

TIME PARTITIONING FAVORS THE COEXISTENCE OF SYMPATRIC CRAB-EATING FOXES (*CERDOCYON THOUS*) AND PAMPAS FOXES (*LYCALOPEX GYMNOCERCUS*)

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Crab-eating foxes (*Cerdocyon thous*) and pampas foxes (*Lycalopex gymnocercus*) are very similar in body size and food habits, with distributional ranges that overlap extensively in South America. We used camera-trap records of both species obtained at the Iberá Nature Reserve (INR), northeastern Argentina, to test the hypothesis that, when living in sympatry, they reduce competition by using different habitats and by being active at different times. Camera-trap records obtained at 2 additional sites inhabited by only 1 of these species, the Atlantic Forest of Misiones (AF) and Lihué Calel National Park (LCNP), were used to determine the activity patterns of these foxes when living alone. At INR, we set 41 camera-trap stations in 2 habitats (shrubland forest and flooded grassland), and in 2 treatments per habitat (with or without cattle). Three stations also were set in gallery forests. We obtained 540 photographs of crab-eating foxes (289 records) and 175 photographs of pampas foxes (115 records) in 1,521 camera-trap days. At LCNP, 27 camera-trap stations (1,002 camera-trap days) provided 109 records of pampas foxes. At AF, 195 camera-trap stations (11,689 camera-trap days) provided 103 records of crab-eating foxes. At INR, crab-eating foxes were more frequently recorded in forest habitats, whereas pampas foxes preferred opened grasslands. However, both species were found in all habitats and their recording rates were not negatively correlated. At INR, crab-eating foxes were nocturnal, with peaks of activity after dusk and before dawn, a pattern similar to that observed at AF and elsewhere. At INR, pampas foxes showed a peak of activity between 0000 and 0400 h and another between 1000 and 1300 h, a pattern that differed from that observed at LCNP and other places, where the species is mostly nocturnal. At INR, pampas foxes reduced their activity at times when activity of presumably dominant crab-eating foxes was high, which may facilitate their coexistence.

Key words: *Cerdocyon thous*, competitive exclusion, habitat use, Iberá Nature Reserve, interspecific competition, *Lycalopex gymnocercus*, maned wolf, South American foxes, species coexistence, time partitioning

The competitive exclusion principle is often used to explain the conditions under which similar species may coexist and, consequently, the patterns of biodiversity observed in nature (Davies et al. 2007). One of the consequences of interspecific competition is that 2 species cannot occupy the same ecological niche without exerting strong negative effects on each other

(e.g., limiting their population sizes). Thus, when resources are limiting, species can coexist if they differ morphologically or behaviorally and consequently use different resources or use them in different areas or at different times (Brown and Wilson 1956; Davies et al. 2007; Dayan and Simberloff 2005; Schoener 1974).

This theoretical framework has promoted research on the comparative ecology and behavior of closely related and morphologically similar species living in sympatry. Competition between pairs of canid species living in the same location can take several forms, from indirect, exploitative competition for resources to direct, aggressive interactions (Linnell and

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Strand 2000). For example, foxes in Patagonia (culpeo foxes [*Lycalopex culpaeus*] and South American gray foxes [*Lycalopex griseus*]) and northern Europe (red foxes [*Vulpes vulpes*] and arctic foxes [*Vulpes* {formerly *Alopex*} *lagopus*]), jackals (*Canis adustus* and *Canis mesomelas*) in Africa, and wild dogs and dingoes (*Canis lupus familiaris* and *Canis lupus dingo*) and red foxes in Australia may live in sympatry and their diets overlap to a large degree (Macdonald et al. 2004b; Mitchell and Banks 2005; Novaro et al. 2004; Tannerfeldt et al. 2002). However, there is spatial avoidance at the microhabitat scale (e.g., their territories do not overlap) as a result of the subordinate species being excluded by the dominant one from the more productive or more secure areas (Jiménez et al. 1996; Johnson and Franklin 1994a; Loveridge and Macdonald 2003; Mitchell and Banks 2005; Tannerfeldt et al. 2002). Interference competition may even take the extreme form of interspecific killing, where a larger and dominant species slays the smaller, weaker species (Linnell and Strand 2000; Macdonald and Sillero-Zubiri 2004; Palomares and Caro 1999; Wang et al. 2004).

The crab-eating fox (*Cerdocyon thous*) and the pampas fox (*Lycalopex gymnocercus*) are 2 widespread and relatively common South American foxes (Langguth 1975; Redford and Eisenberg 1992; Vieira and Port 2007). In a large portion of northern Argentina, western Paraguay, northern Uruguay, eastern Bolivia, and southeastern Brazil the distributional ranges of the 2 species overlap extensively (Langguth 1975; Macdonald and Sillero-Zubiri 2004; Redford and Eisenberg 1992), which provides the opportunity to compare their ecology and behavior under similar conditions and understand what factors facilitate their coexistence.

The crab-eating fox ranges from northern South America to northern Argentina and Uruguay (Berta 1982; Macdonald and Sillero-Zubiri 2004; Medel and Jaksic 1988; Nowak 2005). This fox has been described as a habitat generalist, using humid and dry forests, forest edges, wooded savanna, and grassland habitats to different degrees (Brady 1979; Jácomo et al. 2004; Macfadem Juarez and Marinho-Filho 2002; Maffei and Taber 2003; Vieira and Port 2007). It is a nocturnal or crepuscular species that usually lives in pairs that share a territory and usually travel together (Brady 1979; Macdonald and Courtenay 1996; Medel and Jaksic 1988; Montgomery and Lubin 1978; Sunquist et al. 1989; Yanosky and Mercolli 1990). Its broadly omnivorous diet, composed of small mammals and other vertebrates, fruits, and arthropods, shows variation from one study site to another (Berta 1982; Bisbal and Ojasti 1980; Bueno and Motta-Junior 2004; Gatti et al. 2006; Jácomo et al. 2004; Macdonald and Courtenay 1996; Macfadem Juarez and Marinho-Filho 2002; Medel and Jaksic 1988; Montgomery and Lubin 1978; Pedó et al. 2006; Rocha et al. 2004; Sunquist et al. 1989).

The pampas fox is found in eastern Bolivia, western Paraguay, Uruguay, southeastern Brazil, and central and northern Argentina (Crespo 1975; Macdonald and Sillero-Zubiri 2004; Nowak 2005). The pampas fox usually has been described as a grassland species, but it also inhabits wooded savannas, deserts, and open forests (Crespo 1975; García and

Kittlein 2005; Lucherini and Luengos Vidal 2008; Nowak 2005; Redford and Eisenberg 1992; Vieira and Port 2007). Although no detailed studies of its social behavior have been carried out, it is thought to form monogamous pairs. However, it seems to be a solitary forager that could be active during both day and night (Branch 1994; Brooks 1992; Lucherini et al. 2004). Studies of its diet indicate that pampas foxes are omnivorous, with small mammals, insects, and fruit being the main food items recorded in stomach contents and feces, with important variation among study sites (Crespo 1971, 1975; Farias and Kittlein 2008; García and Kittlein 2005; Lucherini and Luengos Vidal 2008; Medel and Jaksic 1988).

A few studies have compared the diet and habitat use of the crab-eating fox with those of other sympatric canids (Bueno and Motta-Junior 2004; Jácomo et al. 2004; Macfadem Juarez and Marinho-Filho 2002). Only 1 recent study (Vieira and Port 2007) is focused on the comparative ecology of crab-eating and pampas foxes living in sympatry. Although variation among sites in the composition of the diet of the crab-eating fox has been noted, its diet is strikingly similar to that of the pampas fox when they live in sympatry, which suggests that the 2 species may be strong competitors for food (Vieira and Port 2007). Vieira and Port (2007) also suggest that both species prefer grassland habitat, but the crab-eating fox also makes use of forests and forest edges to a lesser degree. Differences in their daily activity patterns also are suggested, with the crab-eating fox being more nocturnal than the pampas fox. Because the study by Vieira and Port (2007) relied on sightings of animals and feces in habitats with different visibilities, these results may include some biases and should be corroborated with other studies.

We used camera-trap records of the crab-eating fox and the pampas fox obtained at 3 study sites to analyze if (and how) they partition their ecological niche in the spatial and temporal dimensions when living in sympatry. We also compared their social behavior (solitary foraging versus in pairs) as a potential variable explaining the observed patterns. A 3rd species of canid, the maned wolf (*Chrysocyon brachyurus*), also is found in sympatry with both species at 1 of our study sites, the Iberá Nature Reserve (INR), but its low frequency of occurrence in our photographic records precludes an analysis of its pattern of habitat use and daily activity in relation to the foxes. However, we discuss some potential competitive relationships between maned wolves and the foxes.

We specifically tested the following hypotheses and predictions: 1) The 2 fox species will segregate spatially, using the different habitat types within the INR to different degrees in order to minimize competition for food or other resources. Two predictions from this hypothesis are tested. First, the crab-eating fox will have a relatively higher recording probability in stations located in the structurally more complex forest habitats, whereas the pampas fox will be recorded relatively more frequently in the more open grasslands (Langguth 1975). Second, the probability of recording these species and their recording rates at the sampling stations will be negatively correlated. 2) The 2 species will segregate their daily activity patterns such as to minimize the probability of encounters

while foraging. We predict a different and nonoverlapping daily activity pattern for these species at INR. If 1 of the species is actively switching its daily activity pattern to reduce encounters with the other, its pattern will differ from that observed in the study areas where it is the only fox species present. 3) We tested the prediction that the crab-eating fox will be photographed in pairs with a frequency similar to that observed in other social species, but the pampas fox, being a species that forages solitarily, will be recorded in pairs with a lower frequency, similar to that of other solitary species.

MATERIALS AND METHODS

Study sites.—We conducted camera-trap surveys in 3 separate regions of Argentina: the INR in Corrientes Province, inhabited by both foxes plus the maned wolf; the Atlantic Forest of Misiones Province (AF), where the crab-eating fox is the only canid that reaches biologically meaningful population densities (the bush dog [*Speothos venaticus*] is extremely rare and was never photographed); and Lihué Calel National Park (LCNP) in La Pampa Province, where only pampas foxes are found (Fig. 1).

The INR is a 1,300,000-ha multiple-use protected area (Canziani et al. 2003). The core of this reserve is comprised of the large Iberá marsh, which is surrounded by terrestrial ecosystems speckled with lakes and crossed by small rivers and streams, constituting a highly diverse mosaic of habitats (Neiff and Poi de Neiff 2006). The climate is humid and subtropical, with a mean annual precipitation that ranges between 1,500 and 1,800 mm, and mean daily temperatures that range from 16–17°C during the winter months (June–July) to 27–28°C during the summer months (January–February—Neiff and Poi de Neiff 2006).

Three main types of terrestrial habitat are found within the study area (Fig. 2). The 1st terrestrial habitat is a thorny, deciduous shrubland forest typical of the Argentine Espinal ecoregion (hereafter, shrubland). This is a dry open forest or wooded savanna habitat dominated by a few species of short (<8 m tall) legume trees in the genus *Prosopis* and *Acacia* (Tressens et al. 2002). The 2nd main terrestrial habitat is a temporarily flooded grassland, locally called malezal, having *Andropogon lateralis* as the dominant species in a complex community composed of a diverse range of aquatic and terrestrial plant species. We will refer to this habitat type as the grassland. The 3rd terrestrial habitat is the narrow gallery forest that borders the streams that drain both the shrubland and the grassland, and flow toward the marshes and rivers. These gallery forests, although they represent a small proportion of the study area, are highly diverse in plants and animals. They are relatively tall (canopy layer at 10–15 m) forests characterized by the presence of the pindó palm (*Syagrus romanzoffianum*), typical of the Atlantic Forest (Tressens et al. 2002).

The most common economic activity within the INR is cattle ranching, which is usually practiced on large, extensive properties and combined with annual anthropogenic fires.

Thus, most areas of shrubland and grassland in the INR show the effects of cattle grazing and burning, where the former appear as open savannas with isolated trees, no understory strata, and very short grasses, and the latter as short-grass, temporarily flooded pampas. As an exception to this general pattern, 1 of our sampling areas, Rincón del Socorro (RS), is a former cattle-grazing estancia converted into a 13,000-ha private nature reserve where livestock has been excluded since 2002 (Fig. 2). Because of this exclusion, small trees of different sizes, shrubs, and tall grasses now close the gaps among older trees in the shrubland habitat, whereas a continuous 1.2- to 1.5-m-tall layer of grass is covering the grassland areas in RS. The eastern portion of the cattle-grazing Estancia Iberá, called Reserva Miriñay, also is excluded from livestock grazing and tall grasses dominate this portion of grassland.

The surveyed area is located in the southeastern portion of the INR, southwest of the small town of Colonia Carlos Pellegrini (28°39'S, 57°23'W). Camera-trap stations were placed in 5 conditions or treatments: uninhabited grassland used for cattle grazing in Estancia Iberá, uninhabited shrubland free of cattle at RS, uninhabited gallery forest free of cattle at RS, uninhabited grassland free of cattle at RS and Reserva Miriñay, and inhabited shrubland used for cattle grazing in the Paraje Uguay (a hamlet). RS, Estancia Iberá, and Reserva Miriñay are owned by The Conservation Land Trust, a conservation foundation. Hunting is strictly prohibited and controlled by park rangers and employees in these areas. Paraje Uguay experiences significant hunting pressure by local people living around the hamlet. Dogs and cats are very common in this area and extremely rare on RS, Estancia Iberá, and Reserva Miriñay.

At AF we conducted 4 camera-trap surveys at 3 large areas of the Green Corridor of Misiones Province (25°30'–27°00'S, 53°50'–54°30'W) in the Upper Paraná Atlantic Forest ecoregion. The area is located in the most interior portion of the Atlantic Forest of South America and is characterized by a continuous subtropical rain forest (Galindo-Leal and de Gusmão Câmara 2003). The climate is humid with an average annual rainfall that ranges between 1,700 and 2,000 mm, and with strong seasonality in day length and temperature that determines a marked seasonality in fruit and arthropod availability (Di Bitetti 2001; Di Bitetti and Janson 2001). The surveyed areas comprise protected areas and private forests with different degrees of human intervention (logging and hunting; for details see Di Bitetti et al. [2008] and Paviolo et al. [2008]).

Lihué Calel National Park is a 9,900-ha, strictly protected area located in the Monte ecoregion of central Argentina (37°57'S, 65°33'W). The area is characterized by flat terrain, with relatively low mean annual precipitation (about 500 mm) and mean daily temperatures that range from <8°C in winter to >25°C in summer. The vegetation is composed of a mosaic of creosote bush flats (*Larrea*), grasslands dominated by bunch grasses (*Stipa*), and mixed shrub patches (e.g., *Condalia microphylla* and *Prosopis flexuosa*). There is no poaching within the park and the pampas fox is the only native canid present in the region. For details of the study site see Pereira et al. (2006).

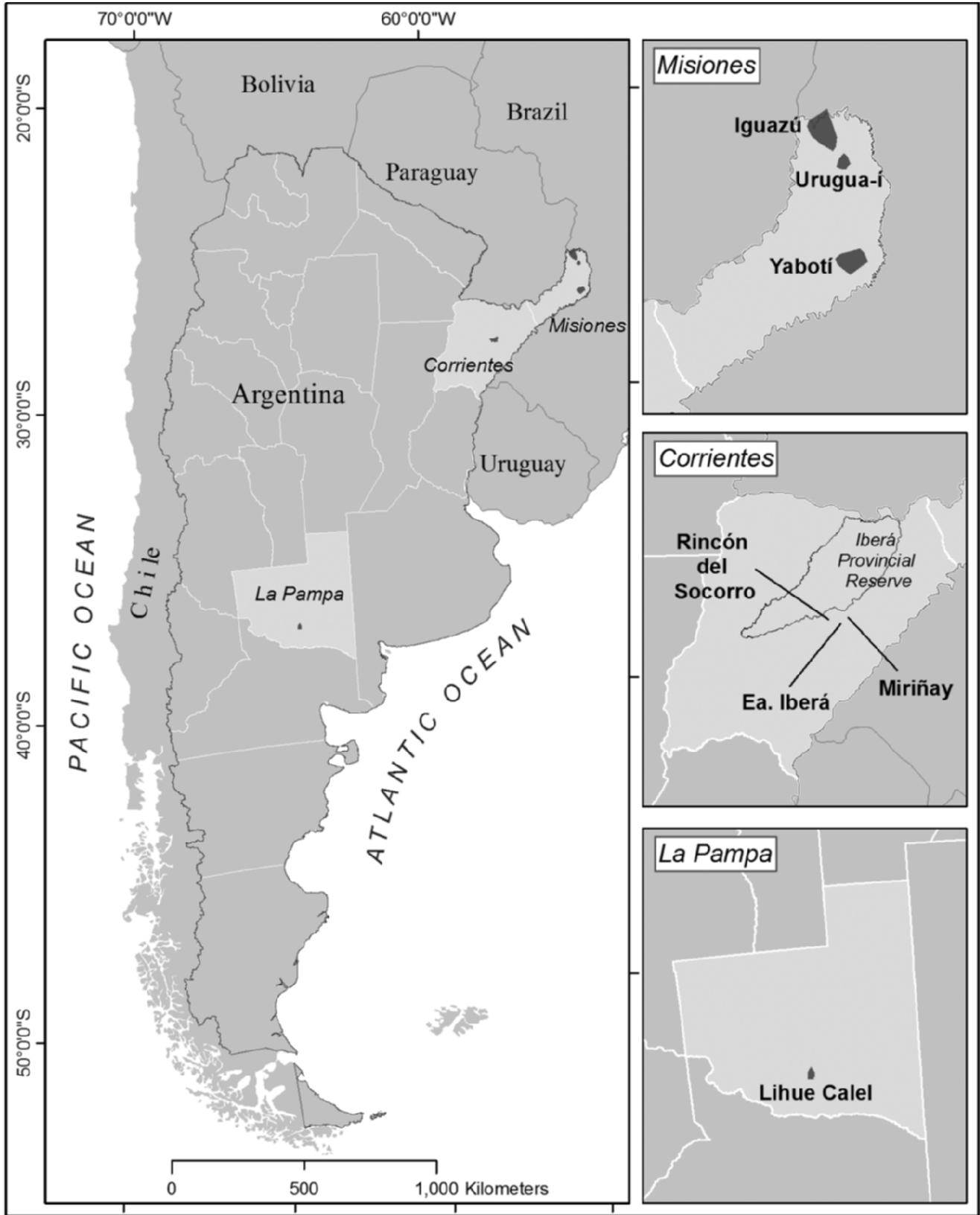


FIG. 1.—Location of the 3 study areas in South America.

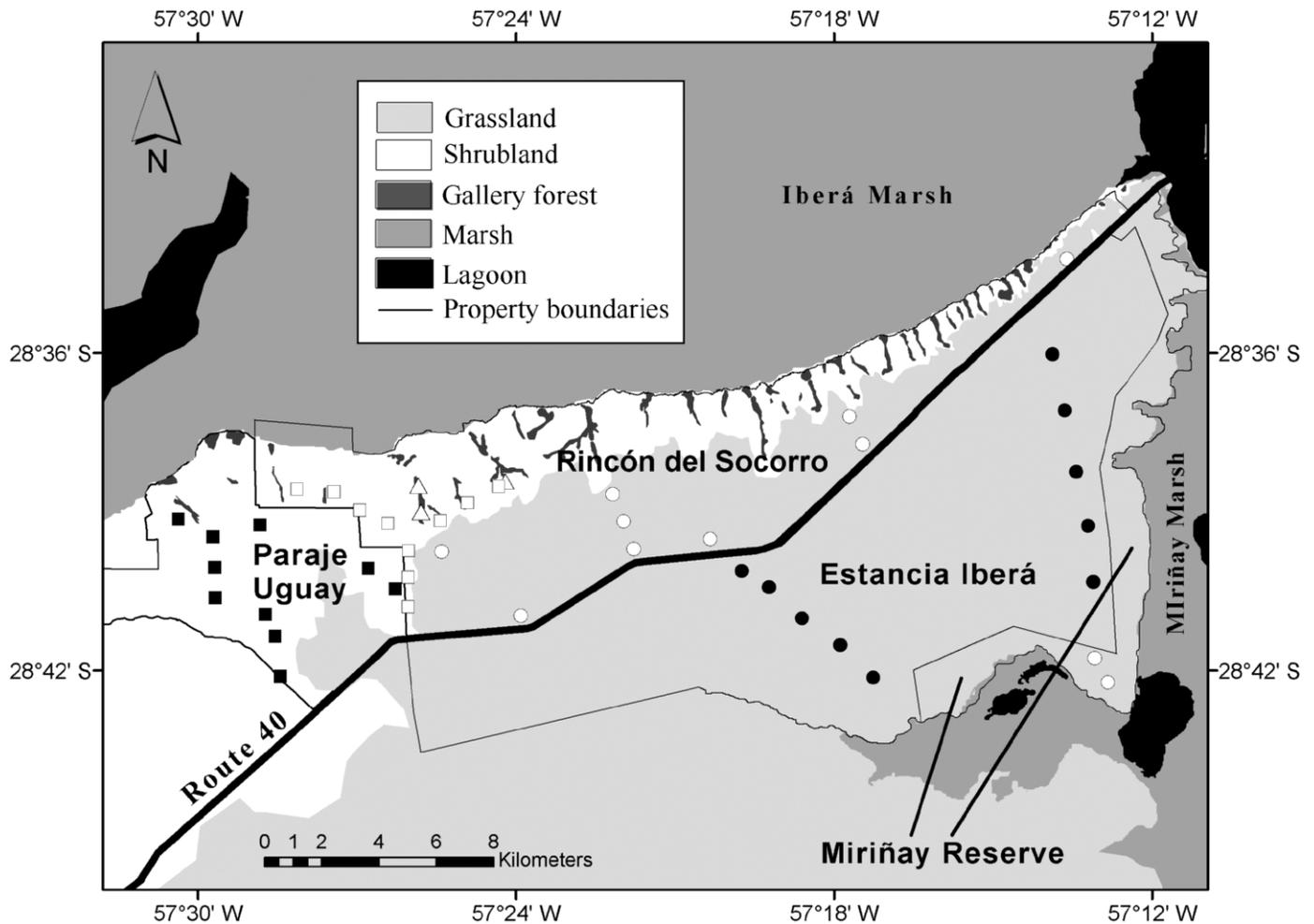


FIG. 2.—Location of the study site and the camera-trap stations within the Iberá Nature Reserve, Corrientes Province, Argentina. Camera-trap stations were located in 3 different habitats: grassland (dots), shrubland (squares), and gallery forest (triangles), and in areas with (black symbols) and without (white symbols) cattle. Stations located in Paraje Uguay (black squares) also have a higher presence of people and domestic animals.

Study methods.—We conducted camera-trap surveys to record medium- to large-size mammals in the 3 study areas. At INR, the survey was conducted between 12 August and 30 September 2007. Forty-four camera-trap stations were deployed in 5 different situations (hereafter, treatments): shrubland without people and domestic animals ($n = 10$ stations), shrubland with people and cattle ($n = 10$), grassland with cattle ($n = 10$), grassland without cattle ($n = 11$), and gallery forests ($n = 3$; Fig. 2). Stations consisted of 1 camera-trap deployed >50 m from the nearest unpaved road. Camera-traps were Leaf River Trail Scan Model C-1 units (Vibra Shine, Taylorsville, Mississippi), except for 3 TrailMAC 35 mm Standard Game Scouting Cameras (Trail Sense Engineering, LLC, Middletown, Delaware). Camera-traps located in the shrubland and gallery forest were set to be active 24 h per day, but those deployed in the grassland were set to be active only at night because light reflection in this habitat often triggered photographs without any animal stimulus. Camera-traps were set to have a delay of 5 min between successive photographs (4 min in the TrailMAC units). Camera-traps were placed 25–50 cm above ground and attached to a tree trunk or wooden

post. A perforated can of tuna fish was fixed, as bait, 2–3 m in front of the camera to attract carnivorous and omnivorous species. The vegetation in the area between the can and the camera was cleared with a machete. Fish cans were replaced every 9–13 days.

Camera-trap stations at INR were placed at a mean (\pm SD) distance of $1,217 \pm 631$ m apart. The radius of the mean home-range estimate for pampas foxes in Buenos Aires Province (153 ha, $n = 2$ studies—Lucherini et al. 2004; Lucherini and Luengos Vidal 2008) is 641 ± 387 m. The radius of the mean home range of crab-eating foxes based on estimates from 4 studies (Brady 1979; Macdonald and Courtenay 1996; Maffei and Taber 2003; Sunquist et al. 1989) was 772 ± 390 m. Thus, the mean distance among camera-traps was probably not ideal to ensure complete independence of records for both species, because some individuals may have been recorded at >1 station. However, it is our impression that the density of foxes at INR was very high and thus, home ranges would have been at the lower end of sizes, which may have improved the independence of records. Camera-traps were checked every 3–7 days to replace film or batteries if needed. The 2 fox

species were easily identified in the photographic records by their physical appearance (body-size proportions and coloration).

Total sampling effort at INR was 1,521 camera-trap days. On average, the camera-trap stations were active for (mean \pm SD) 34.6 ± 5.9 days but there were differences among treatments: stations in the grassland with cattle were active for a longer period (38.9 ± 6.1 days) than those in the shrubland with people and domestic animals (31.8 ± 5.0 days) and those in the gallery forests (25.0 ± 2.0 days; analysis of variance, $F = 6.61$, $d.f. = 4, 40$, $P = 0.004$).

At AF the camera-trap surveys were conducted between 2003 and 2007 and encompassed all seasons. We set 195 camera-trap stations with 2 camera-traps facing each other (and no bait), and located along sides of unpaved roads or trails opened with machetes in the forest. Camera-trap stations were located >1 km apart. Total sampling effort was 11,689 camera-trap days. Most stations ($n = 185$) were active 24 h and those that were not ($n = 10$) were excluded from this analysis. For details on the methodology used during these surveys see Di Bitetti et al. (2008) and Paviolo et al. (2008).

At LCNP, we conducted a 3-month-long survey (January–April 2006) during which we set 27 camera-trap stations, totaling 1,002 camera-trap days. Stations were located >1 km apart and consisted of 2 camera-traps facing each other, without bait, and located along sides of unpaved roads or trails inside the park. At 12 of these 27 stations 1 of the 2 camera-traps was set to be active only at night, but records from these cameras were excluded from the analysis.

We followed in all our procedures the guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Data analyses.—To test for habitat segregation by sympatric fox species, we relied only on the records obtained at INR. Not all photographs obtained at this area were included in this analysis, because baited stations tended to produce successive pictures of the same individual at short time intervals (usually 5 min apart), and because stations in the grassland were active only at night. Hence, we only used nocturnal records obtained >12 h apart (i.e., no more than 1 record per species per night) in the statistical tests testing for an effect of habitat and treatment in the probability of recording foxes. The frequency of these records was transformed to a daily rate by dividing the frequency of records per station by the number of days the station was active.

Only the photographic records from INR were used to assess if 1 species had a higher chance of being recorded in pairs than the other, because the camera-trap stations were baited and this increased the chances of attracting potential foraging pairs or groups. For this analysis, we used all photographs obtained.

Camera-traps were set to print the time of the day in the photographs. The photographic records of the 2 foxes at the 3 study sites were used to compare the activity patterns in regions inhabited by only 1 of the species (AF and LCNP) with those where both species were present (INR). We also compared the pattern of records of pampas foxes at RS, where crab-eating foxes were abundant, with that observed at Paraje Uguay,

where crab-eating foxes were less frequently recorded. We only used photographs from stations that were active 24 h (shrubland and gallery forest). In all cases, >1 h had to pass between successive photographs of a species to be considered independent records.

To test for differences in the intensity of habitat use by the 2 fox species at INR, we made comparisons among the 3 habitat types (grassland, shrubland, and gallery forest) and the 5 treatments using independence (likelihood ratio) tests in contingency tables, with presence–absence of the species and habitat type or treatment as categorical variables. Despite differences among treatments in the mean duration (days) the stations were active, duration of activity had no statistical effect on the probability of recording either of the 2 fox species, either when tested alone or as a covariate in logistic regression models with habitat type or treatment as the main effect, so this variable was not included in the statistical models. As a 2nd test of differences in habitat use, we used the recording rate of the species per day (number of records/days the station was active) as the dependent variable. Because this variable was not normally distributed due to the relatively high frequency of 0 values, we used the Kruskal–Wallis test (Sokal and Rohlf 1995).

To test the hypothesis that the 2 species made different use of the habitat at a fine scale (microhabitat), we used tests of independence using the presence–absence of the species at the different camera-trap stations. We also tested for a negative correlation of the recording rate of both species using linear regression. To make this test more conservative, we excluded stations where both species were not recorded.

Because the daily activity patterns of the foxes were not unimodal and did not follow a von Mises distribution (Fisher 1993), we used the Mardia–Watson–Wheeler statistical test (Batschelet 1981) to test the null hypothesis that the distributions compared were identical, that is, that there were no differences in the activity patterns of both species at INR. We then compared the daily activity pattern of crab-eating foxes at INR with that observed at AF and the daily activity pattern of pampas foxes at INR with that observed at LCNP.

To test for differences in the social system of both species (solitary foraging versus pairs) and to compare their social systems with those of other solitary or gregarious species photographed at the study site, we used tests of independence in 2×2 contingency tables, with the frequency of photographs with 1 versus >1 individuals and species as categorical variables.

The alpha level for committing a type I error in the statistical tests was set at 0.05. Statistical tests, with the exception of the Mardia–Watson–Wheeler test, were performed with JMP (version 3.2.2; SAS Institute Inc., Cary, North Carolina) statistical software.

RESULTS

Patterns of habitat use.—We obtained 540 photographs of crab-eating foxes, 175 photographs of pampas foxes, and 5 photographs of maned wolves at INR. When considering only nocturnal records obtained >12 h apart (1 record per night), we

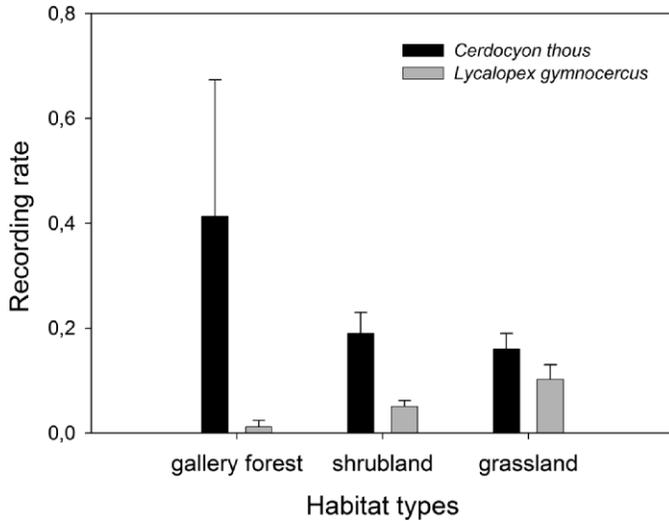


FIG. 3.—Recording rate (records per camera-trap night \pm 1 standard error of the mean) of crab-eating foxes (*Cerdocyon thous*; black bars) and pampas foxes (*Lycalopex gymnocercus*; gray bars) in 3 different habitat types at the Iberá Nature Reserve: gallery forest ($n = 3$ camera-trap stations), shrubland ($n = 20$ stations), and grassland ($n = 21$ stations).

obtained 289 records of crab-eating foxes, 115 records of pampas foxes, and 4 records of maned wolves. The 4 records of maned wolves were obtained within RS private reserve, at 2 stations located in the grassland and 1 located in the shrubland. At the 2 grassland stations where maned wolves were recorded, no records of pampas foxes or crab-eating foxes were obtained. At AF, we obtained 155 photographs (103 records) of crab-eating foxes, and at LCNP, 140 photographs (109 records) of pampas foxes.

At INR, crab-eating foxes showed a tendency for having a higher recording rate at stations located in the gallery forest than in the shrubland and grassland (Fig. 3), but these differences were not statistically significant (Kruskal–Wallis test, chi-square approximation, $\chi^2 = 1.603$, $df. = 2$, $P = 0.449$). Pampas foxes showed a tendency for the opposite pattern (Fig. 3), having a higher recording rate in stations located in the grassland and a very low rate of records in the gallery forest (this species was recorded only once in this habitat type) but again, differences were not statistically significant ($\chi^2 = 2.054$, $df. = 2$, $P = 0.358$).

The 2 species of foxes were recorded in all 5 treatments. The probability of recording the crab-eating fox at a sampling station was not independent of the treatment, being lower in the shrubland with people and in the grassland without cattle (likelihood ratio test, $G = 16.301$, $df. = 4$, $P = 0.003$; Fig. 4A). The probability of recording the pampas fox was also dependent on the treatment, being highest in the grassland with cattle than in the other situations ($G = 16.317$, $df. = 4$, $P = 0.003$; Fig. 4A). In the shrubland, the probability of recording the 2 species showed an opposite pattern in relation to treatment, with crab-eating foxes having a higher probability of being recorded in the shrubland without cattle

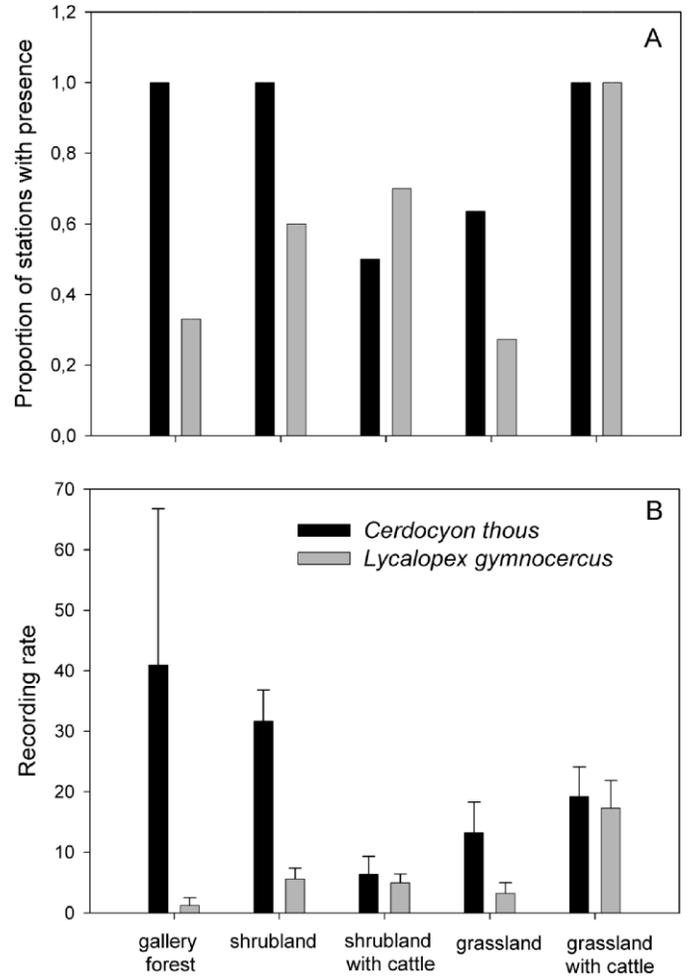


FIG. 4.—A) Proportion of stations where foxes were recorded and B) recording rate, measured as the mean number of records per 100 night traps \pm 1 standard error of the mean of crab-eating foxes (*Cerdocyon thous*; black bars) and pampas foxes (*Lycalopex gymnocercus*; gray bars) at 5 different treatments that result from combinations of habitat types and the presence of anthropic effects (people, hunting, domestic animals, and livestock; indicated by “with cattle”) within the Iberá Nature Reserve.

and people and pampas foxes having a higher probability of being recorded in the shrubland with cattle and people (Fig. 4A).

The recording rate of crab-eating foxes was higher in the gallery forest and the shrubland without people and domestic animals and lower in the shrubland with people and domestic animals (Kruskal–Wallis test, $\chi^2 = 15.221$, $df. = 4$, $P = 0.004$; Fig. 4B). The recording rate of pampas foxes was >3 times higher in the grassland with cattle than in any other situation and was very low in the gallery forest ($\chi^2 = 12.663$, $df. = 4$, $P = 0.013$; Fig. 4B).

The probability of recording the crab-eating fox at a sampling station did not reduce the chances of recording the pampas fox but, on the contrary, there was an almost positive association between the species ($G = 3.750$, $df. = 1$, $P = 0.053$). When the stations with no records of both species were

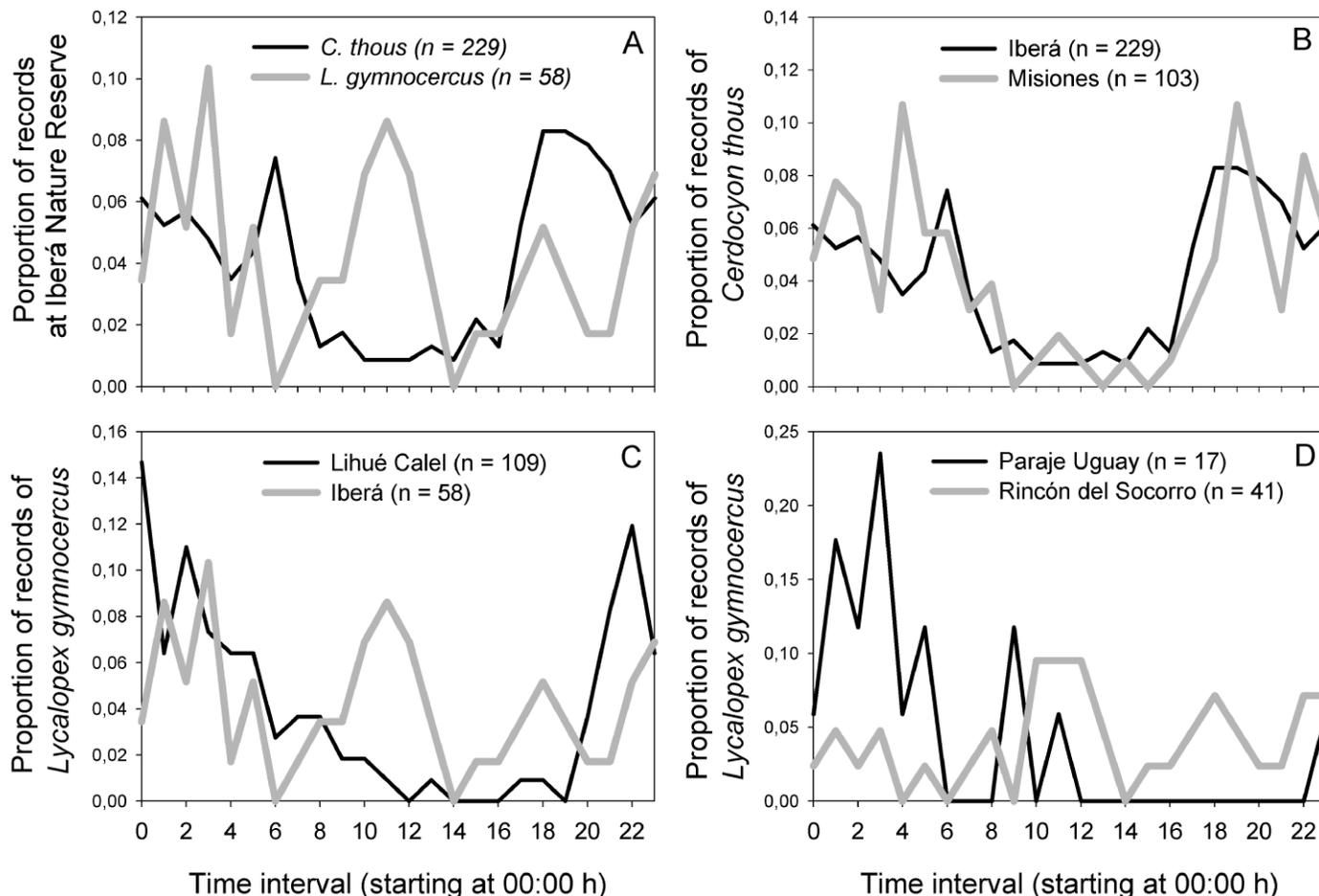


FIG. 5.—Daily camera-trap records A) of crab-eating foxes (*Cercdocyon thous*) and pampas foxes (*Lycalopez gymnocercus*) at Iberá Nature Reserve; B) of crab-eating foxes at 2 different study sites, the Iberá Nature Reserve and the Atlantic Forest of Misiones; C) of pampas foxes at 2 different study sites, the Iberá Nature Reserve and Lihué Calel National Park; and D) at 2 different contiguous areas within the Iberá Nature Reserve, Rincón del Socorro, where crab-eating foxes were relatively more abundant, and Paraje Uguay, where they were less frequently recorded.

excluded ($n = 6$), there was no relationship between the natural logarithm of recording rate of pampas and crab-eating foxes ($F = 0.320$, $df. = 1, 36$, $P = 0.575$).

Daily patterns of records.—At INR, the daily patterns of records of the 2 species were different (Mardia–Watson–Wheeler test, $\chi^2 = 7.423$, $df. = 2$, $P < 0.025$) and complementary (Fig. 5A). The records of crab-eating foxes were mostly nocturnal, with a main peak between 1900 and 2200 h and a 2nd peak at dusk (0600–0700 h). Pampas foxes showed 2 peaks of records, a nocturnal one between 0000 and 0400 h, and a diurnal one between 1000 and 1300 h, occurring at time intervals when crab-eating foxes showed a relatively low level of records. Both species showed little activity between 1400 and 1700 h.

The daily pattern of records of crab-eating foxes at INR was similar to that observed at AF ($\chi^2 = 2.918$, $df. = 2$, $P > 0.20$; Fig. 5B). The activity pattern of pampas foxes at INR was very different from the one observed at LCNP ($\chi^2 = 13.387$, $df. = 2$, $P < 0.005$), where the late-morning peak of activity observed at INR disappears and shows a pattern that resembles that of crab-eating foxes (Fig. 5C). Records of pampas foxes

were mostly nocturnal in Paraje Uguay and mostly diurnal in RS ($\chi^2 = 18.310$, $df. = 2$, $P < 0.001$; Fig. 5D).

Photographs of 1 versus 2 individuals.—At INR, the probability of recording 2 individuals in a photograph was much higher for crab-eating foxes (60 of 540 photographs = 11.11%) than for pampas foxes (2 of 175 photographs = 1.14%; likelihood ratio test, $G = 23.057$, $df. = 1$, $P < 0.0001$). The percentage of pictures with >1 individual for crab-eating foxes was not different from that recorded in 2 other social species: capybaras (*Hydrochoerus hydrochaeris*; 21 of 285 photographs = 7.37%; $G = 3.078$, $df. = 1$, $P = 0.079$) and vizcachas (*Lagostomus maximus*; 23 of 144 photographs = 15.97%; $G = 2.377$, $df. = 1$, $P = 0.123$). Other presumably solitary species showed a very low frequency of photographs with >1 individual, a proportion that was similar to that observed for pampas foxes, including hog-nosed skunks (*Conepatus chinga*; 4 of 318 photographs = 1.26%), nine-banded armadillos (*Dasyus novemcinctus*; 1 of 68 photographs = 1.47%), white-eared opossums (*Didelphis albiventris*; 0 of 85 photographs = 0.00%), and six-banded armadillos (*Euphractus sexcinctus*; 3 of 234 photographs = 1.28%).

DISCUSSION

Habitat use.—The crab-eating fox has usually been associated with forests, forest edges, and wooded savannas, whereas the pampas fox has mostly been associated with grasslands (Langguth 1975; Redford and Eisenberg 1992). Differences in the physical appearance of the 2 species also point to adaptations to different environments, with the crab-eating fox having relatively shorter legs, snout, and ears than the pampas fox, morphological characteristics typical of forest-living species (Langguth 1975). The results of our study show that at the scale of the landscape, the 2 fox species use the available habitat in relatively different ways. Crab-eating foxes were more frequently recorded in the thicker and structurally more complex environments, the gallery forests and the shrubland without cattle. Pampas foxes were more frequently recorded in the very open grassland with cattle. The presence of people and domestic animals in the shrubland of Paraje Uguay had a negative effect on the recording rate of crab-eating foxes, but no effect on the recording rate of pampas foxes. In the grassland, both species were recorded more frequently where cows were present.

Thus, patterns of habitat use by these fox species at INR conform, in general, to what was predicted based on previous studies. However, some of the patterns observed need further explanation. First, why did the presence of people in the shrubland have a strong negative effect on crab-eating foxes but not pampas foxes? Second, why did the lack of cattle in the grassland seem to negatively affect both species, especially the pampas fox, which is considered to be more adapted to the native grasslands?

A tentative answer to the 1st question is that the presence of domestic animals in the shrubland creates a very open environment, structurally more similar to a grassland habitat than to a forest, which favors the presence of pampas foxes but not crab-eating foxes. However, crab-eating foxes reached relatively high recording rates in the open grassland with cattle. Another possibility is that crab-eating foxes are behaviorally less able to cope with people and dogs than are pampas foxes.

A speculative answer to the 2nd question is that ungrazed grassland is not a good habitat for either fox species. Except for a short time after they are burned, these grasslands are dominated by dense and tall grasses (1.2–1.5 m), which likely make it very difficult for foxes to travel through them. The grassland is also flooded a good part of the year. Thus, both species may need a terrain that is relatively open and easy to travel through, which is more common in heavily grazed grassland. Moreover, the tall grassland is the habitat type to which maned wolves seem to be best adapted (Mendes Coelho et al. 2008; Nowak 2005). In fact, of the 4 photographic records of maned wolves obtained during this study, 3 were taken (at 2 different stations) in ungrazed grassland. In a study of interspecific killing in carnivores, Donadio and Buskirk (2006) found that the probability of a larger species killing a smaller one is higher when the mass of the larger species was 2–5.4 times that of the smaller one. Both fox species are 3–5 times smaller than the much heavier (20–30 kg) maned wolf (Macdonald and Sillero-Zubiri 2004; Redford and Eisenberg 1992). Although

little is known about the behavioral interactions between these foxes and maned wolves, there are several reports of medium- to large-size mammals in the wolf's diet, including brocket deer (*Mazama*), pampas deer (*Ozotoceros bezoarticus*), grisons (*Galictis cuja*), coatis (*Nasua nasua*—Bueno and Motta-Junior 2004; Macfadem Juarez and Marinho-Filho 2002), and even hoary foxes (*Lycalopex vetulus*—Jácomo et al. 2004). Avoidance of maned wolves may be another reason why these 2 foxes are relatively rare in the grassland without cattle. In fact, at the 2 stations in the grassland without cattle where we recorded maned wolves, we did not record any of the 2 fox species, an event that only happened at 6 of 44 camera-trap stations.

At the microhabitat level, we predicted that the recording rate of 1 fox species at a camera-trap station would be negatively correlated with the recording rate of the other. This prediction did not hold. In contrast, recording rates of both species tended to be positively (although not significantly so) correlated. In a study of habitat use by red foxes and wild dogs (or dingoes) in southeastern Australia, Mitchell and Banks (2005) found that, at the landscape level, both species were found in similar habitat types, but at a smaller spatial scale; visitation of baiting stations by dogs was negatively associated with visitation by foxes, suggesting that at a microhabitat level foxes avoid dogs. The crab-eating fox (5–7 kg) is only about 10–20% heavier than the pampas fox (4–7 kg—Crespo 1971; Lucherini and Luengos Vidal 2008; Lucherini et al. 2004; Macdonald and Sillero-Zubiri 2004; Redford and Eisenberg 1992). At INR, it is possible that even though both foxes may aggressively compete for food, their differences in body size are not large enough for 1 species to be a real danger to the other, as was the case for the relationship between wild dogs and red foxes (Mitchell and Banks 2005) and several other pairs of canid species (Macdonald and Sillero-Zubiri 2004).

Daily activity patterns.—The daily activity patterns of both species were complementary when living in sympatry. The crab-eating fox was the more nocturnal of the 2 species, with peaks of activity after dusk and before dawn, a relatively high level of activity during the whole night, and very little activity during the day. Vieira and Port (2007) also found that crab-eating foxes are more nocturnal than pampas foxes when living in sympatry in southeastern Brazil. However, the patterns of daily activity described by these authors may not be comparable to the ones described here as a result of methodological biases (Vieira and Port 2007). Crab-eating foxes at INR showed a daily activity pattern strikingly similar to that observed in populations inhabiting other habitats where pampas foxes are absent, the Atlantic Forest (Fig. 5B), flooded savannas and forests in the Brazilian Amazon (Macdonald and Courtenay 1996), the dry forests of Bolivia (Maffei and Taber 2003), and the Venezuelan Llanos (Sunquist et al. 1989), with almost exclusively nocturnal activity and peaks after dusk and before dawn.

At INR, pampas foxes showed a bimodal pattern, with a peak of nocturnal activity in the middle of the night and another peak of diurnal activity between midmorning and noon. However, when we compared the daily pattern of records of pampas foxes at INR between areas where crab-eating foxes were frequently recorded (RS) and areas where they were

uncommon (Paraje Uguay), a striking contrast emerges: pampas foxes become more diurnal in areas where crab-eating foxes are relatively more abundant. At LCNP, where the pampas fox is the only wild canid present, its activity pattern is different from the one observed at INR, resembling that of the crab-eating fox. In protected areas of Buenos Aires Province, where the pampas fox is also the only wild canid present, it shows a daily pattern of activity similar to the one observed at LCNP (Araujo 2004; Lucherini and Luengos Vidal 2008). This suggests that if one of these species is switching its daily activity pattern to avoid encounters with the other species, this would be the pampas fox.

Social structure.—The high relative frequency of photographs with >1 individual of the crab-eating fox, which was similar to the incidence observed in other social species, suggests that this fox forages in pairs that travel together, as has been previously reported in other populations (Brady 1979; Macdonald and Courtenay 1996; Montgomery and Lubin 1978; Yanosky and Mercolli 1990). The pampas fox, on the other hand, seems to be a solitary forager, because the frequency of photographs with >1 individual was very low and similar to that observed in other solitary species (see also Branch 1994).

Concluding remarks.—Both species of fox used all habitat types monitored in our study, although they did so to a different degree, and their use also depended on the extent of human impacts. As expected, crab-eating foxes tended to make more intensive use of forest habitats, whereas pampas foxes tended to use to a higher degree the more open grasslands with livestock grazing. However, the trend toward a positive (although not statistically significant) relationship between the recording rates of both species at baiting stations, and observations of both species in close proximity (about 50 m—M. S. Di Bitetti, pers. obs.), suggests that spatial avoidance is not an important mechanism that these foxes use to reduce the chance of encounters with individuals of the other species.

Temporal partitioning is 1 mechanism that closely related species can use to avoid competition (Kronfeld-Schor and Dayan 2003), with the less-competitive (subordinate) species usually switching its activity to suboptimal times of the daily cycle in order to reduce interference competition by the dominant one (Carothers and Jaksic 1984; Gutman and Dayan 2005). However, phylogenetic constraints on activity patterns usually make closely related species show similar patterns, limiting the opportunities for temporal partitioning among closely related competitors (Roll et al. 2006). This may explain why most studies of potentially competing canids living in sympatry have shown spatial segregation of the species at a microhabitat level (with similar daily activity patterns) as the main mechanism used to avoid competition (Macdonald et al. 2004a). The activity pattern of crab-eating foxes at INR was similar to that described for populations of this species in other neotropical sites. Conversely, pampas foxes had different activity patterns at different study sites (Fig. 5C), being mostly nocturnal when no other fox species was present, and showing diurnal activity when living in sympatry with crab-eating foxes (Vieira and Port 2007; Fig. 5A).

Despite differences in the patterns of relative habitat use between crab-eating foxes and pampas foxes, we suggest that the main mechanism that facilitates the coexistence of these foxes is time partitioning. We further suggest that it is the pampas fox's behavioral plasticity, mainly its ability to adjust its activity pattern to avoid encounters with other sympatric canids, what allows this species to live in sympatry with the crab-eating fox and share the same microhabitats. Pampas foxes resort to this mechanism of interspecific avoidance because, due to their smaller size and because they forage solitarily, they may be competitively subordinate to crab-eating foxes (see Carothers and Jaksic 1984; Johnson and Franklin 1994b; Linnell and Strand 2000; Macdonald et al. 2004a; Wang et al. 2004). This hypothesis should be further tested with detailed studies of the diet, activity patterns, social interactions, and home-range use of both species living in sympatry and allopatry across different study sites.

RESUMEN

El zorro de monte (*Cerdocyon thous*) y el zorro pampa (*Lycalopex gymnocercus*) son similares en tamaño corporal y dieta. Sin embargo, solapan sus rangos de distribución en Sudamérica. Usamos registros de cámaras-trampa de ambas especies obtenidos en la Reserva Natural del Iberá (RNI), noreste de Argentina, para poner a prueba la hipótesis de que, en simpatria, reducen la competencia interespecífica usando hábitats distintos y/o evitando superponer sus patrones de actividad. Usamos registros de cámaras-trampa obtenidos en 2 sitios adicionales habitados por solo 1 de estas especies, el Bosque Atlántico de Misiones (BA) y el Parque Nacional Lihué Calel (PNLC), para describir el patrón de actividad diario de estos zorros cuando viven solos. En RNI establecimos 41 estaciones de muestreo en 2 hábitats (bosque de Espinal y pastizales), y en 2 tratamientos por hábitat (con o sin ganado y pobladores). Tres estaciones fueron instaladas en bosques en galería. Obtuvimos 540 fotografías de zorro de monte (289 registros) y 175 fotografías de zorro pampa (115 registros) en 1521 días-cámara. En PNLC, 27 estaciones de muestreo (1002 días-cámara) produjeron 109 registros de zorro pampa. En BA, 195 estaciones de muestreo (11.689 días-cámara) brindaron 103 registros de zorros de monte. En RNI, el zorro de monte fue registrado con mayor frecuencia en ambientes de bosque, mientras que el zorro pampa lo fue en los pastizales abiertos. Sin embargo, ambas especies fueron registradas en todos los hábitats y sus tasas de registros no estuvieron negativamente correlacionadas entre sí. En RNI, el zorro de monte fue nocturno, con un pico de actividad luego del anochecer y otro antes del amanecer, un patrón similar al observado en BA y otras regiones. En RNI, el zorro pampa mostró un pico de actividad entre las 0000 y las 0400 h y otro entre la 1000 y las 1300 h, un patrón que difiere del observado en PNLC y en otros sitios, donde la especie es mayormente nocturna. En RNI, el zorro pampa reduce su actividad diaria en los horarios en que el posiblemente dominante zorro de monte está activo, lo cual facilitaría su coexistencia.

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