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MATEUS ZIMMER

A COEXISTÊNCIA DE GRAXAINS-DO-MATO (Cerdocyon thous) E CACHORROS

(Canis familiaris) NO LIMITE AUSTRAL MATA ATLÂNTICA

Porto Alegre, Dezembro de 2019

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Trabalho de Conclusão de curso apresentado como requisito parcial para obtenção do título de Bacharel em Ciências Biológicas na Universidade Federal do Rio Grande do Sul. Orientadora: Maria João Ramos Pereira Co-orientadora: Flávia Pereira Tirelli

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FORMATAÇÃO

Este trabalho foi redigido em inglês seguindo, nas páginas numeradas, as regras de formatação e publicação da revista Iheringia – Série Zoologia, como visualizadas em 30/11/2019 através do link:

<http://www.scielo.br/revistas/isz/iinstruc.htm>.

De acordo com as regras para diagramação da revista, figuras e tabelas não seriam inseridas no texto e sim enviadas em arquivos separados. Contudo, para este trabalho, optamos por incluir as figuras e as tabelas ao longo do texto para facilitar a leitura. Crab-eating foxes and dogs (Carnivora: Canidae) in the southern limit of the Brazilian Atlantic Forest: Coexistence facilitated by spatio-temporal segregation?

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Abstract: Humans (Homo sapiens) and dogs (Canis familiaris) have an ancient relationship of proximity, and thus are distributed around the world. Natural areas bordering human occupations, in urban or rural settings may suffer from the presence of dogs. Dogs may compete with wildlife in several ways, but due to their phylogenetic and behavioral proximity wild canids are particularly susceptible to impacts resulting from dogs' presence. Here we assessed spatio-temporal effects of dogs on a species of wild canid, the crab-eating fox (Cerdocyon thous). We detected changes in the behavior of C. thous in the presence of dogs, including changes in temporal activity and spatio-temporal segregation, that is they do not occur in the same place at the same time. However, the two species do not seem to avoid each other spatially; on the contrary, their probability of detection increases with the capture success of the other at sites where both occur. The coexistence of C. thous and C. familiaris seems to be facilitated by spatio-temporal segregation, where C. thous avoids encounters with domestic dogs in sites where both occur. In relation to crab-eating foxes, dogs seem to act as interference competitors, although the possibility of other forms of competition should not be excluded.

Key-words: *Canis familiaris, Cerdocyon thous*, sympatry, co-occurrence, occupancy.

Resumo: Humanos (*Homo sapiens*) e cachorros (*Canis familiaris*) têm uma antiga relação de proximidade, e assim estão distribuídos ao redor do mundo. Áreas

naturais limítrofes de ocupações humanas, urbanas ou rurais, podem sofrer com a presença de cachorros. Os cachorros podem competir com a vida selvagem de várias formas, mas devido à sua proximidade filogenética e comportamental, os canídeos silvestres são particularmente suscetíveis aos impactos resultantes da presenca de cachorros. Aqui avaliamos efeitos espaço-temporais dos cachorros sobre uma espécie de canídeo silvestre, o Graxaim-do-mato (Cerdocyon thous). Detectamos alterações no comportamento de C. thous na presença de cachorros, incluindo alterações na atividade temporal e segregação espaço-temporal, não ocorrendo no mesmos lugares ao mesmo tempo. No entanto, as duas espécies não parecem evitar uma à outra espacialmente; pelo contrário, a sua probabilidade de detecção aumenta com o sucesso da captura da outra nos locais onde ambas ocorrem. A coexistência de C. thous e C. familiaris parece ser facilitada pela segregação espaço-temporal, onde C. thous evita encontros com cachorros em locais onde ambos ocorrem. Em relação aos graxains-do-mato, os cachorros parecem agir como competidores de interferência, embora a possibilidade de outras formas de competição não deva ser excluída.

Palavras-chave: Canis familiaris, Cerdocyon thous, simpatria, coocorrência,

ocupação.

INTRODUCTION

At the end of the last ice age, when all human populations (*Homo sapiens* - Linnaeus, 1758) were hunter-gatherers, their spatial occupation overlapped with that of grey wolves (*Canis lupus* - Linnaeus, 1758), and the coexistence and co-evolution of the two species led to the domestication process that eventually originated domestic dogs (*Canis familiaris*- Linnaeus, 1758) (MOREY, 1994; CLUTTON-BROCK, 1995). With shared evolutionary histories, dogs and humans have a close bond and thus have jointly dispersed globally (GOMPPER, 2014). Currently *C. familiaris* is a ubiquitous species and its global population is estimated in between 700 million and one billion individuals, distributed with greater concentration along with human occupations in urban and rural settings (GOMPPER, 2014).

However, dogs can become free-ranging (HUGHES & MACDONALD, 2013) and, as an invasive species (SILVA, 2012), reaching non-urban areas may negatively impact native fauna through predation, competition, harassment, hybridization, disease transmission (YOUNG *et al.*, 2011; HUGHES & MACDONALD, 2013; DOHERTY *et al.*, 2017) and by forcing behavioral changes in wild mammals (ZAPATA-RÍOS & BRANCH, 2016).

Dogs are undoubtedly the most abundant carnivore in the world (GOMPPER, 2014) and have already contributed to the extinction of at least 11 species of vertebrates worldwide, are confirmed or potential threat to 188 endangered vertebrate species (DOHERTY *et al.*, 2017) and, thus, recognized as a global conservation issue (SILVA, 2012; GOMPPER, 2014). Although, it is surprising that the ecological impacts of domestic-dogs do not get much research effort and are not nearly as well understood as those of domestic-cats (*Felis catus* - Linnaeus, 1758),

another domestic carnivore and invasive species globally widespread (MEDINA *et al.*, 2011; YOUNG *et al.*, 2011; DOHERTY *et al.*, 2017).

Wild carnivores tend to avoid domestic carnivores, and this may cause the replacement of native species by exotic species (FARRIS *et al.*, 2016). VANAK & GOMPPER (2009¹) reported four ways by which dogs may act as competitors affecting sympatric carnivores:

(1) as intraguild predators, by killing and consuming smaller carnivores; in Brazil, CAMPOS *et al.* (2007), found remains of small carnivores such as the coati *Nasua nasua* (Linnaeus, 1766) and the lesser grison *Galictis cuja* (Molina, 1782) in dog scats;

(2) as exploitative competitors, by suppressing limited resources shared with other carnivores; dogs may potentially become stronger competitors regarding species of similar or even larger size, because of the advantage of hunting in packs or because they tend not to show reluctance in approaching humans, for example;

(3) as interference competitors, especially regarding medium-sized and small carnivores, by causing spatial exclusion, harassment, or even death (in extreme cases) to competitors; the subordinate competitor will avoid encounters and potentially modify patterns of use of space or time to reduce competition with dogs;

(4) as apparent competitors, by often acting as reservoir for pathogens (parasites and zoonosis) able to affect the health or body condition of the sympatric wild carnivores; as pathogens multiply and spread amongst the less sensible or more abundant species (dogs; the dilution effect, OSTFELD & KEESING, 2000), the rarer or more susceptible species suffers from the disease.

Wild carnivores within the Canidae are particularly prone to be impacted by the presence of dogs. The phylogenetic proximity results in behavioral similarities in terms of resource use and preference, leading to at least one of the abovementioned competitive interactions. Due to that proximity, dogs and wild canids also have strong compatibility and consequent sharing of diseases and parasites, and the risk of transmission is further increased because communication between canids is based on olfaction of mucous and/or infectious matter, such as urine and feces (BUTLER *et al.*, 2004; WOODROFFE *et al.*, 2004). The presence of dogs may lead to changes in the activity patterns of wild canids, including a decrease in the time used for hunting and foraging, an increase in time spent in state of vigilance and, concurrently, reduced time spent with rest and non-vigilance activities (VANAK & GOMPPER, 2009²). However, the ecological dynamics of spatio-temporal distribution of the potentially conflictive coexistence of domestic-dogs and other canids has not been widely studied yet.

Dogs are extremely widespread in Brazil and the southern region of the country is no exception. In Rio Grande do Sul (RS) state, dogs are probably one of the most widespread invasive exotic species, found even the innermost areas of conservation units (FERREIRA *et al.*, 2005).

There are three extant species of wild canids in RS; the maned wolf (*Chrysocyon brachyurus* - Illiger, 1815), the pampas fox (*Lycalopex* gymnocercus - G. Fischer, 1814) and the crab-eating fox (*Cerdocyon thous* - Linnaeus, 1766). *Chrysocyon brachyurus* is extremely rare in the state (SILVA, 2014), where it is categorized as Critically Endangered (CR) (RIO GRANDE DO SUL, 2014), and the present-day localization of an established population of the species is unknown. *Lycalopex gymnocercus* prefers open areas, and thus, is more restricted to grassland formations,

so typically occurs in the Pampa biome and in high-altitude grasslands (KASPER et al., 2014; SILVA, 2014). *Cerdocyon thous* is the most common, widespread and abundant wild canid of the state. This mesopredator occurs across the two biomes that characterize RS, Pampa and Atlantic Forest; the species occupies several habitats, with open or more cluttered vegetation (TRIGO et al., 2013; KASPER et al., 2014; SILVA, 2014).

While the crab-eating fox is not endangered species in any level (state, federal or global), the species suffers some sort of pressures, such as road kills, death resulting from conflicts with farmers, and dog-borne diseases (KASPER *et al.*, 2014; SILVA, 2014; TRIGO *et al.*, 2013). With this study we aim to evaluate ecological aspects of the coexistence of the domestic dog (*C. familiaris*) and the crab-eating fox (*C. thous*) in the austral limit of the Atlantic Forest, which occurs in the southernmost Brazilian state, RS. We hypothesize that the presence of dogs affects and leads to behavioral changes in the crab-eating foxes. As we assume *C. familiaris* to be the dominant species in a competition situation, we expect *C. thous* to avoid cooccurrence with dogs by not occupying the same sites, or by avoiding occurring in the same sites at the same time.

MATERIAL AND METHODS

Study areas. We sampled three areas in Rio Grande do Sul, southern Brazil (Fig. 1.), as part of a larger project of the Bird and Mammal Evolution, Systematics and Ecology Lab of the Universidade Federal do Rio Grande do Sul (UFRGS). The sampled areas are included in the southernmost limit of the Atlantic Forest biome. The landscape quite differs between areas, from the largest most preserved tropical deciduous forest in the state, to a natural mosaic of altitude forests and grasslands, to an anthropogenic rural matrix. Such differences between areas create a structural

and compositional landscape complexity inside the sample universe. Beyond that, the sample universe reflects a gradient of human and dog density and other associated anthropogenic pressures. The areas sampled were: 1) Turvo State Park (TUSP; 27°08'44''S, 53°53'10''W): a state strict protection conservation unit with a total area of 17,491 hectares, it constitutes a forest reserve that has important areas of preserved Decidual Seasonal Forest. Created in 1954, it is the oldest conservation unit in the state. TUSP is located at the northwest of RS, in the municipality of Derrubadas, banks of the Uruguay River, and bordering the Santa Catarina (SC) state and the Argentinean province of Misiones (KASPER et al., 2015; KASPER et al., 2004; MELO et al., 2012). 2) Serra Geral National Park (SGNP; 29°08'2''S, 49°59'40''W): a federal strict protection conservation unit, with an area of 17,300 hectares, covering the municipalities of Cambará do Sul, RS, Praia Grande and Jacinto Machado, SC. The landscape is constituted by high-altitude grasslands, a natural mosaic with forests that includes various vegetation formations, such as Mixed Ombrophylous Forest, also known as Araucaria forest, characterized by the presence of patches of Araucaria angustifolia trees (SANTOS et al., 2004; MMA/IBAMA, 2003). The park portion sampled in this study was an area under government expropriation where cattle still roams in some patches. 3) Teutônia Rural Area (TEUT; 29°26'36''S, 51°47'57''W.): a non-protected area, located in the municipality of Teutônia, central region of RS. Here the landscape is a mosaic of houses and private rural properties with patches of silvicultural (Pinus or Eucalyptus), agricultural and livestock productions and remnants of Atlantic forest on steeper terrain. The area delimited by the outermost sampled points had approximately 1,000 hectares.

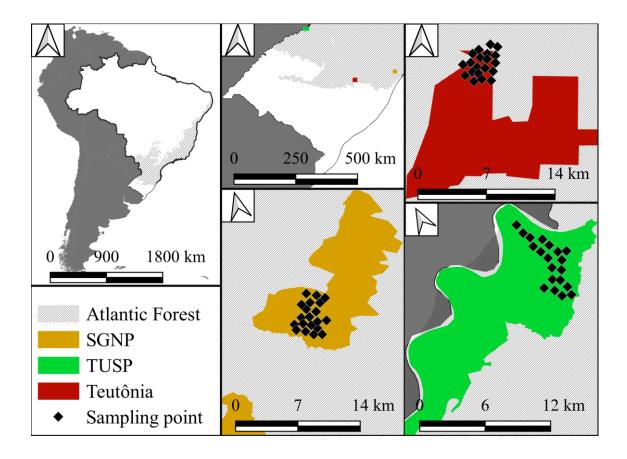


Fig. 1. Location of study areas in Rio Grande do Sul state, Brazil; South America. Note that all the areas occur in the southernmost limit of the Atlantic Forest. In green the Turvo State Park (TUSP), in red the Teutônia municipality and in yellow the Serra Geral National Park (SGNP) as well as the distribution of the sampling points in each area in black diamonds.

Field sampling. We used the camera trapping method to collect our data. Camera traps (Bushnell and/or Moultrie) consist of automatic cameras equipped with a motion sensor. Sampling design was defined by superimposing a 1x1 km grid on the maps of the three areas, selecting - based on environmental integrity and logistical favorability - 20 contiguous sampling cells with one sampling point inside, which were approximately 1km apart from each other. Each sampling point was composed of two passive infrared digital camera-traps, totaling 40 camera-traps per sampling area. The cameras were programmed to capture 10-second videos, with a 5-second interval in-between, were active 24 hours a day, and stamped each record with the date and time of the instant captured. The traps were installed in the trunk of trees, about 30cm above the ground, in places that had evidence of nearby use by mammals (demarcated trails, feces, burrows, etc.) and no baits were used, as to interfere the least with the natural behavior of the animals. The camera traps were active in each area for about two months, not concomitantly. Every 30 days batteries were replaced and the data recorded on the memory cards collected. Our first sampled area was SGNP, where the cameras stayed for 134 days, from September 2017 to January 2018; then we moved the cameras to TUSP, where they remained for 123 days, from March to July 2018; TEUT was sampled last and for just 65 days, from October to December 2018.

Data triage and taxa identification. Every video registered was watched in full, and the ones that contained any faunal records were identified and processed by a qualified member of the lab crew, with the help of literature and/or a specialist if necessary. For this study's species of interest, the information of the records used in subsequent analysis was the sampled point, the date and time of the record. We considered an independent record those of a given species in a given sampled point separated by at least a 30-min interval (DI BITETTI *et al.*, 2006), and a trap interval as a 24-h period during which at least one of the two cameras at the sampled point functioned properly; sampling occasion is the trap interval of a certain sampled point. A matrix of 'capture history' was built for each species, and consists of a value of (1) for presence of at least one independent record at a sampling occasion and (0) for the absence of any record. We calculated the sampling effort as the sum of the trap intervals, and we defined capture success for each species by dividing the sum of 1's of the capture history by the sum of occasions of a certain sampled point, then multiplied by 100. The capture success of the species was used as a detection variable in single-species occupancy models, of *C. familiaris* for *C. thous* and viceversa, as detailed below.

Temporal activity and its overlap between species. We estimated the percentage of overlap in the period activity of the two species using i) the total time data and ii) only records from sampled points where both species were registered, with the "overlap" package from R. Overlap percentage results are given by two different indexes; (1) 'Dhat1' to be used when one of the samples is smaller than 50, and (2) 'Dhat4' to be used when both samples are equal to or greater than 50 (MEREDITH & RIDOUT, 2018). Bootstrap (1000 simulations) tests were done to obtain confidence intervals.

First, all time data was treated with function "sunTime" of package "overlap" version 0.3.2 (MEREDITH & RIDOUT, 2018) in software R version 3.6.1 (R CORE TEAM, 2019); this function converts the clock time to sun time, by adjusting sunrise to 6am and sunset to 6pm. The adjustment is based on the dates and coordinates of every record provided (MEREDITH & RIDOUT, 2018). This was done because animal activity patterns are, in fact, regulated by daylight intensity and not by the time shown at any clock (NOUVELLET *et al.*, 2012).

Then, for obtaining each species period of activity we generated rose diagrams using the "circular" package 0.4-93 (LUND, 2017) of the software R. This was done using the time data from each species' independent records; in the first test the total time data obtained for each species was used (A), alternatively we tested time data from sampled points where (B) both species were registered, (C) only one of them was registered. Rayleigh tests were performed in order to test for uniformity in the temporal distribution of the records.

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Inter-species record intervals and spatiotemporal segregation. We assembled the set of observed time intervals between records of the two species in all sampled points where both species occurred. Two kinds of event are possible: a record of *C. thous* detected after a record of *C. familiaris* in the same sampled point, and a record of *C. familiaris* detected after a record of *C. thous* in the same sampled point. To assess spatiotemporal segregation between the two species we generated an expected statistical distribution of intervals between records from the observed time intervals (1000 simulations). Then, we tested for normality in the distribution of the observed time intervals by analyzing QQ-plots done in R. As the distribution was not normal, but instead skewed towards the upper values, we compared the observed and the estimated distributions of time intervals between records of the two species using Komolgorov-Smirnov one-side tests.

Hierarchical occupancy models and set of detection/occupancy variables. To estimate site occupancy and detection for the two species, we used the "unmarked" package 0.13-0 (FISKE *et al.*, 2019) from software R, as it fits hierarchical models of unmarked animals' (i.e. not identified at individual level) occurrence for data collected with imperfect detection, allowing the input of covariates as parameters influencing the observation and biological processes (FISKE *et al.*, 2019). We built single-season single-species occupancy models for each species, using the capture history matrix per species and a set of covariates selected as explanatory for the detection and occupation models that would follow. In table I we present the full set of site associated variables selected for the detection (observation process) and occupancy (ecological process) models and the corresponding prediction. All variables were scaled, as the different units could cause deviations on their individual influence in the models. Using the function 'vifcor' from the R package "usdm" version 1.1-18 (NAIMI, 2017) we calculated the variance inflation factor (VIF) for the set of variables. VIF allows detecting multicollinearity and excluding highly correlated variables (VIF>7) from the set (NAIMI, 2017). We built the models for each species using all possible combinations of the variables, which we then ranked by the Akaike Information Criterion (AIC), and considered models with Δ AIC < 2 as equally well fit. Still, when more than one model showed Δ AIC < 2, we used the highest variable significance in the model as a form of tie-breaker. Following the hierarchical approach, the best detection model for each species was subsequently inserted in the occupancy models. The naïve occupancy probabilities were obtained by simply dividing the number of sites with at least one record for each species by the total number of sites.

Variable	Code	Description or source (Value range [unit])	Prediction
Trigger speed	t_cam	Mean value for trigger speed of the two camera- traps brand/model at a sampling point, and time delay necessary for the camera to shoot a picture once an animal has interrupted the infrared beam within the camera's detection zone (0,2-30 [s]) (HORN, 2019)	Shorter response time will increase the detection of both species
PIR detection range	d_cam	Mean value of Passive Infra-Red (PIR) distance detection range of the two camera-traps brand/model at a sampling point (12 – 30 [m]) (HORN, 2019)	Higher PIR detection range will increase the detection of both species
Distance to roads	d_est	Euclidean distance raster created in ArcGis based on shapefile from the Regional Executive Organization for	Smaller distances will facilitate dogs' detection and road buzz may scare away <i>C. thous</i> , decreasing its detection

Table I. Selected predictor variables and respective predicted effects on detection and occupancy models.

Capture success of <i>C. familiaris</i> Capture success of <i>C. thous</i>	sc_c_fam sc_c_tho	Environmental Protection; missing roads included manually through own observations (3 - 1800 [m]) (HORN, 2019) Capture success = (sum of 1's of the capture history / sum of occasions of a certain sampling point) times 100 (0 - 21 [%])	Used in <i>C. thous</i> detection model; will decrease detection as avoidance is expected Used in <i>C. familiaris</i> detection model; will decrease detection as avoidance is expected or will increase detection resulting from intra-guild predation
	(Decupancy models	î
Vegetation Index	NDVI	Normalized Difference Vegetation Index, values range from non-forest to dense forest (0-1) MODIS Product generated by the Land Processes Distributed Active Center (LP-DAAC)	<i>C. thous</i> occupancy will increase in denser forest, while <i>C. familiaris</i> occupancy will decrease
Distance to nearest human facility	d_inst_h	Distance measured by satellite imagery (Google Earth) from sampling point to the nearest building (24 – 7226 [m])	<i>C. thous</i> occupancy will decrease near humans, while <i>C. familiaris</i> occupancy will increase
Number of human facilities	n_inst_h	The number of human buildings counted by satellite imagery (Google Earth) in a 500-meter radius around each sampling point (0-38)	<i>C. thous</i> occupancy will decrease with increasing human density, while <i>C.</i> <i>familiaris</i> occupancy will increase
Distance to forest interruption	d_b_mt	Distance measured by satellite imagery (Google Earth) from sampling point to the nearest forest edge or interruption (0 – 7060 [m])	As this distance relates with edge effects intensity, <i>C. thous</i> occupancy will decrease in sites close to forest edges, while <i>C. familiaris</i> occupancy will increase

RESULTS

Our total sampling effort was 5101 trap intervals (SGNP = 1941, TEUT = 1235, TUSP = 1925). From the total 60 sampled points, 29 did not record any of the

studied species, and 31 recorded at least one of the species, 18 just recorded *C. thous* and 3 just *C. familiaris*. In 10 sampled points both species were recorded. We obtained 191 total independent records (30 min. interval) of the both species, *C. thous* with 133 and *C. familiaris* with 58. Seventy-three percent of the total records were obtained in TEUT, 16% in SGNP and 11% in TUSP. In all three areas the proportion of *C. familiaris* records was lower than that of *C. thous* (TEUT: *C. thous* = 71.43% / *C. familiaris* = 28.57% | SGNP: *C. thous* = 70% / *C. familiaris* = 30% | TUSP: *C. thous* = 57.24% / *C. familiaris* = 42.86%). Species capture success varied between 0 and 21%, with the highest values obtained in TEUT (Fig. 2).

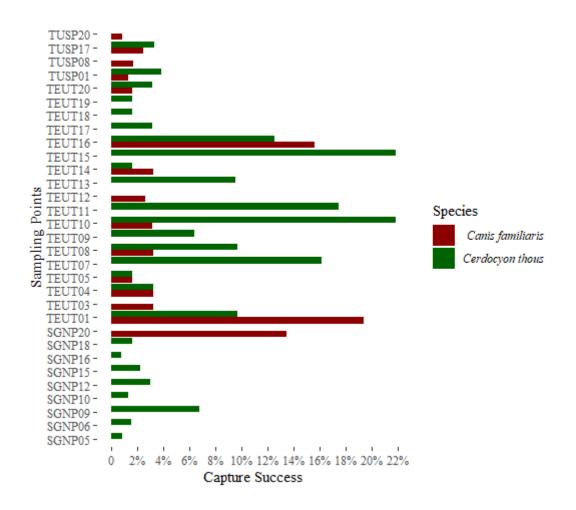


Fig. 2. Capture success of *Cerdocyon thous* and *Canis familiaris* in sampling points where at least one of them was recorded in Turvo State Park (TUSP), the Teutônia municipality (TEUT) and the Serra Geral National Park (SGNP).

The temporal activity for *C. thous*, had non-uniform distribution being predominantly nocturnal, reaching peaks right after the sunset and at dawn (Fig. 3). Using the entire set of time data, the angular average of the set of frequencies was between 0 and 1am and (Rayleigh test = 0.277 | p<0.001), when co-occurring with *C. familiaris* the angular average was at 2am (Rayleigh test: 0.459 | p = 0.000), and when occurring solo the angular average was at 22pm (Rayleigh test: 0.256 | p = 0.007). *Canis familiaris* temporal activity had trimodal distribution, apparently cathemeral, starting activity in the morning just after sunrise, diminishing at noon, then rising again at mid-afternoon and decreasing at early evening, and then showing additional activity peak at dawn (Fig. 3). Using the entire time data, the angular average of the frequencies was at 11am and showed marginally non-significant non-uniformity (Rayleigh test = 0.227 | p = 0.051), when co-occurring with *C. thous* the angular average of the frequencies was between 8 and 9am and had a more uniform distribution (Rayleigh test = 0.100 | p = 0.651). For solo activity of *C. familiaris* there were not enough independent records to compute the statistic.

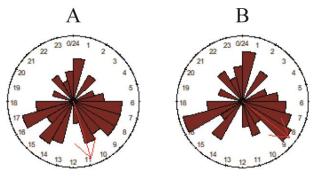


Fig. 3. Distribution of the temporal activity for *Cerdocyon thous* and *Canis familiaris* in a rose diagram ploted with 24 axes representing the 24 hours of the day, The higher the bar the greater the amount of records. For both species (A) total time data, (B) records from sampling points with co-occurrences and (C) records from sampling points with no co-occurrences. The red arrow represents the angular average of the set of frequencies.

The overlap in the period of activity between the two species in all sites was of 61.7% (49.9 – 73.7% Bootstrap 95% CI) (Fig. 4). At the set of sites where the two species co-occurred, average temporal overlap reduced to 55.6% (41.3 – 69.8% Bootstrap 95% CI) (Fig. 5).

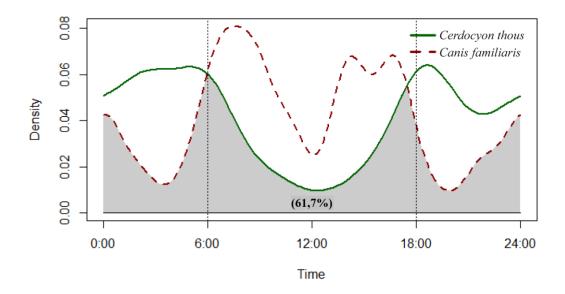


Fig. 4. Overlap in the activity period between *Cerdocyon thous* and *Canis familiaris*, using the total time data. Overlap (grey part) equals 61,7%. The line in 6:00 represents the sunrise and the line at 18:00 represents the sunset.

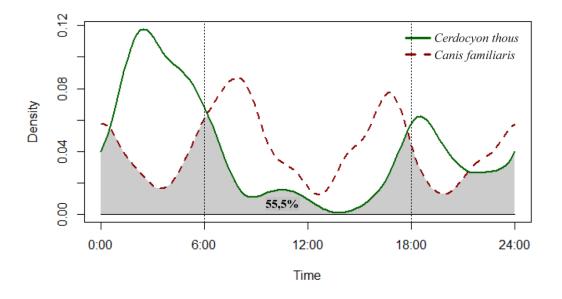


Fig. 5. Overlap in the activity period between *Cerdocyon thous* and *Canis familiaris*, using only time data from sampling points with co-occurrences. Overlap (grey part) equals 55,5%. The line in 6:00 represents the sunrise and the line at 18:00 represents the sunset.

Excluding the sites were only one or none of the species occurred, we obtained 36 events of one species recorded after the other in the same sampled point, ranging

from a minimum of 1h17min and a maximum of 40 days. In Table II we present inter-species record intervals in percentages for three time classes and by event kind. The Komolgorov-Smirnov one-side tests showed that observed time-to-encounter distribution was significantly greater than that of the estimated time-to-encounter distribution (D^=0.670; p<0.001) reflecting species spatio-temporal segregation.

Table II. Percentage of time-to-encounter intervals in three time classes (<24h, >7d, <30d) by event type (first detection *Cerdocyon thous* and first detection *Canis familiaris*).

	Interval				
Event	< 24h	< 7 d	< 30 d		
Cerdocyon thous \rightarrow Canis familiaris	23,53%	82,35%	94,12%		
Canis familiaris \rightarrow Cerdocyon thous	31,58%	73,68%	94,74%		

For all the variables (Tab. I) VIF tests were performed, but none of the detection variables showed multicollinearity (VIF<1.4), so all the five were suitable for use in the selection process of the detection models. As for the occupancy variables, 'Distance to forest edge' showed multicollinearity (VIF>7) and was thus excluded from the subsequent analyses. The remaining three were not multicollinear among them (VIF<1.7) and were thus used as predictors for occupancy.

In Table III we present the detection models for *C. thous* ranked by Δ AIC. The best model included 'PIR detection range' (Est = 0.342 | SE = 0.087 | z = 3.860 | p<0.001) as the most significant variable, this model also included the 'Capture success of *C. familiaris*' (Est = 0.145 | SE = 0.065 | z = 2.20 | p = 0.028).

Table III. Detection models for *C. thous*. (p:detection, Ψ :occupancy). The model in bold - p(d_cam + sc_c_fam) Ψ (.) - was chosen as the best model based on the most significant predictor variable. (t_cam: trigger speed, d_cam: PIR detection range, sc_c_fam: capture success of *C. familiaris*).

Model	nPars	AIC	ΔAIC	AIC	Cumulative
				weight	Weight

$p(t_cam + d_cam + sc_c_fam) \Psi(.)$	5	959	0	0.30	0.30
$p(d_cam + sc_c_fam) \Psi(.)$	4	959.67	0.67	0.21	0.51
$p(t_cam + d_cam) \Psi(.)$	4	960.93	1.93	0.11	0.63
$p(d_cam + d_est + sc_c_fam) \Psi(.)$	5	961.10	2.11	0.10	0.73
$p(t_cam + d_cam + d_est) \Psi(.)$	5	961.47	2.48	0.08	0.82
$p(d_cam + d_est) \Psi(.)$	4	962.11	3.11	0.06	0.88
$p(t_cam + sc_c_fam) \Psi(.)$	4	962.57	3.57	0.05	0.93
$p(t_cam + d_est + sc_c_fam) \Psi(.)$	5	963.36	4.36	0.03	0.96
$p(t_cam + d_est) \Psi(.)$	4	964.28	5.29	0.02	0.98
$p(t_cam) \Psi(.)$	3	965.06	6.07	0.01	1.00
$p(d_est + sc_c_fam) \Psi(.)$	4	970.40	11.40	0.00	1.00
$p(d_{est}) \Psi(.)$	3	972.22	13.22	0.00	1.00
$p(sc_c_fam) \Psi(.)$	3	1086.42	127.43	0.00	1.00
$p(d_cam) \Psi(.)$	3	1094.17	135.17	0.00	1.00
р(.) Ψ(.)	2	1111.14	152.14	0.00	1.00

In Table IV we show the occupancy models for *C. thous*. The best model included the most significant variable – 'Distance to nearest human facility' (Est = -0.839 | SE = 0.349 | z = -2.40 | p = 0.016). Crab-eating fox average probability of detection was 5% (95% CI = 4 - 5.9%) and average probability of occupancy was 44,7% (95% CI = 30.6 - 58.8%); naïve occupancy was 43%.

Table IV. Occupancy models for *C. thous*. (p:detection, Ψ :occupancy). The model in bold - p(d_cam + sc_c_fam) Ψ (d_inst_h) - was chosen as the best model based on the most significant predictor variable. (d_inst_h: distance to nearest human facility, n_inst_h: number of human facilities, NDVI: vegetation index).

Model	nPars	AIC	Δ AIC	AIC weight	Cumulative Weight
p(d_cam + sc_c_fam) Ψ(d_inst_h)	5	954.34	0	0.29	0.29
$p(d_cam + sc_c_fam) \Psi(n_inst_h + NDVI)$	6	954.54	0.21	0.26	0.55
$p(d_cam + sc_c_fam) \Psi(NDVI + d_inst_h)$	6	955.61	1.27	0.15	0.71
$p(d_cam + sc_c_fam) \Psi(n_inst_h)$	5	956.05	1.71	0.12	0.83
$p(d_cam + sc_c_fam) \Psi(d_inst_h + n_inst_h +$	7	956.52	2.19	0.10	0.93
NDVI)					
$p(d_cam + sc_c_fam) \Psi(d_inst_h + n_inst_h)$	6	958.01	3.67	0.05	0.97
$p(d_cam + sc_c_fam) \Psi(.)$	4	959.67	5.33	0.02	0.99
$p(d_cam + sc_c_fam) \Psi(NDVI)$	5	961.59	7.26	0.01	1.00

Among detection models for C. familiaris, the best model included the most significant covariates: 'Distance to roads' (Est = -2.729 | SE = 0.668 | z = -4.08 |

p<0.001) and 'Capture success of C. thous' (Est = 0.802 | SE = 0.166 | z = 4.83 |

p<0.001) (Table V).

Table V. Detection models for *C. familiaris*. (p:detection, Ψ :occupancy). The model in bold - p(d_est + sc_c_tho) Ψ (.) - was chosen as the best model based on the most significant predictor variable. (t_cam: trigger speed, d_cam: PIR detection range, sc_c_tho: capture success of *C. thous*).

Model	nPars	AIC	ΔAIC	AIC	Cumulative
				weight	Weight
$p(d_cam + d_est + sc_c_tho) \Psi(.)$	5	440.04	0	0.47	0.47
$p(d_est + sc_c_to) \Psi(.)$	4	440.91	0.87	0.31	0.78
$p(t_cam + d_est + sc_c_tho) \Psi(.)$	5	441.59	1.55	0.22	1.00
$p(d_cam + sc_c_tho) \Psi(.)$	4	452.85	12.81	0.00	1.00
$p(t_cam + d_cam + sc_c_tho) \Psi(.)$	5	454.30	14.26	0.00	1.00
$p(d_cam + d_est) \Psi(.)$	4	462.33	22.29	0.00	1.00
$p(sc_c_tho) \Psi(.)$	3	462.62	22.58	0.00	1.00
$p(t_cam + d_cam + d_est) \Psi(.)$	5	462.66	22.62	0.00	1.00
$p(d_cam) \Psi(.)$	3	463.42	23.38	0.00	1.00
$p(d_{est}) \Psi(.)$	3	463.88	23.83	0.00	1.00
$p(t_cam + sc_c_tho) \Psi(.)$	4	464.43	24.38	0.00	1.00
$p(t_cam + d_est) \Psi(.)$	4	464.84	24.80	0.00	1.00
$p(t_cam + d_cam) \Psi(.)$	4	465.41	25.37	0.00	1.00
p(.) Ψ(.)	2	469.52	29.48	0.00	1.00
p(t_cam) Ψ(.)	3	471.35	31.31	0.00	1.00

Regarding occupancy models for C. familiaris (Table VI) none of the variables

included in any of the five best models showed significant effects. Dog average

probability of detection was 0.3% (95% CI = 0 - 0.7%); naïve occupancy was 25%.

Table VI. Occupancy models for *C. familiaris*. (p:detection, Ψ :occupancy). None of the predictor variables in any of the models returned significant estimates. (d_inst_h: distance to nearest human facility, n_inst_h: number of human facilities, NDVI: vegetation index).

Model	nPars	AIC	ΔAIC	AIC	Cumulative
				weight	Weight
$p(d_est + sc_c_to) \Psi(.)$	5	440.91	0	0.24	0.24
$p(d_est + sc_c_tho) \Psi(d_inst_h + NDVI)$	6	441.40	0.49	0.19	0.43
$p(d_est + sc_c_tho) \Psi(n_inst_h + NDVI)$	6	441.67	0.76	0.17	0.60
$p(d_est + sc_c_tho) \Psi(n_inst_h)$	5	441.91	1.00	0.15	0.74
$p(d_est + sc_c_tho) \Psi(d_inst_h)$	7	442.15	1.24	0.13	0.87
$p(d_est + sc_c_tho) \Psi(d_inst_h + n_inst_h +$	6	443.38	2.47	0.07	0.94
NDVI)					
$p(d_est + sc_c_tho) \Psi(d_inst_h + n_inst_h)$	4	443.80	2.89	0.06	1.00
$p(d_est + sc_c_tho) \Psi(NDVI)$	5	464.31	23.39	0.00	1.00

DISCUSSION

As hypothesized, the presence of dogs seems to lead to behavioral changes in crab-eating foxes, but not exactly as predicted. The relations between these two species are complex. Crab-eating foxes seem to slightly change their use of time in the presence of dogs, as the percentage of temporal overlap is lower in sites occupied by the two species than in sites exclusively used by crab-eating foxes, and this is caused by changes in the activity pattern of crab-eating foxes but not of dogs. When the two species occur at the same site, they segregate temporally; indeed, observed time-to-encounter distribution was significantly greater than expected by chance, but the two species still seem to seek some sites used by the other after a certain time interval. Although one species or the other uses some sites exclusively, occupancy models did not evidence spatial avoidance between the species; in fact, for both, the probability of being detected positively relates with a site's greater capture success of the other species, though that was only significant for dogs. So, perhaps dogs follow clues (e.g. chemical) left by the crab-eating foxes due to their phylogenetic and eco-physiological similarity.

Crab-eating foxes slightly change their use of time in the presence of dogs. The co-occurrence of the two species seems to cause behavioral changes in *C. thous*, reflected in the distribution of this species temporal activity, which is dislocated by the presence of dogs towards a greater concentration at dawn, when compared to when occurring solo. There seems to be a trend for reduction in time activity overlap from total sites to co-occurrence sites, suggesting potential temporal niche partitioning between crab-eating foxes and dogs. Of the two, only *C. thous* seems to significantly alter its activity patterns. While solo, crab-eating-foxes explore more time during the day; however, in the presence of dogs they reduce their day-time activities, exploring mostly the second half of the night-time (0 to 6am; Figs. 4 and 5). The consequence of strong competition or predation within a predator guild is that the competitively weaker species is often pushed into suboptimal niches, such as being forced to alter its use of time, to conform to the habits of the competitively stronger species (CREEL *et al.*, 2001). Such outcome suggests that, indeed, *C. familiaris* may, at least up to a certain level, act as an interference competitor for another canid species, as reported by VANAK & GOMPPER (2009¹). In Cayambe-Coca National Park, Ecuador, ZAPATA-RÍOS & BRANCH (2016) found similar behavioral responses amongst wild mammals co-occurring with dogs. There, dog activity was bimodal, concentrating between 5 to 9am and 16 to 20pm, making the Andean fox (*Lycalopex culpaeus* - Molina, 1782) to drastically avoid temporal overlap with dogs: the Andean fox response was to move its activity towards periods after the sunset, similarly to the crab-eating fox in our study, and becoming a lot more inactive in co-occurrence areas, particularly when dogs were most active.

Spatio-temporal segregation facilitates the coexistence of crab-eating foxes and dogs. Species avoidance is not solely temporal but also spatio-temporal. Actually, even when the two species occur in the same site, they do not use that site at the same time, presenting significant spatio-temporal segregation. This pattern also supports the assumption of dogs as interference competitors. Indeed, as suggested by KARANTH *et al.* (2017), spatio-temporal segregation in sympatric carnivores serves as way of dodging conflicts and of facilitating the coexistence between competitors.

Despite the evidence of spatio-temporal segregation between crab-eating foxes and dogs as a way to reduce interference competition, the possibility of apparent competition should not be put aside. As referred by VANAK & GOMPPER (2009¹), this pathogen-mediated competition is "perhaps the largest threat that sympatric carnivores face from dogs". This should be even more serious among closely related species; the phylogenetic closeness between crab-eating foxes and dogs, both Canidae within the Carnivora, leads to high, if not complete, compatibility regarding pathogens. Thus, similar use of space, and particularly the use of the same sites and trails, increases the chances of transmission of dangerous dog-borne viruses able to survive for short periods of time in the environment. Take for example the canine distemper virus (CDV), present in all body secretions and excretions, normally transmitted through inhalation or direct contact between individuals, but able to persist in the environment for some hours to a few days depending on environmental conditions (NEWBURY *et al.*, 2009). Actually, besides CDV, also canine parvovirus (CPV) and canine coronavirus (CCoV) have already been found in *C. thous*, as well as in *L. gymnocercus*, in the state of RS (HÜBNER *et al.*, 2010).

Sharing space: good for them, good for us? Perhaps the most popular knowledge about dogs' biology is that they mark their territory with urine. Still, such behavior is not exclusive to dogs (not even to canids), and scent-marking is done with urine, feces and other secretions sources of odor. Scent-marking behavior integrates the complex social systems of the Canidae, involving intricate signals for communication, not only associated with territoriality, on which these species rely (ANISKO, 1976). Besides, scent-marking often involves a circuit to be traversed and several specific points to be marked repeatedly with different types of odors. This chemical communication exchanges different messages between individuals of the same species, but also between individuals of distinct species (MACDONALD, 1980). Indeed, BEKOFF (2001), showed that domestic dogs easily find and discriminate their own urine from that of others, spending more time sniffing

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another's' urine, and re-scenting over more frequently in this latter case. We speculate this chemical communication to be the reason beyond the increased probability of detection *C. familiaris* with the capture success of *C. thous* at the same site, but not necessarily only associated with territorial marking activity. Actually, the mere presence of a different species intrinsic scent may arouse curiosity or the instinctive following of chemical clues by a phylogenetic and eco-physiological similar species. On the other hand, similar space-use may simple result from phylogenetic signal (LOSOS, 2008). But, either way, both thesis need empirical examinations to be confirmed or refuted.

Though we predicted that *C. thous* would avoid *C. familiaris* spatially, this does not seem to be the case, as reflected by the results of the detection models. Scent-stations using an industrialized product for sanitary training of domestic dogs (urea based) seem, instead, to have worked well in attracting *C. thous* (FARIA-CORRÊA, 2004); while here *C. thous* detection was not positively affected by the capture success of *C. familiaris*, it was also not negatively affected in the end.

Dogs probability of being detected increased closer to roads. This use of human infrastructures was not unexpected, given the long-term close relationship between dogs and humans (GOMPPER, 2014). In fact, FOX *et al.* (1975) when observing a small group of urban dogs reported their remarkable abilities to adapt to the urban environment, crossing roads and constantly using them for moving between sites, as well as the fortuitous foraging in garbage disposed on roadsides.

The motion sensitivity of the camera-trap significantly influenced the detection of *C. thous*; the greater the detection range, the furthest will the motion sensitivity of the camera-trap reach. Strangely, it did not seem to influence the detection of *C. familiaris*. Nonetheless, better equipment will make the detections of any animal

likely to occur. Actually, this should always be a key point when choosing field equipment, as it directly affects capture success and, subsequently, the success of the study in question.

"All over" habitat use by crab-eating foxes and dogs. Twenty-one of the sampled points had exclusive records of either crab-eating foxes or dogs, suggesting, at a first sight, spatial exclusion between the two species. However, two thirds of these sampled points showed 3% or less in capture success of the species exclusively captured; also, half of these points were in SGNP, where *C. familiaris* was only sampled at one point. Thus, our data does not support spatial exclusion for these particular sites and, instead, may simply reflect an almost complete absence of dogs in that area.

Dog occupancy was not significantly influenced by any of the evaluated variables. Similarly, the occupancy of the crab-eating fox was also not significantly influenced by the evaluated variables, except by the distance to human facilities, where its occupancy seems to increase. While we did not expect this outcome, FOX *et al.* (1975) has stated that "human activity and constructions may provide a higher density of food and shelter resources, and artifacts in the environment that might be used by animals on occasions". This, along with the known resilience and generalist habits of *C. thous* (KASPER *et al.*, 2014; SILVA, 2014) may explain the observed result. SILVA (2014) also describes as common knowledge among rural dwellers that the species wanders around dwellings, in search of leftover food or small domestic animals as preys. As a fact, TIRELLI *et al.* (2019) found plastic in the species faeces, in a deforestation frontier of the Brazilian Amazon, suggesting some sort of contact with anthropogenic waste. However, these results regarding the modeling of the ecological process should be taken cautiously. The highest amount

of independent records and the highest capture success for both species were obtained in the most human-modified area (TEUT). So, the models may be mostly explaining the specific occupancy of a rural-city adapted population of *C. thous*. Also, being so close to humans, dogs may easily be evenly widespread over the sampled area and, thus, not strongly associated to landscape or any spatially-structured environmental variables. Alternatively, variables capable of explaining the occupancy of crab-eating foxes and domestic dogs in rural areas or, otherwise, highly preserved areas, may be distinct and acting at a much finer scale than those here evaluated. For example, SOTO & PALOMARES (2015) found out the detection of dog tracks in a protected area was associated with the distance from the anthropogenic boundary.

Conclusions. The coexistence of *C. thous* and *C. familiaris* seems to be facilitated by spatio-temporal segregation, where *C. thous* avoids encounters with domestic dogs in sites where both occur. Then, in relation to crab-eating foxes, dogs seem to act as interference competitors, though the possibility of apparent competition should not be neglected. In fact, at the population level, non-lethal effects resulting from the presence of *C. familiaris* are very difficult to access, and will perhaps be subject to evaluation only with long-term monitoring data. But even if *C. thous* reveals to be resilient in a scenario of increased dog occupancy, negative impacts on other more sensitive species (e.g. small felids) may be significant, emphasizing the importance of social awareness programs for dog owners, most urgently for those living around protected or sensitive natural areas. In any case, municipalities, state and federal governments play a crucial role in damage mitigation, and should be investing in the control and castration of feral and roaming domestic dogs. Because this is a sensitive matter, which plays with the emotions of

people towards 'humans best and oldest friend', different stakeholders should be included in this discussion, and once the importance of the cause is understood, ultimate extreme containment measures, that usually generate strong conflicts, may be avoided.

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