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Conservation and ecological implications of the use of space by chilla foxes and free-ranging dogs in a human-dominated landscape in southern Chile

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Abstract We investigated whether domestic dogs (*Canis lupus familiaris*) influenced the use of space by chilla foxes (*Lycalopex griseus*) in southern Chile and tested the hypothesis that dogs interfere with chillas. We used scent stations and occurrence of scats within systematically placed plots to assess habitat use by both species and to test whether dogs were associated to the use of space by chillas. Activity data were obtained from captures for both species, and telemetry for foxes. Diet of both species was analysed in order to tease out the potential existence of exploitation competition. We found that, when active, chillas used prairies more and native forest less than expected according to availability, whereas inactive chillas (during the day) preferred native forest, the only habitat type that dogs did not use. The odds of dog occurrence increased at shorter distance to human houses, whereas the inverse pattern was observed for chillas. Poisson models showed that the number of chilla visits to scent stations was negatively correlated with the number of dog visits. We observed dogs persecuting and/or killing chillas which was also corroborated by local people that used dogs to prevent chilla-related poultry losses, supporting the idea that dogs harass foxes actively. The analysis of scats showed that dogs fed mainly on house food and domestic ruminant carcasses whereas foxes fed on hare, hens, mice and wild birds, thus suggesting that exploitation competition is not a strong alternative hypothesis as a proximate cause for the patterns observed. We conclude that dogs seem to constrain the use of space by wild carnivores via interference.

Key words: *Canis lupus familiaris*, carnivore conservation, interference competition, intraguild killing, *Lycalopex griseus*.

INTRODUCTION

The domestic dog (*Canis lupus familiaris*), a near-ubiquitous companion of humans, can be found in almost every anthropogenic landscape and is considered an important threat to wildlife when allowed to roam freely (Iverson 1978; Boitani 1983; Taborsky 1988; Van't Woudt 1990; Butler & Toit 2002; Manor & Saltz 2004; Laurenson *et al.* 2005; Campos *et al.* 2007; Silva-Rodríguez *et al.* 2009b). Free-ranging dogs negatively affect wildlife through depredation (Iverson 1978; Taborsky 1988; Manor & Saltz 2004; Campos *et al.* 2007; Silva-Rodríguez *et al.* 2009b), fear-related alteration of activity patterns (Miller *et al.* 2001; Banks & Bryant 2007), exploitation competition (Butler & Toit 2002; Butler *et al.* 2004), hybridization (Gotelli *et al.* 1994) and disease spill-over (Laurenson *et al.* 2005), all of which greatly extend the sphere of human-related negative impacts on wildlife (Miller *et al.* 2001). Domestic dogs represent complex ecological threats to wild carnivores; many wild carnivore species are small enough to fall prey to dogs, many can experience competition and interspecific similarity introduces the dangers of disease and genetic swamping. Negative conflicts with dogs are documented or perceived for at least 25 species of canids (see species accounts in Sillero-Zubiri *et al.* 2004). Despite widespread awareness of the potential negative impacts of dogs on carnivores, few studies have characterized their nature beyond the relatively common documentation of disease transmission and genetic hybridization.

The potentially aggressive behaviour of dogs towards wild carnivores fits in the broader context of interference competition and intraguild predation within the order Carnivora, or the reduction in the ability of an organism to make use of a resource

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because of harassment or aggression by a second organism (Carothers & Jaksic 1984; Linnell & Strand 2000). Exploitation competition on the other hand is mediated by efficiency in the use of a limited resource, and may not involve direct confrontation between interacting species (Carothers & Jaksic 1984). Interference competition between carnivores frequently leads to intraguild killing, although this does not necessarily imply consumption of the dead individual (Palomares & Caro 1999). Interference competition and intraguild killing are widely observed among carnivores (Palomares & Caro 1999; Linnell & Strand 2000; Donadio & Buskirk 2006), and are more frequent among confamilial species with intermediate differences in body size and diet (Donadio & Buskirk 2006). In spite of these interactions, different species of carnivores coexist in most landscapes. Understanding the mechanisms that allow their coexistence is important for their conservation, especially considering the widespread distribution and increasing global population sizes of domestic and feral dogs.

Interactions between carnivores are mediated by behavioural responses of an individual towards the threat imposed by individuals of a larger species (Palomares & Caro 1999; Linnell & Strand 2000; Donadio & Buskirk 2006). For these interactions it is expected that the smallest species will attempt to reduce the probability of encountering individuals from a larger species. This can be achieved by increasing the levels of vigilance (Durant 2000) or by moving away from the areas frequently used by the larger carnivore (Johnson & Franklin 1994b; Jiménez *et al.* 1996, Tannerfeldt *et al.* 2002, Mitchell & Banks 2005, see also Sergio *et al.* 2003 for raptors). Such behavioural responses are similar to widely documented anti-predator behaviours (Brown *et al.* 1999; Caro 2005). This will result either in the exclusion of one species by the other or in coexistence by partitioning space-time (Johnson & Franklin 1994a). In this latter scenario, the subordinate carnivore will use lower-quality habitat (Linnell & Strand 2000), or will avoid the larger by temporal shifts in activity patterns (Harrington *et al.* 2009).

The objective of this study was to examine whether dogs affect the use of space by a smaller wild carnivore in southern Chile. Our study species was the chilla (*Lycalopex griseus*), a small-sized South-American fox (2.5–4.0 kg) that is distributed from 17°S in Chile and 23°S in Argentina to 54°S in Tierra del Fuego; the species is native in this range, except in Tierra del Fuego (González del Solar & Rau 2004). Chillas are omnivorous generalists (González del Solar & Rau 2004) and preferentially use open habitats (Johnson & Franklin 1994a; Jiménez *et al.* 1996). The chilla is considered a species of Least Concern by the IUCN which recognizes skin traffic, conflicts with humans, and probable harassment and killing by dogs as its main threats (González del Solar & Rau 2004). Dogs and chillas are sympatric in most of the chillas' range, even within some protected areas where free-ranging dogs owned by rangers, neighbours and tourists can be found (Johnson & Franklin 1994b; Silva-Rodríguez *et al.* 2009b). Considering the differences in body size between chillas and dogs, and the fact that both species are canids, both resource overlap and killing of chillas by dogs are likely to occur (Donadio & Buskirk 2006). In this scenario, we hypothesized that dogs would affect chilla's habitat use by behaviourally mediated effects (interference or predation risk). We predicted that dogs would concentrate their activity close to human houses, and chillas would be more active away from them, in habitat types that dogs do not use and/or at times when dogs are less active, thereby reducing the risk of interaction. To test this prediction, we conducted a comparative-observational study in which we assessed the association of dog activity (and distance to houses) to the presence/absence and activity of chillas, while controlling for several other covariates that could also be important for chillas' habitat use. Additionally, we measured prey distribution (see Supplementary Material) and diet overlap in order to assess if prey selection or exploitation competition could be valid alternative hypotheses to explain the patterns of space use observed.

METHODS

Study site

The research was conducted in Centinela (40°14′S; 73°04′W), a rural area located 6 km north of the city of La Unión, in southern Chile, between January and April 2006. The study site encompassed an extent of about 1500 ha of small, private farms used for agriculture (sheep pastures and wheat fields) and for pulp production. The climate is temperate humid, with yearly average precipitation of 1267 mm and temperatures of 11.6°C (Luebert & Pliscoff 2005). We characterized four land cover types for our analyses (prairie, native forest, plantation and other). The landscape was dominated by prairies of exotic grasses and interspersed with blackberry shrubs (*Rubus* spp.) that cover approximately 35% of the study area. Prairies are used by local people for raising small stock (mostly sheep and some goats) and some dairy and beef cattle (see details in Silva-Rodríguez *et al.* 2009a). Native forest represented 23% of the study area and was primarily composed of *Nothofagus obliqua*, *Laurelia sempervirens* and *Persea lingue* interspersed with bamboo (*Chusquea quila*). In the study area, forest occurred in one larger upland fragment (*c.* 280 ha) and multiple small and isolated fragments located in ravines. Forest plantations were also abundant in the area (22% of the study site) comprised of monocultures of *Eucalyptus* spp. and some pine (*Pinus radiata*). For the purpose of our study stands were considered as forest plantation only if the trees averaged over 10 cm diameter at breast height (dbh). Younger plantations and all

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other habitat types, including wheat fields, sugar beet fields, orchards, roads and streams, were grouped into the 'other' category (20% of the area).

Dog density in the study area was estimated previously, through the use of questionnaires, to be approx. 7.3 dogs/km^2; similar to that reported by other authors for comparable rural areas (5.1–7.5 dogs/km^2, Harrison 1993; 7.2 dogs/km^2, Butler & Toit 2002). Although all dogs had owners, 87.8% ranged free (Silva-Rodríguez 2006). Dogs were of mixed breeds and ranged in size from those of fox terriers (6–10 kg) to Rottweilers (40–60 kg), with most of them being of medium size (10–25 kg). All dogs were fed by their owners (Silva-Rodríguez 2006). Feral dogs were absent, as they were either eliminated to avoid livestock damage, or adopted as pups (E. Silva-Rodríguez, unpubl. data, 2006).

Habitat use estimates

We used three methodologies to assess habitat use. The first was the scent station method (Linhart & Knowlton 1975; Roughton & Sweeny 1982; Conner *et al.* 1983) that has been previously used to study habitat use by wild carnivores (Jiménez 1993; Acosta-Jammet & Simonetti 2004). We used fatty acid scent (FAS, USDA Pocatello Supply Depot, ID, USA) diluted in glycerine at 15% and applied to chalk tablets as a lure. FAS act as a lure by mimicking the odour of rotten food. Tracks were identified using the guide of Acosta and Simonetti (1999) and our previous field experience. Chilla tracks were distinguished from dog tracks because of their smaller size, more elongated shape (Miller & Rottmann 1976), and relatively larger impression of the toes in relation to the pad (J.E. Jiménez, pers. obs., 2006). No other canid was present in the area. One hundred and twenty-two different scent stations were placed systematically every 300 m, covering a total area of *c.* 1300 ha (see Supplementary Material for analysis of spatial dependence). Because of logistical constraints, the area was subdivided in five grids each covering 130–145 ha. Monitoring was conducted during two periods of three consecutive days between January and March 2006. After discarding non-operative scent stations (those destroyed by birds or cattle) a total of 690 scented stations day were used in the analysis. A station was considered to be visited by a chilla or a dog if we found their tracks at least once during the 6-day period. In addition, we recorded the total number of days that each station was visited.

We used the occurrence of scats as a second method to evaluate habitat use. We recorded the presence of recent chilla and dog scats within 20-m-radius plots centred at each scent station, prior to the application of scent in order to keep independence among methods. Thus, we did not consider all the scats that appeared after scent stations were activated because they could be correlated with visits to the station during the same time interval. Analysis was performed considering the presence/absence of scats at each station. Recording the presence of scats within systematically placed stations to explore habitat use has proven to be a reliable technique (Weckerly & Ricca 2000) by reducing the problems of differences in probability of detection among habitats (Virgos *et al.* 2002).

Radio-telemetry was the third method used to study habitat preferences of chillas. This method provided information on both active and inactive animals. Animals were captured with fish-baited soft Victor leg-hold (77 traps/night) and Tomahawk traps (145 traps/night). Traps were checked at least every 12 h (7:00 and 19:00). Seven chillas – four females and three males – and six dogs – five males and one female – were captured. Although traps were run on daily cycles, chillas were only captured at night, whereas, all but one of the dogs were captured during the day. Five chillas – three females and two males – were radio-collared. One of the non-collared chillas was maimed and killed by local people when in the trap and the other was released after it was measured (mean weight of the seven captured adult chillas = 3.3 ± 0.2 kg (SD)). Chillas were chemically immobilized using a ketamine hydrochloride (10 mg/kg) and xylacine (1 mg/kg) protocol, weighed, measured, fitted with a numbered ear tag and with 30–38 g activity-mode 148–150 MHz Wildlife Materials (Carbondale, IL, USA) and ATS (Isanti, MN, USA) transmitters and released at the capture site after recovering from the drug. Other species that were trapped including domestic dogs and cats were released without chemical immobilization.

Telemetry fixes were taken from mid February to April 2006. Locations of foxes were estimated from triangulations obtained with three-element handheld Yagi antennas and Telonics TR-2 receivers from at least three points (White & Garrot 1990). Locations of points were determined using a GPS unit and azimuths were obtained using a compass. Animal activity was determined through the activity mode of the radio collars. To minimize errors because of animal movement, only bearings taken within 15 min where the angle of intersection was between 45° and 135° were included in the results (Horner & Powell 1990). To account for potential temporal dependence (Swihart & Slade 1985), no more than one location was obtained daily. Between 30 and 32 fixes were obtained for each fox. Fixes were evenly distributed between day and night (46.7–63.3% of locations were nocturnal). Female fox F5 was not included in the analysis because it was killed by domestic dogs within a week of being radio-collared. Locations were estimated with LOAS (3.02) and home ranges with BIOTAS (1.03) (Ecological Software Solutions, Urnäsch, Switzerland). The 95% fixed kernel (FK) algorithm was used as the home range estimator. Bandwidth was estimated using the minimum square cross-validation. For comparative reasons minimum convex polygons were also computed. The habitat in which each animal was located was assigned to each location and was confirmed by plotting all fixes onto a digital vegetation map of the area (scale 1:20 000). Available habitat was estimated at the individual level as the proportion of each habitat type within the fox home range (third order habitat selection, *sensu* Johnson 1980). Through interviews, we collected information and estimated the number of houses, dogs and persons located within the home range of each individual fox.

Habitat characterization

Habitat type (as described above), distance to closest road, distance to nearest house and presence of a hedgerow within 25 m were computed for each scent station. Vegetation struc-

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ture was evaluated at each station using the line-intercept technique (Brower *et al.* 1990) measuring the proportion of the ground projection of the vegetation at one metre height across four lines of 15 m each (Mueller-Dombois & Ellenberg 1974; Larson & Bock 1986). Transects began at each station and were directed towards the four cardinal points. Canopy closure was estimated in each spot by taking photos of the canopy from ground level with a 35 mm lens and analysed with Adobe Photoshop (Adobe Systems, Mountain View, CA, USA). We also estimated a horizontal visibility index as the proportion of a white and black painted one-metre stick located at the centre of each scent station that could be seen from 50 cm – height of the head of a chilla – 15 m away from the scent station in the direction of the four cardinal points (Jiménez 1993).

Diet

We collected 69 scats of dog and 223 of chilla across the study site. Scats were identified based on diameter (chillas <15 mm, Jiménez 1993), shape and odor, and by other cues such as presence of fresh tracks or direct collection from the animal (traps or detection of the animal when defecating). The content of the scats was not used as a criterion for discriminating scats. We discarded scats collected in the vicinity of one house that had fox-terrier dogs – given that they were more likely to be confounded with fox scats because of their smaller diameter – and those that could not be easily attributed to each of the species. Prey items were identified by comparing the remnants against determination keys, reference collections and samples collected in the field. Food remains were prepared following standard procedures (Day 1966; Coman & Brunner 1971) and identified to the highest taxonomic level possible using keys available for the region (Chehébar & Martin 1989; Reyes 1992; Pearson 1995). As most dogs in the area were fed by local people, we considered the presence of any items that do not occur in the area as proof of human-provided food (e.g. rice, corn, legumes, wheat bran, etc.). The presence of sheep or cattle bones with evidence of saw marks was identified as human-provided food, otherwise such bones were considered as eaten from a carcass (no domestic ruminant were killed by predators in the area). During the study, poultry losses affected some houses (Silva-Rodríguez *et al.* 2009a). Thus, the finding of chicken remains was highly likely to be related to predation either by dogs or foxes. However, dogs are commonly fed with chicken bones (Silva-Rodríguez 2006). Thus, as a conservative measure, we only considered the finding of chicken remains as predation when feathers were also present; otherwise chicken bones were considered as human-provided food.

We calculated the percent frequency of occurrence (FO) as the frequency of scats that had each prey type. We also calculated the frequency by number (FN) as the number of times a prey item occurred as a percentage of the total number of prey items across all samples (Donadio & Buskirk 2006). The calculation of %FN only considered vertebrate items (Jiménez 2007) and human-provided food when evidence was found. To estimate the similarity between dog and chilla diet we calculated the Schoener index of percent overlap (Schoener 1970):

$$P_{jk} = 100\sum^{n} \min(p_{ij}, p_{ik})$$

where P_{jk} is the dietary overlap between species j and k; p_{ij} is FN of item i for species j; p_{ik} is FN of item i for species k; and n is the total number of categories. For the purpose of calculating this index and avoiding bias in terms of taxonomic resolution, we used order as the unit for analysis. This can lead to overestimation of the true overlap, and thus, we are confident that our estimates are conservative. Human-provided food was considered a valid food item for the estimation of niche overlap, given that most householders do feed their dogs (Silva-Rodríguez 2006), and thus, its exclusion could lead to overestimating the overlap. However, the occurrence of human-provided food is likely to be underestimated given our inability to identify human-provided food that do not produce solid residues.

Data analysis

Habitat selection for all three methods was estimated following Neu *et al.* (1974). This method consists in comparing the use of habitats against their availability in the area, by using goodness-of-fit tests (chi-square). If significant, multiple comparisons are performed by constructing confidence intervals for each observed proportion of occurrence in each habitat type in order to determine whether expected values (p_0) lie within the magnitude of the significant effects (Neu *et al.* 1974). Given that the level of significance is influenced by the number of simultaneous comparison performed, we adjusted the z-values used to calculate the confidence intervals by applying the Bonferroni correction (Neu *et al.* 1974). This is a conservative method that provides reasonable type I error rates (Bingham & Brennan 2004) as well as consistent habitat selection patterns across levels of habitat availability (McClean *et al.* 1998). For the analysis of scent stations and scat data, habitat use is represented by the presence or absence of signs in or around the stations, and availability corresponds to the proportion of scent stations in each habitat type. For the analysis of telemetry data, use was analysed at the level of individual locations and availability was measured as the proportion of the home range composed by each habitat type. Differences in vegetation structure across habitat types were compared by using the nonparametric Kruskal–Wallis test (Zar 1999), and pairwise comparisons were tested a *posteriori* using multiple comparisons of mean ranks. For the purpose of our study, we considered differences to be significant at $\alpha < 0.05$.

To assess the effects of habitat variables on chilla and dog habitat use, we used generalized linear models assuming binomial distribution and logit link (logistic regression) for presence-absence data and Poisson distribution and log link for count data (Agresti 2007). Models were run separately for scats, visits and count data (number of visits) for dogs and chillas. Independent variables assessed include habitat type, visibility, presence of a hedgerow within 25 m, distance to closest road and distance to closest house as predictors for the presence of foxes or dogs at stations. In addition, we considered whether a station was positive for dogs as a predictor variable for chilla occurrence and the number of dog visits as a predictor for the number of visit by chillas (count data). We dealt with multicollinearity by dropping from the

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model all predictor variables whose variance inflation factor (VIF) was higher than 2.5 (Tolerance <0.4; Allison 1999). There were three variables with high VIF (Table 1). After removing canopy cover and vegetation cover from the analysis, VIF for the visibility index dropped to 1.2, and thus was allowed in the analysis. Given that the interest in the analysis of the number of visits by both canids was to have an estimate of visit rate, we included the number of days each scent station was active as an offset term to the models based on count data (Agresti 2007).

For model selection purposes we utilized the Akaike information criterion (AIC) corrected for small sample size (AIC_c) when using logistic regressions, and quasi-AIC ($QAIC_c$) that considers a variance inflation factor $\hat{c}$ (as χ^2/d.f., using the global model) as a parameter to account for overdispersion in the case of Poisson regressions (Burnham & Anderson 2002). We estimated Akaike differences (Δ_i) and weights (w_i) to determine the level of support for each of the candidate models, and the sum of Akaike weights ($w_+(j)$) obtained as the sum of w_i across all models where variable j occurs, as an estimate of the relative importance of each predictor variable (Burnham & Anderson 2002). Estimates and standard errors presented are conditional on the best AIC model. Model effects for the best AIC model were tested using the likelihood-ratio test, and goodness of fit was assessed using the Hosmer-Lemeshow statistic for binomial models and the deviance for Poisson models (Agresti 2007). Analyses were performed using SPSS 16.0 (SPSS Inc. Headquarters, Chicago, IL, USA).

RESULTS

Habitat structure

Most variables measured differed between habitat types. Native forest had the lowest visibility indexes and the highest canopy and vegetation cover in the other layers whereas prairies had the lowest values in all vegetation-related variables. Scent stations located in forest plantation were located closer to the roads than the scent stations located in the remaining habitat types, whereas stations located in native forest were farther away from houses than stations located in other habitat types (Table 1).

Habitat use *versus* availability

Twenty-two stations were visited only by chillas, 32 only by dogs and 20 by both canids. Scent stations were never visited simultaneously by chillas and dogs. Sixteen stations had only chilla scats, 16 only dog scats and six had scats of both species. Chillas used prairies more and native forest less than expected (for visits: $\chi^2 = 11.34$; d.f. = 3; $P = 0.01$; for scats: $\chi^2 = 9.81$; d.f. = 3; $P = 0.02$; Fig. 1). Dogs used habitat types according to their availabilities (for visits: $\chi^2 = 6.96$; d.f. = 3;

Table 1. Differences in habitat variables measured at scent stations among the main four habitat types available at Centinela, southern Chile ($n = 122$)

	Habitat type						Collinearity statistics	
	Forest plantations	Native forest	Prairies	Others	H	P	Tolerance	VIF
Visibility (%)	46.3 ± 5.8^a	11.5 ± 3.0^b	51.5 ± 4.8^a	48.6 ± 4.6^a	29.69	<0.001	0.4	2.8
1-m vegetation cover (%)	9.2 ± 1.7^a	20.2 ± 2.0^b	6.2 ± 1.2^a	3.9 ± 1.4^a	38.14	<0.001	0.2	4.8
Canopy cover (%)	19.7 ± 1.9^a	60.8 ± 2.3^b	1.4 ± 0.6^c	5.7 ± 2.6^c	93.15	<0.001	0.1	8.5
Distance to nearest road (m)	89.7 ± 16.6^a	311.6 ± 52.0^b	$208.9 \pm 24.9^{b,c}$	$121.3 \pm 26.5^{a,c}$	4.383	0.222	0.6	1.6
Distance to nearest house (m)	304.5 ± 32.0^a	601.8 ± 69.0^b	285.9 ± 30.0^a	$342.3 \pm 51.0^{a,b}$	17.32	<0.001	0.6	1.8

Data are presented as mean ± 1 SE. Kruskal–Wallis H values and probabilities are shown. Same letter within a row indicate that differences are not significant (Multiple comparison of mean ranks, $P > 0.05$). The tolerance and VIF are shown for each variable. VIF, variance inflation factor.

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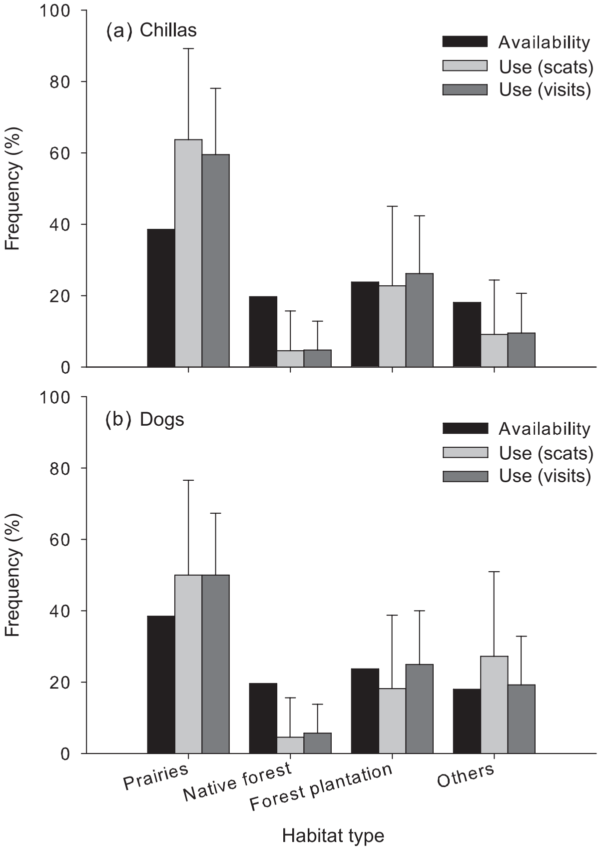

Fig. 1. Habitat use and selection by chillas and dogs. Availability corresponds to the proportion of scent stations in each habitat type. Use is shown as the proportion of scent stations were scats or visits were registered. Error bars correspond to 95% Bonferroni confidence intervals on the observed frequencies.

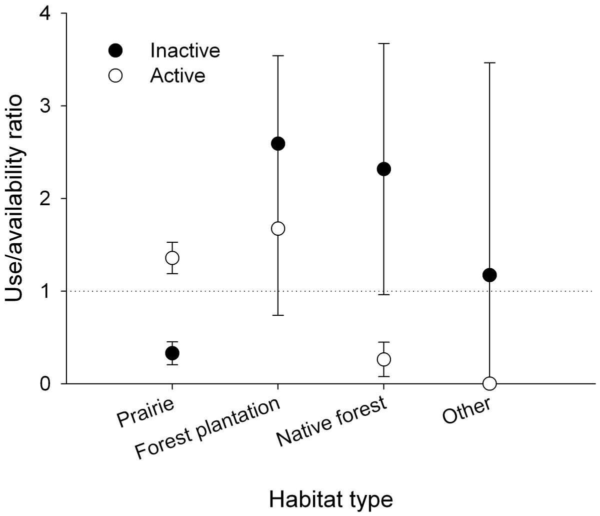

Fig. 2. Habitat preference by active and inactive chillas ($n = 4$) as measured using radiotelemetry. The use-availability ratio represent the proportion of locations in a given habitat type divided by the proportion of the home range composed by that habitat type, averaged across individuals foxes. Error bars represent 95% confidence intervals. The dotted line indicates use-according to availability. Use-availability ratios above and below the dotted line indicate preference and selection against, respectively.

$P = 0.073$; for scats: $\chi^2 = 4.64$; d.f. = 3; $P = 0.20$), except for native forest that was used less than expected (Fig. 1).

Telemetry showed that all foxes were more likely to be active at night (76.3% ± 7.1%) than during the day (27.3% ± 8.7%). Active foxes spent most of their time in prairies. Inactive chillas were more likely to be recorded in native forest or forest plantation (Fig. 2). Fox home ranges (95% FK) were between 103.5 and 279.9 ha (Table 2). The density of houses and dogs within chillas home-ranges varied between 2.9 and 3.8 houses/km^2 and 5.4–8.8 dogs/km^2, respectively (Table 2).

Habitat use models

For chillas two visit-based binomial models were substantially supported by the data, and six similar models were supported by the analysis of scat data (Table 3). Both the best AICc model and the sum of AICc weights provide strong evidence for the relative importance of habitat, presence of hedgerows and distance to houses as predictor variables for the presence of chilla signs (visits and scats, Table 4). The logistic regression conditional on the best model selected for each of the methods showed that prairies, closeness to a hedgerow and larger distance to houses increased the odds of detecting chillas at scent stations (Table 5). The analysis of visit rates by chillas (Poisson regressions) provide substantial support for six models (Table 3) and strong evidence for the relative importance of habitat type and number of dog visits as predictors for chilla visit rate (Table 4). Given the best QAIC$_c$ model, visitation rates by chillas were higher in prairies, forest plantation, when hedgerows were present and at larger distance to roads, and were lower when dog visitation rates increased (Table 5). There was no evidence of lack of fit (Visits, Hosmer-Lemeshow, $\chi^2 = 3.664$, d.f. = 8, $P = 0.886$; Scats, Hosmer-Lemeshow, $\chi^2 = 7.307$, d.f. = 8, P= 0.504; Count, Deviance, $\chi^2 = 81.582$, d.f. = 115, $P = 0.992$) for any of the chilla models.

In the case of dogs, 10 visit-based models were equally supported given the data. For the analysis of scats two models were substantially supported by the data (Table 3). Both visit and scat models provide strong support for the effect of distance to houses, and to a lesser extent, distance to road as important predictors for habitat use, whereas only scat data provided

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Table 2. Home range size (ha) of Centinela chillas (southern Chile) as computed by fixed kernel (FK 50% and 95%) and minimum convex polygon (MCP 95%) estimators

	MCP 95%	FK 50%		FK 95%		Density (ind/km^2)		
Fox	Ha	*n*	Ha	*n*	Ha	Dogs	People	Houses
F1	41.7	18	15.9	32	103.5	5.8	7.7	2.9
F2	115.9	15	45.9	31	279.9	7.1	7.9	2.9
M1	82.8	16	38.3	30	226.0	8.8	9.7	3.5
M2	79.2	13	14.6	30	130.8	5.4	9.2	3.8

Densities of dogs, people and houses were computed based on FK 95% and data from surveys. F, female; M, male.

Table 3. Summary of model selection to evaluate the effects of candidate predictors on the use of space by chillas and dogs in a rural area in southern Chile

Species	Method	Model	*K*	AIC$_c$	Δ_i	w_i
Chilla	Visits	Habitat, hedgerow, house	6	135.6	0.00	0.59
		Habitat, hedgerow, house, road	7	137.1	1.48	0.13
	Scats	Habitat, hedgerow, house	6	104.2	0.00	0.45
		Habitat, hedgerow	5	105.6	1.42	0.11
		Habitat, hedgerow, road	6	105.8	1.60	0.09
		Dog, habitat, hedgerow, house	7	105.9	1.72	0.08
		Habitat, hedgerow, house, road	7	106.1	1.93	0.07
		Dog, habitat, hedgerow, house	7	106.1	1.94	0.06
	Count	Dog, habitat, hedgerow, road	7	153.1	0.00	0.25
		Dog, habitat, house	6	153.4	0.32	0.19
		Dog, habitat	5	153.4	0.36	0.18
		Dog, habitat, hedgerow	6	153.9	0.79	0.12
		Dog, habitat, hedgerow, house	7	153.9	0.81	0.11
		Dog, habitat, road	6	154.4	1.34	0.07
Dog	Visits	Habitat, house, road	6	152.1	0.00	0.21
		House, road	3	152.2	0.10	0.19
		House, road, visibility	4	152.7	0.57	0.12
		Hedgerow, house, road	4	153.2	1.09	0.07
		Hedgerow, house, road, visibility	5	153.3	1.16	0.07
		Habitat, road	5	153.5	1.34	0.05
		House, visibility	3	153.6	1.43	0.05
		Hedgerow, house, visibility	4	153.6	1.45	0.05
		House	2	153.7	1.59	0.04
		Habitat, hedgerow, house, road	7	153.8	1.64	0.04
	Scats	Hedgerow, house, road	4	102.5	0.00	0.58
		Hedgerow, house	3	103.5	0.98	0.22
	Count	House, road	3	155.2	0.00	0.52
		House, road, visibility	4	156.3	1.15	0.16
		Hedgerow, house, road	4	157.1	1.89	0.08
		Habitat, house, road	6	157.1	1.94	0.07

Only models with substantial support ($\Delta_i \leq 2$) are presented. For count data AIC$_c$ correspond to QAIC$_c$, to account for overdispersion, and the variance inflation factor $\hat{c}$ was calculated for the global model (chillas $\hat{c} = 1.692$; dogs $\hat{c} = 1.709$). AIC, Akaike information criterion; Δ_i, difference between AIC$_c$ best model and model *I*; *K*, number of parameters; w_i, Akaike weight.

important evidence for an effect of hedgerows (Table 4). The analysis of the best model selected using both methods showed that the odds of detecting dogs increased as distance to road and distance to house decreased (Table 5). The visit-based best model also suggested that the odds of detecting dogs increased in prairies relative to native forest, whereas the scat-based model suggested that the odds of detecting dogs increased when hedgerows were present. Similarly, for count data four models were equally supported by the data (Table 3), and there was strong evidence for the relative importance of distance to houses and distance to roads as predictors for dog's habitat use (Table 4). The Poisson regression on the best model suggests that the visit rate by dogs increased as distance to closest road and house

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Table 4. Relative support for predictors of chilla and dog habitat use as measured through three different methodologies, in southern Chile

		$w_+(j)$					
Species	Method	Dog	Habitat	Hedgerow	House	Road	Visibility
Chillla	Visit	0.099	0.999	0.999	0.887	0.243	0.101
	Scat	0.153	0.961	0.999	0.706	0.230	0.124
	Count	0.957	0.999	0.525	0.340	0.373	0.033
Dog	Visit	–	0.388	0.276	0.915	0.804	0.339
	Scat	–	0.032	0.948	0.993	0.735	0.122
	Count	–	0.139	0.136	0.960	0.921	0.246

$w_+(j)$ = sum of Akaike weights across all models where variable *j* occurs.

Table 5. Fitted generalized linear models for habitat use by chillas and dogs in a rural area of southern Chile

					Model effects		
Species	Method	Predictor	Estimate	SE	LR	df	*P*
Chilla	Visits	Intercept	−1.739	0.557			
		Habitat			22.709	3	<0.001
		Forest plantation	0.797	0.422			
		Prairies	1.563	0.403			
		Other	−0.579	0.521			
		Hedgerow (presence)	0.753	0.254	9.396	1	0.002
		House (km)	2.427	1.096	5.389	1	0.020
	Scats	Intercept	−2.661	0.669			
		Habitat			11.364	3	0.010
		Forest plantation	0.555	0.543			
		Prairies	1.412	0.481			
		Other	−0.548	0.683			
		Hedgerow (presence)	0.859	0.279	10.065	1	0.002
		House (km)	2.253	1.203	3.591	1	0.058
	Count	Intercept	−6.704	0.358			
		Habitat			17.352	3	0.001
		Forest plantation	0.821	0.337			
		Prairies	0.807	0.283			
		Others	−0.290	0.478			
		Hedgerow (presence)	−0.258	0.158	2.568	1	0.109
		Road (km)	1.545	0.992	2.333	1	0.127
		Dog count	−0.369	0.193	4.389	1	0.036
Dog	Visits	Intercept	0.706	0.431			
		House (km)	−2.019	1.115	3.515	1	0.061
		Road (km)	−3.354	1.646	4.550	1	0.033
		Habitat			6.520	3	0.089
		Forest plantation	−0.009	0.366			
		Prairies	0.777	0.349			
		Other	0.161	0.396			
	Scats	Intercept	0.380	0.540			
		Hedgerow (presence)	0.596	0.270	4.838	1	0.028
		House	−4.216	1.813	7.306	1	0.007
		Road	−3.826	2.350	3.079	1	0.079
	Count	Intercept	−5.100	0.200			
		Road (km)	−2.556	0.945	7.756	1	0.005
		House (km)	−2.170	0.639	5.037	1	0.025

Estimates are conditional on the best Akaike model. Models for visits and scats assume a binomial distribution and logit link, whereas models based on count data assume a Poisson distribution and log link. SE estimates for count data were adjusted by $\hat{c}$ (for chillas $\hat{c} = 1.692$; for dogs $\hat{c} = 1.709$). Model effects were tested using the LR. LR, likelihood-ratio test.

Table 6. Diet of chillas and dogs at Centinela, southern Chile, based on the analysis of 223 and 69 scats, respectively

	Chilla			Dog		
	n	FO (%)	FN (%)	*n*	FO (%)	FN (%)
Mammals						
Carnivora[†]	0	0.0	0.0	2	2.8	3.4
Artiodactyla[†]	1	0.4	0.8	13	18.8	22.0
Lagomorpha[†]	20	9.0	15.2	3	4.3	5.1
Rodentia	46	20.6	34.8	4	5.8	6.8
Undetermined	4	1.8	3.0	4	5.8	6.8
Birds						
Passeriformes	19	8.5	14.4	2	2.9	3.4
Columbiformes	2	0.9	1.5	0	0.0	0.0
Charadriiformes	0	0.0	0.0	2	2.9	3.4
Piciformes	1	0.4	0.8	0	0.0	0.0
Tinamiformes	1	0.4	0.8	0	0.0	0.0
Eggs	3	1.3	2.3	0	0.0	0.0
Anseriformes[†]	1	0.4	0.8	0	0.0	0.0
Galliformes[†]	19	8.5	14.4	3	4.3	5.1
Undetermined	6	2.7	4.5	1	1.4	1.7
Reptiles						
Squamata	7	3.1	5.3	0	0.0	0.0
Amphibians						
Anura	2	0.9	1.5	0	0.0	0.0
Insects						
Dermaptera	9	4.0		0	0.0	
Orthoptera	91	40.8		1	1.4	
Coleoptera	124	55.6		5	7.2	
Hymenoptera	13	5.8		0	0.0	
Undetermined	9	4.0		0	0.0	
Plant						
Fruits/seeds	148	66.4		18	26.1	
Others						
House food	0	0.0	0	25	36.0	42.4

[†] Only non-native species. FO, frequency of occurrence estimated as the proportion of scats that contained each prey item; FN, frequency by number as the number of times a prey item occurred as a percentage of the total number of prey items in all samples; *n*, number of scats that contained each prey item.

decreased (Table 5). There was no evidence of lack of fit for the models selected for dogs (Visits, Hosmer-Lemeshow, $\chi^2 = 4.242$, d.f. = 8, $P = 0.835$; Scats, Hosmer-Lemeshow, $\chi^2 = 5.163$, d.f. = 8, $P = 0.740$; Count, Deviance, $\chi^2 = 87.632$, d.f. = 119, $P = 0.982$).

Diet

The diet of chillas in the area was numerically dominated by insects (71.3% FO) and fruits (66.4% FO), in particular by the red cricket *Cratomelus armatus* (Orthoptera: Anostostomatidae; 36.8% FO), the ground beetle *Ceroglossus* spp. (Coleoptera: Carabidae; 32.7% FO), the bromeliad *Greigia sphacellata* (26.9% FO) and cherries (26.5% FO). Among vertebrate items, the most frequent items were rodents (20.6% FO), hares (*Lepus europaeus*, 9.0% FO) and chickens (9.0% FO). For the dogs the most frequent items in their diet were house food (36% FO), fruits (26.1% FO; particularly cherries, 13.0% FO) and cattle carcasses (18.8% FO). According to the Schoener index, foxes and dogs overlapped in 25.8% of their diet (see data in Table 6).

DISCUSSION

Habitat use by chillas

Many fox species have been reported to be habitat generalists (i.e. Jiménez 1993, 2007, Crooks 2002; Acosta-Jammet & Simonetti 2004), and are considered less sensitive to habitat loss than are habitat specialist carnivores (Crooks 2002; Acosta-Jammet & Simonetti 2004). Moreover, foxes and other small and medium-sized carnivores might actually benefit from habitat fragmentation through mesopredator release (Crooks & Soulé 1999), subsidies in the form of

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anthropogenic and non-native food (Fedriani *et al.* 2001) and even by the creation of suitable open habitats (Crooks 2002). Habitat use and diet of chillas at Centinela were consistent with these patterns as they selected habitat types created by humans (i.e. prairies) over native forest (Figs 1,2) and an important proportion of their diet was composed by non-native species (such as hens and hares). Within individual home-ranges chillas used prairies most of the time when active and selected native forests or plantations when inactive (Fig. 2). The prey items used by chillas were also more associated with prairies, and concentrated in hedgerows (see Supplementary Materials). Consistent with this, prairies had high visibility (Table 1), which could increase the probability of prey detection relative to other habitat types with lower visibility such as native forest. It is possible therefore that habitat preferences by chillas are partially driven by food availability (but also see discussion on interference interactions below).

Habitat use by dogs

Dogs used habitat according to its availability, except for the native forest that was used less than expected (Fig. 1). Avoidance of native forest could be an artifact of higher distance of this habitat type to houses (Table 1) rather than selection against. The only variables that were consistently associated with the odds of dog occurrence, as well as visitation rates, were proximity to houses and proximity to roads (Table 5). Different authors have reported that free-ranging owned-dogs concentrate activity around their owners' houses (Daniels & Beckoff 1989; Meek 1999; this study) defending only a small area nearby (Daniels & Beckoff 1989). This could be explained by the fact that people provide their dogs with shelter and food. Dogs seemed to have diurnal activity patterns as reflected by their captures and by the fact that – during nocturnal telemetry – dogs in 19 houses (those that were along the road that we travelled along all nights) were almost always resting at close distance from their houses (usually <50 m; E. A. Silva-Rodríguez, pers. obs., 2006). This is likely to be associated with the diurnal activity patterns of their owners.

Non-lethal effects of dogs on chillas' use of space

At a coarse spatial scale, dog and chilla habitat use overlaps. This is supported by the fact that almost half of the stations visited by chillas were also visited by dogs. Although we did not radio-track dogs, the fact that within the home range of each fox the density of dogs was between 5.4 and 8.8 individuals/km^2 (Table 2) suggests that there is major overlap between the home ranges of chillas and dogs. Thus, at the scale of home-ranges and given our data there is no evidence of segregation in terms of the use of space.

At finer scales, however, chillas and dogs differ in their use of space. During daytime (when dogs seem to be more active), inactive chillas used native forest, the only habitat type that dogs did not used (Fig. 2). Furthermore, the odds of detecting dogs increased as distance to house decreased, whereas the inverse pattern was observed for chillas (Table 5). This suggests that dogs could be constraining the use of space of chillas at short distance from houses and probably during daytime. Harrison (1993, 1997) reported that gray foxes (*Urocyon cinereoargenteus*) tolerated moderate housing densities. Gray foxes avoided houses during daytime, which was attributed to the higher dog activity (Harrison 1993, 1997). The findings of the present study are also consistent with data available for other carnivores such as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) whose percentage of daily activity was found to be negatively correlated to dog and human activity in an urban nature reserve in California (George & Crooks 2006), and were also are more likely to use developed areas during the night than during the day (Riley *et al.* 2002).

Although the distribution of dogs and foxes relative to houses suggests an effect of dogs on foxes, the same pattern could be expected if chilla's prey avoid human houses or if chillas avoid people. The spatial distribution of prey does not seem to be a strong alternative hypothesis, given that some prey items were not affected by the location of houses whereas others – in contrast – were more frequent close to houses (see Supplementary Material). This suggests that in the absence of risk the pattern could be the reverse, as reported for other carnivores (Prange *et al.* 2003; Deplazes *et al.* 2004; Killian 2005) and anecdotally observed for the chilla in several areas (J. E. Jiménez, pers. obs., 2006). To tease out the potential effect of people on foxes from the effects of dogs is difficult, given that both of them are associated to houses. However, dog visit rate was negatively associated to chilla visit rate (Table 5). Furthermore, the second QAIC$_c$ model shows that the association of dogs and chillas held when accounting for distance to houses and habitat type (Table 3). In addition, scent stations were never visited by both species during the same night. Other important evidence in this direction is the difference in activity patterns between people (diurnal) and chillas (nocturnal). Even though dogs also seemed to be diurnal, they are kept outside and unleashed at night (Silva-Rodríguez 2006), which would allow them to harass foxes if they approach houses at night when people are sleeping. Finally, and anecdotally, we observed chillas escaping from dogs and one of the radio-collared chillas was killed by a dog. But we also

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observed chillas approaching people at close distance (E. A. Silva-Rodríguez *et al.*, pers. obs, 2006). Although our data strongly suggest that dogs affect the use of space by chillas, the strength of our conclusions is limited by the design and localized scale of the study. Conclusive evidence on the effects of dogs on the behaviour of foxes should be provided by controlled experimental studies, and larger scale, longer-term field studies in diverse landscapes.

Ecological and conservation implications

Our results suggest that chillas manage to coexist with domestic dogs by avoiding them at fine spatial and probably temporal scales. This finding, and the work of other authors (Murray Berger & Gese 2007), suggests that home-range and even core area overlap does not falsify the existence of interference competition between carnivores as implicitly suggested by other authors (Gehrt & Prange 2007), because avoidance can occur at finer temporal or spatial scales. Fine scale habitat preferences by chillas seem to be the result of a spatial trade-off between resource availability (represented by habitat type) and intraguild predation risk (represented by dogs and distance to houses). Similar observations have been reported for raptors: black kites (*Milvus migrans*) select habitat according to food availability and the risk imposed by eagle owls (*Bubo bubo*), an important black kite predator (Sergio *et al.* 2003). These authors suggested that coexistence between these species was possible because most kites nested in the areas located between owls' home ranges and hypothesized that their results could apply to other vertebrate mesopredators. Our results seem to support their hypothesis given that areas located far from houses – and native forest during daytime – could act as spatial refuges for chillas. This could allow chillas to coexist with dogs and probably profit from a human-dominated landscape.

Most research on interspecific interactions between carnivores has focused on wild species, ignoring domestic dogs. Yet, domestic dogs are the most abundant and ubiquitous carnivores worldwide and probably coexist and interact with most if not all living carnivores (see Sillero-Zubiri *et al.* 2004). This is one of the few studies that have addressed the potential effects of owned domestic dogs on small carnivores in the context of intraguild killing and interference interactions. Our results strongly suggest that the effects of dogs on wildlife deserve attention from a conservation perspective, given that they are subsidized by people and therefore their populations are decoupled from prey abundance. This allows them to reach high densities which could threaten wild carnivore persistence in the long term. Coexistence between dogs and wild carnivores seems possible at low to moderate dog densities (see above). However, if the spatiotemporal extent of dog influence increases beyond some currently unidentified thresholds it is possible that coexistence will no longer be possible (Harrison 1993, 1997). In this study we only explored the potential effects of dog presence on the use of space by chilla. However, other factors such as infectious disease spill over are known to be important and should be more broadly addressed (Sillero-Zubiri *et al.* 2004; Laurenson *et al.* 2005). As a consequence, understanding the ecology, management and human dimensions of the problem of domestic dogs will be important in conservation practice.

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