.500	0.4795
Hind foot length	106.63	2.00	103.83	0.73	1.125	0.2888
Ear length	68.38	2.26	68.17	1.20	0.125	0.7237
Upper canine length	13.33	0.92	13.50	0.70	0.127	0.7213
Lower canine length	10.73	0.38	10.63	0.41	0.125	0.7237
Upper intercanine distances	21.40	0.44	20.33	0.32	4.500	0.0339
Lower intercanine distances	19.10	0.80	19.07	0.43	0.125	0.7237
Carnassial length	13.10	0.17	12.93	0.50	0.127	0.7213

Means, 1 SE and comparison between gender (*n* for males 4; *n* for females 3) are shown (Kruskal–Wallis test with χ^2 approximation). Weights in g and lengths in mm.

Table 2 Home range size (ha) of Ahuenco foxes as computed by FK (50 and 95%) and MCP (95%) estimators

Fox	FK 50%		FK 95%				MCP 95%, home range
	Core area	Locations	Home range	Locations	Length	Width	
F1	130.4	41	487.8	64	3657	1913	270.7
F5	60.8	62	273.2	92	2543	1442	177.0
F6	49.3	12	157.7	13	2565	891	24.9
M0	131.6	39	384.3	51	3225	1608	242.2
M2	109.7	63	427.8	84	4227	1660	284.7
M3	29.5	30	103.2	42	1773	1206	49.8
M4	53.2	17	174.6	19	2544	973	37.2
CV	52.3	52.9	51.9	58.0	28.1	27.2	74.5

Length and width (m) for kernel home ranges are shown.

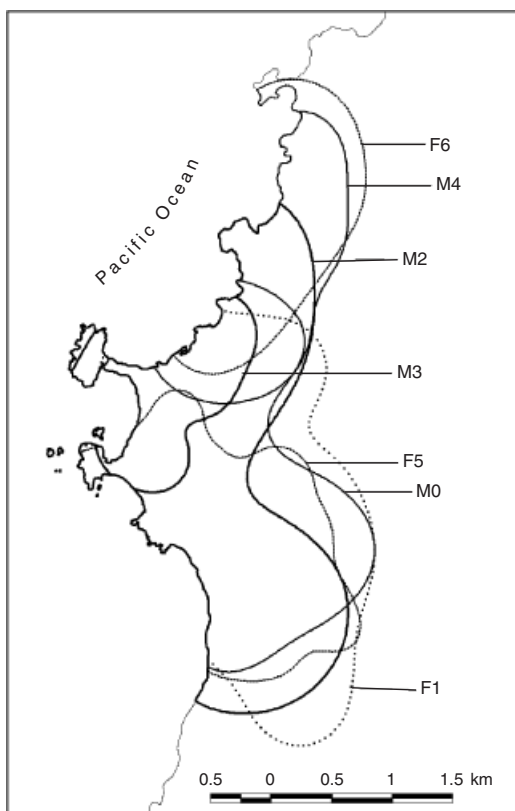FK, fixed kernel; MCP, minimum convex polygon; F, female; M, male; CV, coefficient of variation.

Figure 6 Home range (95% fixed kernel) contours of Ahuenco foxes. Acronyms as in Fig. 5.

and that subordinate individuals, either males or females, stayed within their presumable parent's or relative home range. Kinship is only assumed. Large overlaps even in their core areas (more than 10 out of 42 dyads overlapped more than 75%) indicate that foxes share rather than defend and monopolize the exclusive use of space, indicating a lack of territorial behavior.

Computed as the total number of known foxes that live in the total area used by them (considering overlapping areas), there was an ecological density of 0.92 foxes km^{-2} at Ahuen-co. This is a conservative estimate given that other foxes might be living in this same area and might have remained undetected. This was more likely in the northern and
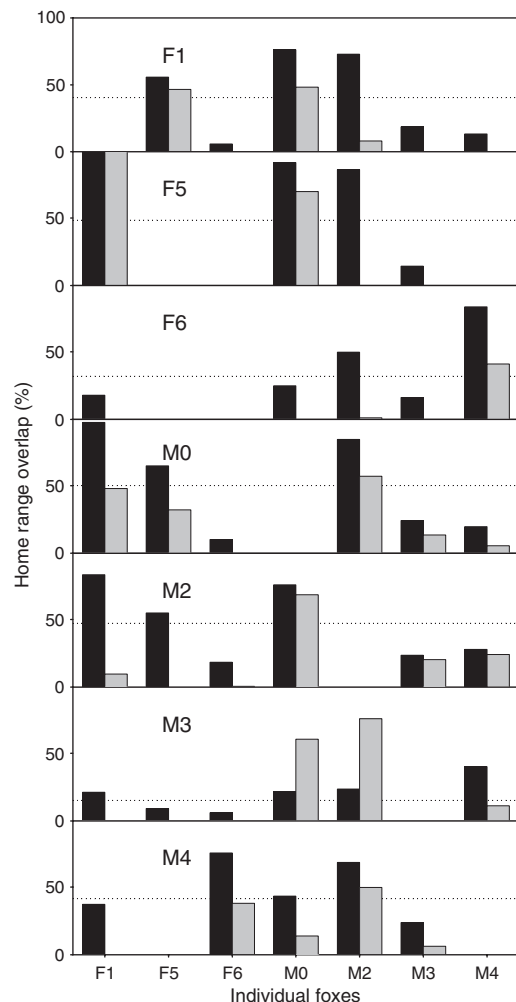

Figure 7 Home range (95% kernel, black) and core areas (50% kernel, gray) overlaps of each Ahuenco fox with the others. M, male; F, female.
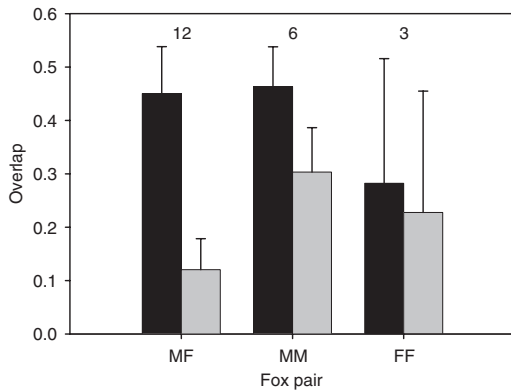
Figure 8 Minta's home range and core areas overlaps (mean and 1 SE) between foxes of the same and of different gender (shadings as in Fig. 6). Sample sizes are shown. M, male; F, female.

southern extremes or at the borders, rather than in the central area. Nonetheless, a high ecological density resulted because foxes overlapped extensively in space.

Habitat use and selection

Foxes did not use the environment homogeneously ($G = 85.54$, d.f. $= 12$, $P < 0.001$; estimated as locations). SGF, SHR and OTL (chiefly shores) were used by all
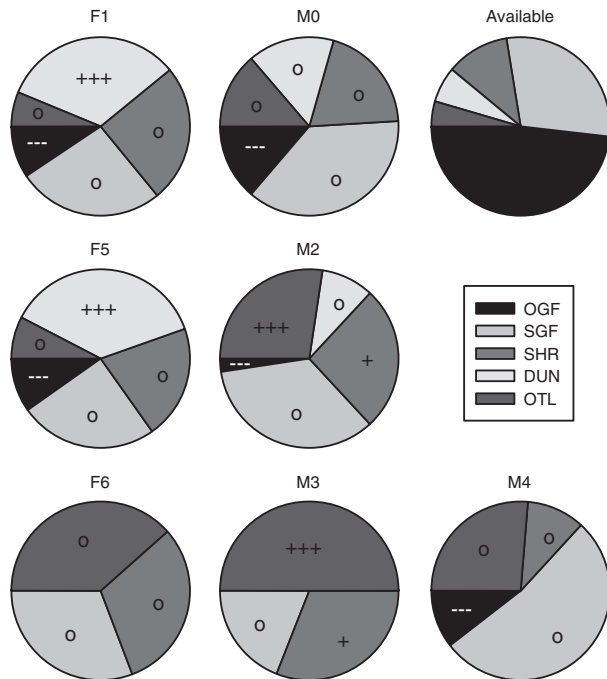

Figure 9 Habitat use and selection by individual Darwin's foxes *Pseudalopex fulvipes* and availability measured at the population level at Ahuenco. For each habitat type, the preference levels computed using Bonferroni confidence intervals are shown as 'o' for used as available, '–' for avoided and '+' for preferred. One, two and three signs represent $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively. Acronyms as in Fig. 5 and Materials and methods.

individuals. In contrast, DUN, located in the southern part of the study area (Fig. 1), was used by four foxes (intensively by F1 and F5), whereas OGF was used by five individuals (Fig. 9). Analyzing the habitat use at the core areas level did not change much the proportions of the different habitat types used by the different foxes. Three (out of seven) foxes did not include any part of OGF in their core areas.

When comparing the use and availability of the different habitat types, a high variability in habitat selection by individual foxes was evident. However, all foxes used the habitat types in proportions different from those available in the environment, and these patterns were consistent irrespective of whether the selection was estimated at the individual home range level or at the core area and whether the availabilities were computed at the individual or at the population scale (over an area of 13.6 km^2; all χ^2s > 10, all Ps < 0.03, d.f. = 4; Fig. 9). OGF was consistently avoided by all foxes. SGF and SHR, in general, were used as available. The selection of DUN and OTL was mixed. DUN was preferred by two females, used as available by two or three others and avoided by the rest. Conversely, OTL was consistently preferred by two males, whereas the rest used it as available.

Habitat diversity H' regressed on home range size was significant ($F = 9.51$, $P = 0.027$) and the relationship had a positive slope ($t = 3.084$, $P = 0.027$; Fig. 10). Habitat diversity explained 65.5% of the variability of home range sizes of foxes. This means that home range increases in size with increase in habitat diversity. Examining the contribution of each habitat type used to home range size, OGF and DUN were positively related and SGF and SHR were negatively related to home range size (borderline significant to this latter; Fig. 11). Out of the available amounts of each habitat type, however, only SHR was significant and it was negatively related to the size of home ranges (the available area includes the area within each home range in addition to a buffer strip, and thus is not independent of the amount used). The above patterns suggest that OGF and DUN appear to be 'non-essential' habitat types. Conversely, a certain amount of SGD and SHR appeared as necessary
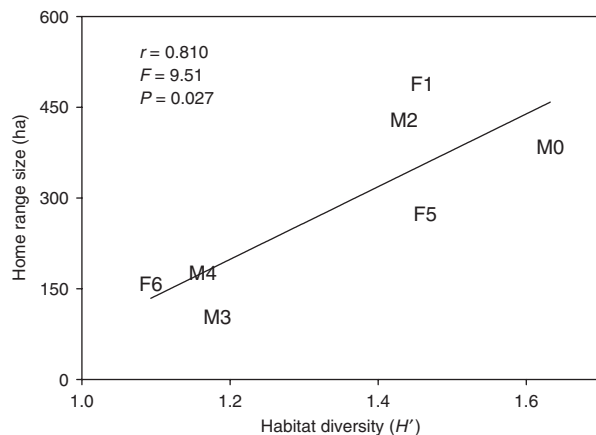

Figure 10 Regression of habitat diversity and home range size of Ahuenco foxes. Acronyms as in Fig. 5.
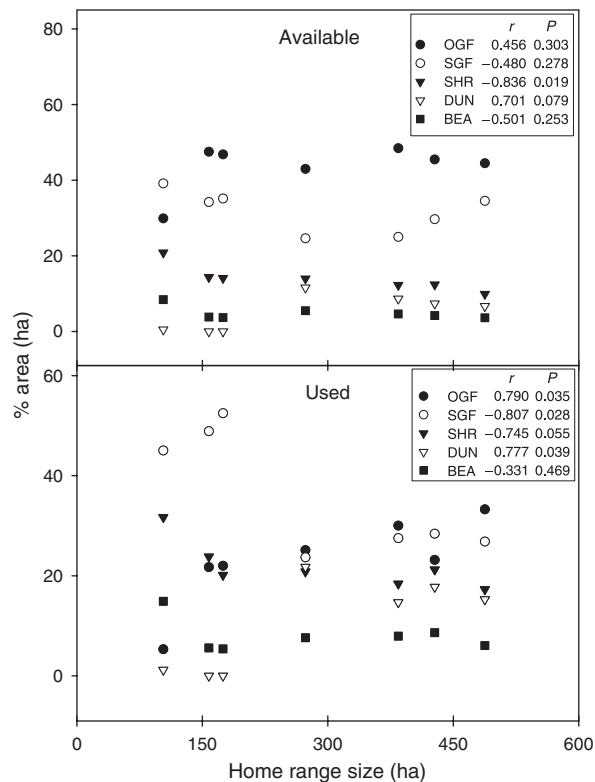
Figure 11 Fox home range sizes and habitat types used and available in Ahuenco. Correlation coefficients are shown in the upper right corner. *P*-values were not corrected to account for increased experimentwise error rate. For acronyms see Materials and methods.

habitats, and after a certain threshold was reached, foxes did not incorporate them any further into their home ranges.

Discussion

Although the Darwin's fox is a species of high conservation concern, thus far no detailed ecological studies are available that provide biological information to base conservation actions. This is the first published account on the ecology of the species on Chiloé Island and represents a study of a coastal population.

Trophic ecology and feeding behavior

In Ahuenco, the Darwin's fox behaved as a generalist predator, in line with other previous studies (Jiménez *et al.*, 1990; Medel *et al.*, 1990; Rau & Jiménez, 2002). It preyed on a large array of different prey types, including ungulates, small mammals, birds, reptiles, amphibians, crustaceans, insects, and fruits. This behavior was maintained throughout the study period, apparently not selecting any specific prey type or prey class. I did not evaluate the availability of prey for the foxes given the difficulties of assessing prey offer for a generalist predator that has a broad and diverse diet (Macdonald, 1981; Geffen *et al.*, 1992), and thus could not

evaluate prey selection. The Darwin's fox, as also found in other foxes (Greenberg, Pelton & Parr, 1988; Cavallini & Lovari, 1994; Moore & Collins, 1995) and in a previous study on this species, also behaved as an opportunistic predator (Jiménez *et al.*, 1990), apparently tracking different food resources as these fluctuated and became available in the environment over the different months studied. This fox is the largest terrestrial predator on Chiloé and, by being a generalist and opportunistic predator, pressurizes and may impact several prey populations in all the different habitat types found on the island.

With the exception of crustaceans (see below), the prey types and diversity eaten by foxes at Ahuenco generally concur with previous accounts on fox diet from other inland (Jiménez *et al.*, 1990) and coastal populations (Rau & Jiménez, 2002) from Chiloé or from the mainland (Jiménez *et al.*, 1990; Medel *et al.*, 1990). Compared with inland foxes, for similar seasons, however, Ahuenco foxes consumed more birds and fewer insects.

The Darwin's fox is a solitary forager that has seldom been reported by more than one individual during the breeding season. Although there are convergent reports of locals that foxes are capable of hunting down adult pudus (Jiménez *et al.*, 1990), the largest prey taken by foxes at Ahuenco, the *Pudu* deer and the penguins *Spheniscus magellanicus*, may have been consumed as carrion, but I did not find evidence to confirm this.

According to the prey activity patterns, foxes appeared to prey on diurnal (birds) and nocturnal prey (most of the other animals fed upon). The activity patterns studied by tracking individuals agreed well with this temporal behavior. In addition, given the prey types and behavior, foxes fed on all environments found in the area. This generalist habitat behavior was also found through telemetry. The type of habitats where foxes caught prey ranged from forest understory (most insects), scrublands (upland bromeliad), marshes (e.g. coipus *Myocastor coipus*, birds such as ducks Anatidae and a great grebe *Podiceps major*), and both rocky (rock bromeliads and penguins) and sandy shores (crustaceans). Darwin's foxes also showed the ability to feed on prey both at the ground level (most insect beetles, rhinocriptid birds such as *Pteroptochos tarnii* and *Scelorchilus rubecola*, and the litter-inhabitant mole mice *Geoxus valdivianus*) and at least on the forest understory shrubs (the arboreal marsupial *Dromiciops gliroides* and the arboreal rat *Irenomys tarsalis*).

It is noteworthy that foxes consumed the fruits of two terrestrial bromeliads abundantly. These are ripe and available during the summer and fall months. There is no previous account that documents that the fleshy fruits of these plants were consumed or dispersed by animals. It is in fact hard for humans to pull out the fruits from the plant, given the spiny leaves and fruit groups held together at the base of the plants. Local people commonly report that foxes pull the fruits from the plant by standing backward and using their muzzle and teeth between the hind legs, while separating the spiny leaves with their back. Given that feces with seeds are dispersed throughout the study site, the

Darwin's fox can be considered as a specialized mutualist that disperses the seeds of these plants. All previous reports on fox diet mentioned the consumption of fleshy fruits (Jiménez *et al*., 1990; Medel *et al*., 1990; Rau & Jiménez, 2002), but none listed bromeliads in the diet.

This is the first report of Darwin's foxes feeding on marine crustaceans. Rau & Jiménez (2002) described the winter diet of the fox in a similar coastal area at Tricolor beach (*c.* 72 km south) and did not find crustaceans preyed upon by foxes. Perhaps foxes feed on marine invertebrates only during the summer months and when they have access to sandy beaches. Marine prey items taken by foxes were also anecdotally reported by locals (Jiménez *et al*., 1990). Foxes and their tracks were commonly seen along and across sandy beaches in Ahuenco and often 'going in and out of the ocean', indicating an active searching or screening behavior for marine organisms. The observation of Osgood (1943, p. 74) on the resemblance of the premolars and mandible of Darwin's fox to that of the crab-eating fox *Cerdocyon thous*, and the implication of this species as a crab eater, supports the findings of this fox feeding on crustaceans. This feeding habit might be more pervasive for coastal populations than currently thought. Given that *Emerita* lives buried in the sand and close to where the waves break, to access them foxes must actively search for this prey by digging it out of the sand. The other crustacean, *Orchestoidea*, is very abundant at night when feeding on stranded brown algae along the shores (J. E. Jiménez, unpubl. data). When disrupted by a predator, the *Orchestoidea* swarm disperses, jumping haphazardly in all directions on the moist sand, and thus can easily be taken by foxes.

Marine items in the form of crustaceans, carcasses of marine vertebrates, and marine birds might be an important component of the diet of coastal fox populations, and marine organisms might serve as alternative or supplemental prey when terrestrial prey are scarce. Further, as reported for other coastal canids (e.g. Hersteinsson & Macdonald, 1992; Rose & Polis, 1999), the subsidy of resources from the sea might be significant, allowing the maintenance of denser coastal fox populations compared with those from inland sites. Further, it has been shown that the abundance and dispersion of resources determine a different social and population structure for coastal Arctic foxes – more packed, and having smaller and overlapping home ranges – than for more inland populations (Eide, Jepsen & Prestrud, 2004). It is likely that a similar scenario under parallel contrasting settings might occur in the Darwin's fox in Chiloé. This hypothesis, however, remains to be tested and should be explored, because it might have important consequences for the conservation of this critically endangered species.

Morphology

Basic morphological information on the Darwin's fox was reported from two individuals by Osgood (1943), one each in Pine, Miller & Schamberger (1979) and Medel *et al*. (1990), and from 16 individuals (including six from this study) by Jiménez & McMahon (2004) for Chiloé. The corresponding measurements of Ahuenco foxes fell well within the range reported by these authors. As found in the island fox (Moore & Collins, 1995), the tail in the Darwin's fox is notoriously short, being 45.2% of the head and body length (Table 1) compared with 59.7 and 60.2% for congeneric mainland culpeos and chillas, respectively (Jiménez, 1993). Similarly, as for island foxes (Moore & Collins, 1995), standardized by head and body length, the length of the legs in the Darwin's fox (20.5% in hind foot length) is shorter than in culpeos and chillas (23.3 and 23.4%, respectively). Having relatively shorter limbs and a more compact body shape represents an adaptation to its life in the dense forest understory and a means of avoiding heat loss in a cold and moist environment as in the rainforest (Jiménez & McMahon, 2004). The lack of notorious sexual dimorphism and the social system found in the Darwin's fox conform to predictions and studies in other small fox species (Geffen & Macdonald, 1992; Crooks & Van Vuren, 1996; Geffen *et al*., 1996; Roemer *et al*., 2001) that small-sized canids show little or no sexual dimorphism and are generally monogamous.

Space use and social structure

The predicted home range size would be 66.5 and 60.3 ha according to Swihart *et al*. (1988) for a hunter of the size of a Darwin's fox; 120 and 109 ha according to Kelt & Van Vuren (2001) for an omnivore of that size; and 143 and 133 ha according to Carbone & Gittleman (2002) for average males and females, respectively. The home range sizes of foxes at Ahuenco were about twice as large as that empirically or theoretically predicted, which is closer to their core area sizes, whether calculated as MCPs or as FKs. This is not an artifact of the number of locations to estimate home range given that a Monte Carlo simulation with telemetry data from a male and a female Darwin's fox from another study site using MCPs and kernel estimates produced home range sizes that converged and stabilized at a sample size of 20–30 locations (J. E. Jiménez, unpubl. data).

Social and behavioral interactions may explain why home range sizes are larger than expected by energetic considerations (Lindstead, Miller & Buskirk, 1986; Zoellick & Smith, 1992). To have very large range overlaps and sharing space with several conspecifics (i.e. sharing resources) may be the reason for having larger individual ranges than predicted on the basis of energetics alone. Perhaps resources are scarce (which is contrary to predictions for island mammals according to Stamps & Buechner, 1985, and findings by Roemer *et al*., 2001) or too dispersed to allow individuals to fulfill their needs in smaller ranges (Eide *et al*., 2004). The latter hypothesis is supported by the fact that habitat types such as dunes and old-growth forest patches, which are interspersed with the other habitat types, appear to contribute little to explain the size of foxes ranges, but are traversed by foxes (and included in their home ranges) in order to reach the 'more useful' patches such as secondary forests and shrublands (Geffen *et al*., 1992; Atwood & Weeks, 2003), which also agrees with the resource dispersion hypothesis proposed by Macdonald (1981, 1983).

The above is also in line with the fact that the size of home ranges is proportional to the diversity of habitat types within each animal range, which is opposite to the pattern shown by red foxes in Italy for habitat richness (Lovari, Lucherini & Crema, 1996; Lucherini & Lovari, 1996). At Ahuenco, for instance, the inclusion of old-growth forest and dunes, which contribute to habitat diversity (and richness) by only five and four foxes, respectively, but apparently did not provide key resources (Cavallini & Lovari, 1994), in fact adds area to the home ranges of these foxes. Thus, a mosaic of fewer habitat types with only the necessary habitat types rather than large patches of resource-poor habitats would result in smaller home ranges and explains the patterns found in Ahuenco.

The amount of time spent in a habitat type or the amount of it used (such as moving through or used while resting) do not necessarily indicate that it is key to the animals (Cavallini & Lovari, 1994). In fact, because of constraints or perceived risks, foxes might hardly use the most productive patches as found in other small canids (Geffen et al., 1992; Warrick & Cypher, 1998; List & Macdonald, 2003). However, this may not be the case with Darwin's foxes, which have few natural enemies on the island, but instead could be the response to the occasional presence of people or stray dogs in open areas and beaches.

As found in red foxes in Finland (Kurki et al., 1998), foxes at Ahuenco may be favored by a patchier or fragmented landscape than by continuous forest. This appeared to be the case in this study, where foxes did not venture much into the continuous OGF and used more the fragmented, landscape closer to the shore, which may also be related to a landscape with more productive patches. Given this and assuming that habitat use is translated into fitness, it would be interesting to evaluate whether more continuous OGFs actually support less foxes than patchy, fragmented and more open habitats. This hypothesis could be easily tested by studying foxes in areas with more continuous forests. If this is the case, then the Darwin's fox would benefit from more fragmented, and open spaces. Thus, from the landscape perspective, foxes would be favored by human disturbances rather than by having extensive and pristine forests. This is contrary to what has been repeatedly described in earlier accounts (Miller et al., 1983; Jaksic et al., 1990; Jiménez et al., 1990; Yahnke et al., 1996; Jiménez & McMahon, 2004), but has not been directly quantified as yet.

Ahuenco fox home ranges were linear and appeared to be shaped according to habitat features as described for red foxes (Ables, 1969; Macdonald, 1981) and were likely to allow an easier and faster movement through more open terrain. Whether this is associated to the constraints imposed by the coastal environment could be proven by studying inland populations.

The basic social unit of the Darwin's fox is not clear. It appears that pairs are monogamous (only one male and one female breed), but they allow other individuals of the same or of different gender in the same range; biparental care is expected, as occur in small canids (Geffen et al., 1996; Roemer et al., 2001). However, as no reproduction was directly studied, this could not be confirmed in this study. Darwin's foxes appear to have relaxed territories, if any, which is also in line with studies that demonstrate that, under low and dispersed resources, foxes have large and non-defended ranges (Angelbjörn, Ströman & Becker, 1997; Eide et al., 2004). This is also what is expected for island species (Stamps & Buechner, 1985). To verify whether this is in line with the theory, the size and amount of overlap in island foxes could be compared with those of the mainland population (Jiménez et al., 1990). The lack of strict territorial behavior is in opposition to space use by congeneric culpeos and chillas that maintain exclusive and non-overlapping territories (Johnson & Franklin, 1994; Jiménez et al., 1996; Salvatori et al., 1999).

At another scale and as expected by Samuel et al. (1985), and found in kit foxes (Zoellick et al., 2002), culpeos (Salvatori et al., 1999), and coyotes (Chamberlain, Lovell & Leopold, 2000), Darwin's foxes had smaller core area overlaps than home range overlaps. Thus, even though individuals were not territorial at the home range scale, they still appeared to maintain small exclusive areas for themselves.

I could not find any other study of foxes that live in such a moist, cool, and forested island environment to compare with. The only other well-studied island fox, the island fox Urocyon littoralis, lives in a more open and drier environment, is considerably smaller, has much higher densities and smaller home ranges and, unlike the Darwin's fox, is highly territorial (Roemer et al., 2001). In contrast, mainland gray foxes Urocyon cinereoargenteus that inhabit deciduous forest environments showed no territoriality and have large and overlapping home ranges (Haroldson & Fritzell, 1984; contrary to what was predicted by Stamps & Buechner, 1985). Hence, the forested environment may favor large home ranges and no territoriality (but see Greenberg et al., 1988).

The patterns of activity of Darwin's foxes, to be active throughout the day but more so at night, concur well with previous reports on this species (Jiménez et al., 1990) and on other canids (Haroldson & Fritzell, 1984; Cavallini & Lovari, 1994; Jiménez et al., 1996).

Abundance

Density estimation using telemetry is considered one of the best methods available for animals such as canids that are secretive and have sparse populations (Gese, 2004). However, it is unknown how biased or representative the estimated density figure is for the entire fox range. The ecological density of 0.92 individuals km^{-2} obtained for the Ahuenco foxes is not high, as expected for an island mammal (Stamps & Buechner, 1985; see also Roemer et al., 2001), and might be an underestimate as individuals may have escaped trapping and be undetected. However, the intensive trapping efforts and the high recapture rate, as well as the repeated observations of known foxes, make this unlikely. The assumption of closure of the population was likely true given that all foxes were captured within 4 weeks and no transient individuals were detected in this study. However, it is important to note that the area estimated is

affected, among other things, by the bandwidth (or smoothing parameter *h*) of the kernel home range estimator (Kernohan *et al.*, 2001), and this will influence the density estimated. Given that there is no variance associated with the density estimate and that the area surveyed was relatively small compared with the ranging behavior of the foxes, it is not known how representative this estimate is for the entire population. As pointed out above, because of the ocean-food subsidy and the effect of food resources on density (Rose & Polis, 1999; Eide *et al.*, 2004), it is likely that this coastal population might be denser than more interior populations. Previous studies pointed out that Darwin's foxes were literally unknown by locals and the few individuals observed or captured were usually from coastal populations (Osgood, 1943; Pine *et al.*, 1979; Miller *et al.*, 1983; see also Darwin's quote above), suggesting that they were more abundant in coastal environments than elsewhere on Chiloé.

In addition to the potential food supply, the large amount of edge and habitat ecotones at the site also appeared to favor a higher number of individuals compared with foxes that live in more homogeneous interior OGFs (Kurki *et al.*, 1998). Lastly, as found by Smallwood & Schonewald (1998), given that Ahuenco was chosen because it had foxes, it might represent a spot with higher fox numbers than a randomly chosen site for Chiloé. Hence, extrapolations of densities from this small site to the whole island will likely overestimate abundances.

The fact that most aspects of the ecology of Darwin's foxes (diet, activity patterns, habitat use and selection, home range size and shape, etc.), either in this study or compared with previous studies, show high variability and great differences among individuals or populations indicate that this is a generalist species that adapts readily to local conditions to exploit resources opportunistically. This same individualistic behavior, which may seem to be highly adaptive for facing natural conditions, makes it difficult when it comes to generalizing and proposing the best environmental conditions for the species in order to suggest management actions to help conserve this critically endangered species.

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Supplementary material

The following material is available for this article online:

Appendix S1 Diet composition of foxes at Ahuenco, Chiloé. Monthly totals as percent frequency by number and as frequencies of occurrence in the feces are shown. Subtotals are in bold.

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-7998.2006.00218.x

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