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1 Patch characteristics and domestic dogs differentially affect carnivore space use in fragmented
2 landscapes in Southern Chile

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24 **Abstract**

25 In an increasingly anthropogenic world, native species face multiple interacting threats. Habitat
26 fragmentation and domestic dogs are two such perturbations threatening terrestrial mammals
27 globally. Here, we implemented a camera trap survey in the fragmented central valley/Andean
28 foothills transition of the Los Lagos Region in Southern Chile to evaluate space use of native
29 carnivores in a landscape comprised of patches of native forest amidst a matrix of pastureland.
30 Using an occupancy modeling framework to account for imperfect detection, we examined the
31 impacts of dogs and landscape metrics of fragmentation on three mesocarnivores – the foxes
32 culpeo (*Lycalopex culpaeus*) and chilla (*Lycalopex griseus*) and the wild cat güiña (*Leopardus*
33 *guigna*). Factors driving occupancy differed for each of the native species, while detection rates
34 for both canid species increased with dog occupancy. We found that a small (12%) simulated
35 increase in dog occupancy negatively impacted the spatial use of the culpeo. Habitat loss and
36 fragmentation were positive drivers for the chilla and the dog, and indirectly impacted the culpeo
37 through the domestic dog. The güiña did not respond to fragmentation and other habitat
38 covariates or dog occupancy. Instead, all native carnivore species temporally partitioned diel
39 activity with dogs. We highlight that the effects of dogs or fragmentation are not ubiquitous
40 across the carnivore guild with varied tolerance. However, future conditions of increased
41 fragmentation and habitat loss will likely increase the potential contact between domestic dogs
42 and native carnivores.

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54 **1. Introduction**

55 Fragmentation and habitat loss remains a global threat to biodiversity, increasing isolation
56 between suitable habitat with emergent consequences from edge effects (Haddad et al. 2015;
57 Pfeifer et al. 2017). These physical changes to landscapes also impact abiotic factors, altering
58 radiation fluxes, wind patterns, and the hydrological cycle to increase heterogeneity within and
59 across habitats (Saunders et al. 1991; Schmidt et al. 2017). Globally, 70% of forests are within 1
60 kilometer of an edge and are becoming increasingly fragmented resulting in abundances for over
61 85% of vertebrates being impacted by edge effects (Haddad et al. 2015; Pfeifer et al. 2017;
62 Montibeller et al. 2020). The negative effects of fragmentation remain highly debated given
63 idiosyncratic impacts across species and ecological interactions (Fahrig 2013; Rielly-Carroll &
64 Freestone 2017; Fletcher et al. 2018; Fahrig et al. 2019; Harrison & Banks & Leite 2020). While
65 species may be able to inhabit edge habitats, they may be excluded via biotic factors such as
66 competition or predation (Michel et al. 2016). Additionally, fragmentation may interact with
67 other factors such as habitat loss, fire prevalence, and hunting, exacerbating impacts or making it
68 difficult to ascertain the individual drivers that alter species or interactions (Cochrane 2001;
69 Peres 2001; Bartlett et al. 2016).

70 Domestic dogs (*Canis lupus familiaris*) represent another global threat to biodiversity as
71 the most abundant carnivore worldwide with a global population estimated at 700 million
72 (Hughes & Macdonald 2013). Therefore, dogs are a widespread invasive species that can
73 commonly exploit fragmented landscapes as they more easily permeate from areas of human
74 residence (Oehler & Litvaitis 1996; Broadbent et al. 2008; Paschoal et al. 2018). Dogs
75 commonly harass and kill native carnivores, compete for prey species, and transmit pathogens to

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76 wild populations, threatening native carnivores (Laurenson et al. 1998; Vanak & Gompper 2009;
77 Doherty et al. 2017). These disturbances can alter activity patterns and reduce relative abundance
78 of native carnivores. For example, native carnivores in Madagascar exhibited spatial avoidance
79 when domestic dogs were present, and were more likely to be replaced by dogs in degraded
80 forests near human settlement (Farris et al. 2016, 2017). Similarly, chilla fox (*Lycalopex griseus*)
81 visits to scent stations in Southern Chile were negatively correlated with dog presence, and
82 telemetry data showed that foxes rested in a habitat type that was not preferred by dogs (Silva-
83 Rodríguez et al. 2010a). In general, how dog-wildlife interactions are facilitated by habitat
84 destruction is largely unstudied, and it is unknown whether habitat destruction and dogs have
85 similar or opposing impacts on native carnivores, or work in concert. Given the pervasiveness of
86 both dogs and fragmentation as major disturbances to native species, it is surprising that few
87 studies measure and compare the synergistic effects of both.

88 The susceptibility to dog harassment/killing is largely size biased and thus, intensified for
89 mesocarnivores. However, the impacts of fragmentation on carnivores is harder to predict
90 because many aspects of their ecology such as prey availability, habitat quality that are also
91 impacted. For example, a disturbance from fragmentations shuffles species distributions and
92 facilitates the invasion of nonnative competitors or other domestic species (Crooks 2002;
93 Echeverría et al. 2007; Jessen et al. 2018). Mammals vary in their sensitivity to fragmentation
94 and in their adaptive responses from fragmentation (Crooks 2002; Janecka et al. 2016; Smith et
95 al. 2019; Palmeirim et al. 2020). Large-bodied mammalian carnivores are particularly susceptible
96 to fragmentation and edge effects due to their relatively small population sizes, slow growth rates
97 and extended habitat requirements and corresponding home ranges (Schipper et al. 2008). The
98 coupling of natural history characteristics, landscape structure, and anthropogenic pressures from

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99 human persecution result in carnivores, of all sizes, being among the most threatened groups of
100 mammals worldwide (Karanth & Chellam 2009; Estes et al. 2011; Ripple et al. 2014). However,
101 the impacts of fragmentation are less clear for mesocarnivores, many of which are generalists
102 and have smaller home ranges than their larger counterparts, and thus may be more resistant to or
103 even benefit from fragmentation (but see Crooks et al. 2017; Rocha et al. 2020). For example,
104 Massara et al. (2016) found that the occupancy of generalist mesocarnivores was negatively tied
105 to reserve size throughout the remnant patches of the Atlantic Forest in Brazil,.

106 Land owned privately by smallholders has been largely omitted from studies on native
107 carnivores and interactions between the carnivore guild and human pressures. These
108 understudied areas represent a later stage of the fragmentation process; rather than a contiguous
109 protected area with an edge riddled with encroaching pastures and other human use Given the
110 increased anthropogenic impacts in these areas, it is likely there is increased dog presence as well
111 (Paschoal et al. 2018). These ‘working’ lands have traditionally been discounted in their value
112 for conservation, being considered largely as the hostile matrix that native species must navigate
113 between protected areas. However, recent findings show that patches within these agriculture-
114 dominated lands can hold considerable biodiversity and can have high conservation value
115 (Kremen & Merenlender 2018; Lindenmayer 2019; Wintle et al. 2019). Given the huge potential
116 of agricultural lands for conservation, comprising a third of the ice-free land on the planet
117 (Ramankutty et al. 2018), there is a increasing recognition that co-production of science with
118 private landowners on working lands is necessary and perhaps unavoidable in efforts to maintain
119 biodiversity (Naugle et al. 2020).

120 In the Valdivian temperate forests biodiversity hotspot of Chile, both fragmentation and
121 the presence of domestic dogs are widespread and potentially devastating endemic species

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122 (Myers et al. 2000). These forests are being rapidly lost and converted to exotic plantations and
123 pasturelands (Echeverría et al. 2008; Echeverría et al. 2012). The current conservation estate is
124 insufficient in meeting goals to maintain the biodiversity value of these forests because protected
125 areas are restricted to the inland Andes rather than the endemic-rich coastal areas (Smith-
126 Ramírez 2004). The central valley, which formerly connected the coastal and montane sections
127 as contiguous forest, has been heavily deforested and now dominated by cow pastures and exotic
128 plantations. Today, only small patches of native forests remain as available wildlife habitat that
129 are interspersed throughout this landscape that are privately-owned and managed (Figure 1).
130 Free-ranging domestic dogs pose a major threat to the persistence of at least two mammal
131 species of conservation concern, pudu (*Pudu puda*, IUCN status of Vulnerable) and Darwin's
132 fox (*Lycalopex fulvipes*, IUCN status of Endangered) (Silva-Rodríguez et al. 2010b, 2016).

133 Here, we determine the relative consequence of fragmentation, the presence of dogs, and
134 the interaction between the two on the spatial use of native carnivores. Specifically, we surveyed
135 privately-owned forest patches that were outside of protected areas or forestry company
136 ownership using remotely-triggered cameras. We expected fragmentation metrics to be more
137 important than dog space use in explaining the occupancy of forest specialists (e.g., güiña,
138 *Leopardus guigna*). In contrast, we also expected that in these largely altered landscapes dog
139 occupancy would be the major driver of native canid spatial use, due to the immediate threat they
140 present, and induced 'fear effects' (Palomares & Caro 1999; Vanak et al. 2009; Vanak &
141 Gompper 2010). We hypothesized that increasing patch isolation and reducing the proportion of
142 forest would be important drivers of dog occupancy, providing evidence that their presence is
143 facilitated by fragmentation (Figure 2). Our work will enhance our understanding of native

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144 carnivore occurrence in the later stages of human-altered landscapes and reconcile the relative
145 contributions of interacting threats from fragmentation and domestic dog presence.

146

147 **2. Methods**

148 2.1 Study area

149 We surveyed the carnivore community in the Los Lagos region of Chile, near the city of Osorno,
150 between Lago Rupanco and Lago Llanquihue (40° 76' to 41° 21' S, 72° 54' to 72° 97' W, Figure
151 1). This area is characterized by Valdivian temperate rain forest (mean temperature 3-23°C) with
152 a cold, rainy winter season between May and September (1346 mm annual rainfall) and mild
153 summers (en.climate-data.org). The landscape, formerly dominated by native forest, is currently
154 dominated by pastures that are used primarily for cattle as well as plantations of pine (*Pinus*
155 *radiata*) and eucalyptus (*Eucalyptus* sp.) with small stands of native forest. The study area is
156 relatively flat and sandwiched between a large protected area (Parque Nacional Vicente Rosales)
157 on the eastern edge and the Osorno metropolitan area on the western edge. Native forest patches
158 were mostly made up of degraded strips along the edges of pastures comprised of a mix of
159 *Lophozonia obliqua*, *Nothofagus dombeyi*., *Persea lingue*, and *Laurelia sempervirens* with a
160 bamboo understory (*Chusquea quila*).

161

162 2.2 Camera trap survey

163 We deployed 50 remotely-triggered cameras (Reconyx© PC 850, 850C, 900, 900C) in native
164 forest patches throughout the study area from June to August 2019, during the austral winter. We
165 affixed cameras to trees (minimum diameter 0.25 m) with cable locks and placed 0.5 m off the

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166 ground. We used signs of animal activity such as game trails and scat to determine the specific
167 micro-site location of camera placement, to maximize detections. Cameras were placed at least
168 0.5 km apart from each other, and efforts were made to place within the core of each patch if
169 minimum spacing allowed. Each camera was baited with canned mackerel placed inside a
170 perforated bottle, wired down to keep animals from accessing or removing the bait. Camera
171 settings included: high sensitivity, one-second lapse between three pictures in a trigger, rapidfire
172 (no quiet period between triggers).

173 At the end of the survey period, images were retrieved from the cameras and identified by
174 a single observer (R. Malhotra) to the species level. After image identification, we applied a 30-
175 minute quiet period to ensure independence of species detections (Wang et al. 2015; Suraci et al.
176 2016). These images and the associated site-level environmental variables (explained below)
177 were used to estimate individual species occupancy. We used Moran's I in ArcPro (vers. 2.3.1)
178 and did not find evidence of spatial autocorrelation. The 'camtrapR' package in Program R was
179 used to organize camera trap images and extract data for modeling.

180 2.3 Occupancy modeling

181 Using single-species single-season occupancy models (MacKenzie et al. 2003), we evaluated the
182 impacts of habitat degradation on the occupancy (Ψ) and detectability (p) of dogs, and evaluated
183 the impacts of habitat degradation and dog occupancy on the occupancy and detectability of
184 three focal native species: the chilla (*Lycalopex griseus*), culpeo (*Lycalopex fulvipes*), and güiña
185 (*Leopardus guigna*) (Figure 3). We expected that increasing habitat loss (*forest*) and patch
186 isolation (*iso*) would reduce native carnivore occupancy, and that native species occupancy
187 would be inversely related to dog occupancy (*dogo*). We first separated species detections into 7-
188 day observation periods. We then modeled detection probabilities for each species holding

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189 occupancy constant, and then used the best detection models to model the occupancy for each
190 species.

191 2.3.1 Detection covariates

192 We modeled detection probabilities with covariates hypothesized to influence visibility of
193 species on camera images. We measured understory cover using a point-intercept method, with
194 the height measured every meter for 10m in the four cardinal directions surrounding each camera
195 (Karl et al. 2017). We then aggregated values for the understory cover into three categories: 0m
196 (no understory), 0.01-0.25m, and 0.26-0.5m. Understory at 10m (*10uds*) is an average of all
197 understory measurements taken every meter within a 10-meter radius of the camera tree (40
198 measurements per camera site). We expected the understory covariate to have a negative
199 relationship with detectability of all species, as animals passing by would be obscured by
200 increased understory towards the height of camera placement. Understory was not included in
201 the detection model for the culpeo, as inclusion prevented convergence of the global model. We
202 first modeled occupancy of dogs using habitat covariates (*10uds*, *forest*, *iso*, *sm*), and then
203 included the resulting site level estimates as the *dogo* covariate for native species models (Figure
204 3). Patches were digitized in ArcPro (vers. 2.3.1) using high resolution satellite imagery from
205 2018 (Maxar Vivid) to obtain proportion native forest cover (*forest*), patch isolation (*iso*) and a
206 metric of edge effects (*edge*) estimates. Patch isolation (*iso*) was measured as the mean border-
207 to-border distance to the nearest patch within a 1-km radius of each camera. The *edge* covariate
208 was measured as the mean ratio of patch perimeter size to patch area for all patches within a 1-
209 km radius of each camera. However, the edge covariate was excluded from the final global
210 model, as it was highly correlated with both *forest* and *iso* covariates ($p < 0.01$). Both *iso* and
211 *forest* covariates were expected to have a positive relationship with native species occupancy.

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212 We estimated relative abundance of small mammals (*sm*), as a metric of prey availability, using
213 the total number of all independent lagomorph, rodent, and shrew opossum triggers per camera
214 standardized by the number of trap nights. Camera type (*cam*) was included to distinguish
215 between white-flash cameras and infrared cameras with the expectation that white-flash cameras
216 would have lower species detection despite better nighttime image quality, due to possibly
217 startling species. Lastly, trap nights (*trap*), the number of nights an individual camera was
218 operational to collect species detections, were included to determine if sampling effort affected
219 detection rates. However, we expected no effect of trap nights, given similar sampling periods
220 for all the cameras.

221 2.3.2 Occupancy covariates

222 Occupancy for each species was modeled with dog occupancy (*dogo*) and habitat covariates
223 (*10uds*, *forest*, *iso*, *sm*); edge was highly correlated with *forest* and omitted from the model . To
224 test whether the impact of dogs on native carnivores was facilitated by lack of understory, we
225 included an interaction term between dog occupancy and average patch understory height within
226 10m (*dogo*10uds*). Individually, we expected dog occupancy to reduce occupancy of all native
227 species, and for understory height to increase the occupancy of the smaller native carnivores
228 (güiña and chilla). As an interaction term, we expected increasing understory to decrease the
229 effect of dog occupancy on native species occupancy. We expected higher prey availability to be
230 a positive driver of native species occupancy, but unimportant for the domestic dog, which in
231 this area would be classified as ‘free-ranging’ by Vanak & Gompper (2010) and thus would rely
232 on human food subsidies.

233 2.3.3 Model evaluation

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234 The dog global model included mean understory height within 10m (*10uds*) and camera type and
235 trap night (*cam, trap*) covariates for detection, and understory (*10uds*), prey (*sm*), and
236 fragmentation (*forest, iso*) for occupancy. Native species global models used the same covariates
237 as the dog model, with the addition of dog occupancy (*dogo*) for detection, and an interaction
238 term for dog occupancy and understory (*dogo*10uds*) for occupancy. All detection and
239 occupancy covariates were tested for correlation by site using Pearson's R. Model ranking was
240 carried out using Akaike Information Criterion, corrected for small sample sizes (AICc), or
241 quasi-AICc (QAICc) if the global model was overdispersed ($\hat{c} > 1.2$), with the top model
242 being defined as the one with the lowest AICc or QAICc score. Goodness of fit was tested for all
243 top models ($< 2 \Delta$ AICcs or QAICcs of the highest rank model) using a Chi-square statistic. All
244 occupancy modeling was completed in the 'unmarked' package in Program R vers. 3.6.2.

245 2.3.4. Threshold response to dogs

246 We interpreted the β coefficient of *dogo* and confidence intervals overlapping zero when
247 occurring in top models to conclude significant effects of dogs on native species occupancy.
248 When the top models included *dogo* as a covariate with a non-significant negative coefficient,
249 we determined the threshold level of dog occupancy required for *dogo* to become a significant
250 negative driver on native species occupancy. We incrementally increased the value of the *dogo*
251 to the maximum occupancy value (1), a single camera at a time. The order was determined by
252 ranking cameras from highest to lowest *dogo* value.

253 2.4 Temporal use

254 As sympatric carnivores may be more likely exhibit temporal instead of spatial partitioning to
255 promote coexistence, we estimated pairwise temporal overlaps for all species, and compared the

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256 overlap of native species pairs with the overlap of native species-dog pairs. We expected native
257 species to have nocturnal activity patterns, dogs to have a diurnal activity pattern, and for native
258 species to overlap more with the other native species than with domestic dogs. We plotted the
259 temporal activity distributions of each species and determined the degree of overlap between
260 pairs (Δ) with 95% confidence intervals generated by 10,000 parametric bootstrap iterations. Δ
261 values range from 0 indicating completely distinct and non-overlapping temporal activity to 1
262 indicating complete overlap between the comparison groups. Δ_1 was used for comparisons when
263 one of the sample groups had less than 50 triggers; otherwise Δ_4 was used to estimate temporal
264 overlap between species pairs (Ridout & Linkie 2009). We then used the Mardia-Watson-
265 Wheeler test to determine if the temporal patterns varied significantly between individual
266 species, which compares two sets of circular data and determines if there is homogeneity in the
267 means or variances. We implemented the temporal analyses using the ‘overlap’ and ‘circular’
268 packages in Program R.

269

270 **3. Results**

271 We detected all three native carnivore species over a total effort of 3500 trap-nights. Naïve
272 occupancy estimates for the güiña (n=56 independent triggers), chilla (n = 225), and culpeo
273 (n=39) were 0.51, 0.59, and 0.16 respectively. Domestic dogs were fairly common (n=64) found
274 at 20/49 camera sites (naïve $\psi = 0.41$). Additional native carnivores that were detected,
275 although rare, included the chingue (*Conepatus chinga*, n=13) and the puma (*Puma concolor*,
276 n=4). We also detected two additional non-native species: the mink (*Neovison vison*, n=20) and
277 domestic cat (*Felis catus*, n=21). Darwin’s fox (*Lycalopex fulvipes*) was not detected during our

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278 camera survey in the area.

279 3.1 Detection of carnivores

280 Our study area was comprised of an understory that ranged from completely open to thickets of
281 dense vegetation with specific camera sites comprising no understory to over two meters in
282 height. As such, we expected detection to vary by understory, depending on species preference
283 on microsite selection for dense vegetation, and the ability of understory to reduce the visibility
284 range for a camera trap. For the chilla ($\beta = -6.16$, SE = 1.38) and dog ($\beta = -7.44$, SE = 1.84),
285 *Iouds* was a strong driver of detection probability, decreasing the detectability for both species
286 (Table S1). For both chilla ($\beta = 1.77$, SE = 0.37) and culpeo ($\beta = 3.23$, SE = 0.834), *dogo*
287 increased detectability. The null model best described güiña detection; that is, no effect of
288 covariates improved model fit.

289 3.2 Occupancy of carnivores

290 Overall, modeling occupancy with covariates and accounting for imperfect detection improved
291 our understanding of carnivore space use. Chilla foxes had the highest overall occupancy ($\psi =$
292 0.67), while culpeos had the overall lowest occupancy, but nearly doubled from the naïve
293 estimate ($\psi = 0.36$). Güiña was the only species for which the null model was the best model,
294 and the occupancy estimate was thus the same as the naïve estimate ($\psi = 0.51$). In comparison to
295 the native species, dog occupancy was higher than the culpeo and güiña, but lower than that of
296 the chilla ($\psi = 0.58$).

297 Factors driving occupancy of native carnivores varied by species (Figure 4, Table 2).

298 Despite the importance of *Iouds* for species detection, it did not appear in the best model for any
299 species. It was however a negative driver of chilla occupancy in 4/10 top models which had

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300 comparable weight to the best model (Table 2). Given the reliance of mammalian carnivores on
301 prey, unexpectedly, *sm* was important only for the occupancy of the culpeo ($\beta = 1.05$, SE =
302 0.53).

303 We aimed to contrast the ecological consequences of habitat destruction (loss and
304 fragmentation), and dog occurrence on the space use of native carnivores (Table 2). Habitat
305 metrics were important drivers of chilla and dog occupancy but did not appear in the model sets
306 for culpeo or güiña. For example, *iso* was in the top two models for the chilla ($\beta = 0.09$, SE =
307 0.04), and was positively correlated with occupancy. *Forest* did not appear to be important for
308 occupancy of any native species. We found that *forest* was however important for dogs ($\beta = -$
309 26.06, SE = 12.1), with increasing proportion of native forest decreasing dog occupancy. *Dogo*
310 appeared in 4/5 top models for culpeo (including the best model) and was important for model fit
311 for the culpeo, but was not a significant driver of culpeo occupancy ($\beta = -4.19$, SE = 2.74).

312 Similarly, results varied in quantifying responses of native carnivore occupancy to domestic dog
313 presence. For chilla, *dogo* was not in the best chilla model but appeared as a positive driver in
314 6/10 top models, which had comparable weight to the best model (Table S1). The *dogo*
315 covariate was not influential, positive or negative, on occupancy for güiña. Culpeo was the only
316 species with *dogo* in the top model with a negative (non-significant) β coefficient. The dog
317 landscape level occupancy from the top model was 0.58. Increasing dog occupancy to 0.65 (an
318 increase of 12.1%) resulted in *dogo* becoming a significant negative driver of culpeo occupancy
319 (Figure S2).

320 Ultimately, we rejected our hypothesis of dog effects on native carnivores being
321 facilitated by lack of understory. We found no evidence for the interaction of *dogo* and *10uds*
322 affecting occupancy for native mesocarnivore species occupancy. Overall, we conclude that

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323 landscape characteristics via metrics of increasing fragmentation have similar positive effects for
324 both generalist native carnivores and for domestic dogs (Figure 4).

325 3.4 Temporal activity

326 We evaluated temporal activity patterns of all of our study species to determine if there was
327 evidence for temporal avoidance with domestic dogs. Activity patterns for the three native
328 carnivores was largely restricted to the nocturnal and crepuscular hours. Overlap among the
329 native carnivores was high (Δ ranging 0.78 – 0.89) and did not vary significantly among pairs
330 (Table S1: *p values*: 0.08-0.79). In contrast, domestic dog activity was almost entirely diurnal,
331 resulting in significantly different activity patterns from native species (Δ ranging 0.35-0.43; $p <$
332 0.001). Furthermore, 95% confidence intervals for Δ dog-native species pairs and for Δ native-
333 native species pairs did not overlap in a single case, indicating that native species overlapped
334 significantly more with other native species than they did with dogs.

335

336 4. Discussion

337 The threats that mammals face from habitat loss and fragmentation are especially relevant in the
338 context of the temperate rainforests of central Chile, which have included rapid deforestation and
339 fragmentation in the past 50 years (Echeverría et al. 2006; Nahuelhual et al. 2012; Uribe et al.
340 2020). An additional human-related threat is the presence of domestic dogs, which antagonize
341 native species and preferentially use the pasturelands that separate the remaining native forest
342 patches (Silva-Rodríguez et al. 2010a). Our results from the remnant forest patches within an
343 agricultural matrix in southern/central Chile indicate that both fragmentation and domestic dogs
344 have differing effects on native carnivore occupancy.

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345 The effects of habitat loss and fragmentation for native carnivores are important to
346 explore given future trends in the deforestation of the region. Our study site represents a
347 landscape that has already undergone extensive habitat loss and fragmentation; primarily
348 agricultural land with only remnant patches of native forest. However, even in already heavily
349 degraded regions such as our study site, trends indicate that native forest throughout Chile
350 continues to decline, with available habitat patches decreasing in size (Echeverría et al. 2008;
351 Echeverría et al. 2012; Miranda et al. 2015). For the species included in this study, at first glance
352 our results suggest that this landscape degradation does not pose an immediate concern. For the
353 chilla, the positive correlation between patch isolation and occupancy is likely a reflection of the
354 ecology of the fox, which primarily forages in the open fields that comprise the matrix between
355 forest patches (Silva-Rodríguez et al. 2010a). However, this species also utilizes interior habitat
356 of these native forest patches as a refuge, and thus, would likely have negative consequences if
357 forest patches fell below a threshold sizes (Silva-Rodríguez et al. 2010a). Our results for culpeos
358 and güiñas, which did not show any response to either habitat loss or patch isolation could
359 indicate that: a) these species are plastic in their habitat requirements; b) fragmentation and
360 habitat loss have not reached a sufficient threshold to elicit a response; c) there is a time lagged
361 ‘extinction debt’, or d) these species are tracking spatial patterns of prey, predator, or competitor
362 species instead (Hanski & Ovaskainen 2002; Ryall & Fahrig 2006; Swift & Hannon 2010;
363 Halley et al. 2016). The model results for the culpeo seemed to suggest this latter mechanism, as
364 they were positively driven by prey availability and dog occupancy was consistent in the top
365 models having a negative coefficient (though note that it was not significant). While landscape
366 characteristics did not appear as a negative driver in any native species models, the inverse
367 relationship between dog occupancy and proportion of native forest means that as habitat loss

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368 increases in this region, it will likely mean less refuge habitat for native species, and higher
369 exposure to domestic dogs (Torres & Prado 2010; Paschoal et al. 2018).

370 We expected dogs to influence native carnivore occupancy because of their documented
371 impact on small carnivores through interference and exploitation competition, and the increased
372 mortality risk they pose as disease reservoirs and vectors (Laurenson et al. 1998; Rhodes et al.
373 1998; Sillero-Zubiri et al. 2004; Vanak & Gompper 2009, 2010). Dogs are potential competitors
374 with native carnivores and have been linked to the decline of the native pudu, a potential prey
375 item for the two fox species in this study (Silva-Rodríguez & Sieving 2012). Despite the threat
376 that a dog encounter presents, dog occupancy did not clearly present a negative driver of native
377 species occupancy, and only featured as a non-significant negative covariate for culpeo top
378 models. While this partially fit our expectation that native canids would more likely have
379 antagonistic interactions with dogs and exhibit avoidance, we expected the smaller chilla fox to
380 be more susceptible and affected (Donadio & Buskirk 2006; Vanak & Gompper 2009). Previous
381 studies corroborate this expectation as dogs enforce interference competition to alter space use
382 and have been observed harassing and killing chilla (Silva-Rodríguez et al. 2010a). A lack of a
383 negative response from chillas to dogs using an occupancy framework could indicate that foxes
384 were avoiding dogs at finer spatial or temporal scales, or that dog density was not sufficiently
385 high to elicit a spatial avoidance (Zapata-Ríos & Branch 2018; Qi et al. 2020). Indeed our
386 analysis of activity patterns suggests temporal partitioning as a mechanism for avoidance of dogs
387 (Kronfeld-Schor & Dayan 2003; Schuette et al. 2013). In contrast to chillas, culpeos did indicate
388 a potential response to dogs at a landscape level in congruence with recent work in the Andes
389 (Zapata-Ríos & Branch 2018). Despite the differences in the landscape histories with our study
390 conducted in a historically contiguous forest, while the Zapata-Ríos & Branch (2018) study

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391 occurred in the historically patchy Ecuadorian Andes, we both found that culpeos could respond
392 to dogs rather than to habitat loss and fragmentation. Congruent with their dog occupancy
393 estimates ($\bar{\Psi}$ = 0.66, range: 0.53 – 0.73), a projected 12% increase in dog occupancy in our study
394 site for it to significantly reduce culpeo occupancy.

395 While dogs had opposite effects on the occupancies of the native fox species, they
396 increased detection for both the culpeo and the chilla. Movement data for canids highlight
397 quicker speeds through riskier areas, which would likely impact detection rates (Péron et al.
398 2017; Broadley et al. 2019). Thus, increased detection for the fox species may reflect a finer
399 scale response to the risk posed by domestic dogs, rather than a broader change in spatial use
400 (Broekhuis et al. 2013).

401 Fragmentation can facilitate the spread of invasive species through numerous pathways,
402 such as roads increasing the occurrence of dogs (Loss et al. 2013; Moreira-Arce et al. 2015). Yet,
403 few occupancy studies have looked at the impacts of both dogs and habitat loss and
404 fragmentation on native carnivores. Our dog occupancy model revealed that dog occupancy
405 decreased with proportion of native forest, providing evidence for the interaction between
406 deforestation and dogs. Whether this interaction impacts native carnivores can be intuitively
407 answered when we see that dog occupancy can be a negative driver of culpeo occupancy when
408 surpassing a threshold. In ‘working’ landscapes this is particularly relevant as habitat loss and
409 dog occupancy will likely continue to increase over time. Our occupancy results suggest that the
410 spatial use of both native fox species (indirectly in the case of the culpeo, through dog
411 occupancy) is tied to fragmentation and habitat loss. Furthermore, this change in the landscape
412 increases the exposure of both native foxes to the threat of a dog encounter (Farris et al. 2017,
413 2020). In the currently remaining native forest stands that we surveyed, the largely nocturnal

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414 temporal use of native species provides a likely avoidance mechanism (Gerber et al. 2012;
415 Shores et al. 2019). This temporal avoidance mechanism may be particularly important for
416 generalist species such as the chilla, which our occupancy models show is similarly benefitted by
417 habitat degradation as dogs. Future studies that investigate fragmentation on antagonistic
418 interactions would prove beneficial to determining impacts on carnivore community structure
419 (Magrach et al. 2014).

420 Our study gives us insight into the drivers of native carnivore space use in ‘working’
421 landscapes rather than the protected areas that represent ideal and untouched habitats. By
422 situating our study on privately-owned smallholder lands, we also have the unique opportunity to
423 inform the conservation of species in these increasingly anthropogenic landscapes. Many
424 landowners do not have access to camera traps, and thus are unlikely to encounter elusive
425 carnivores that are present even in small patches of native forest along the edges of their
426 pasturelands. While voluntary strategies have greater social acceptance, they are not possible
427 without landowners first having the knowledge of what species are on their land (Kamal et al.
428 2015). By partnering with landowners, scientists and managers can facilitate species
429 conservation in these important landscapes which are not typically considered conservation
430 targets (Naugle et al. 2020).

431

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444

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Figure Legends

Figure 1. a) Study area located in the Los Lagos Region of south-eastern Chile. b) Landscape level distribution of camera deployment throughout patches of native forest straddling the Volcano Osorno.

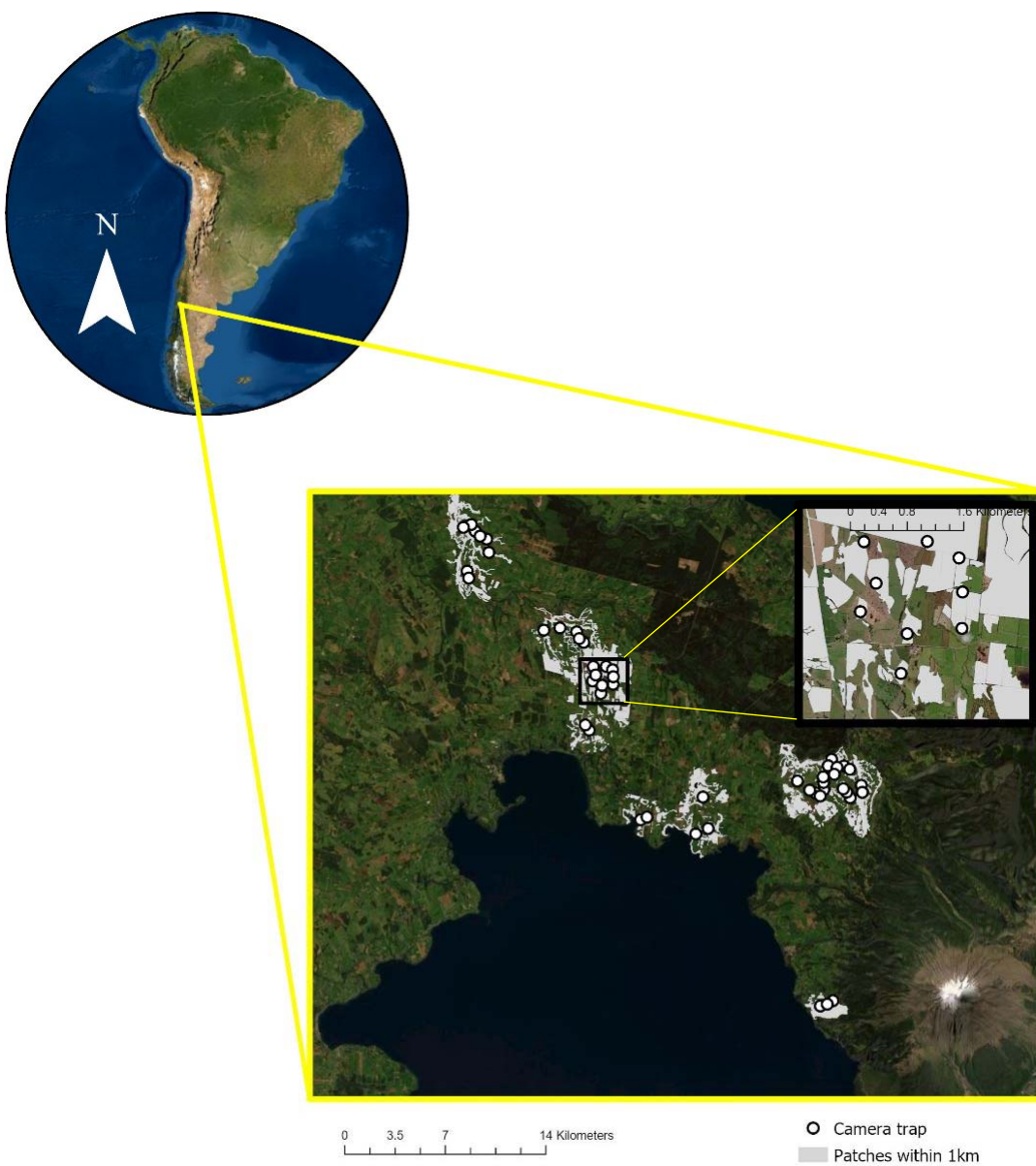
Figure 2. Hypothesized facilitation of dog occupancy by habitat loss and fragmentation with expectation that decreasing proportion of native forest and increasing patch isolation would promote higher dog occupancy. Expectations for native carnivore response to fragmentation were opposite those of domestic dogs, with native carnivore occupancy expected to decrease with decreasing forest and increasing patch isolation.

Figure 3. Focal carnivores in study for size comparison of the three native species relative to and domestic dogs: the güiña, chilla, domestic dog, and culpeo from top left clockwise. Note that the upper weight range of the culpeo likely represents more southern parts of the range than the study area; they are relatively bigger than chillas, and smaller than dogs. Photo credit: Applied Wildlife Ecology Lab.

Figure 4. Relative importance of each covariate on species occupancy based on summed model weights for top model sets ($< 2 \Delta AIC/QAIC$). Positive (+) and negative (-) signs correspond to the direction of beta coefficients from each model set, and were consistent within top model sets.

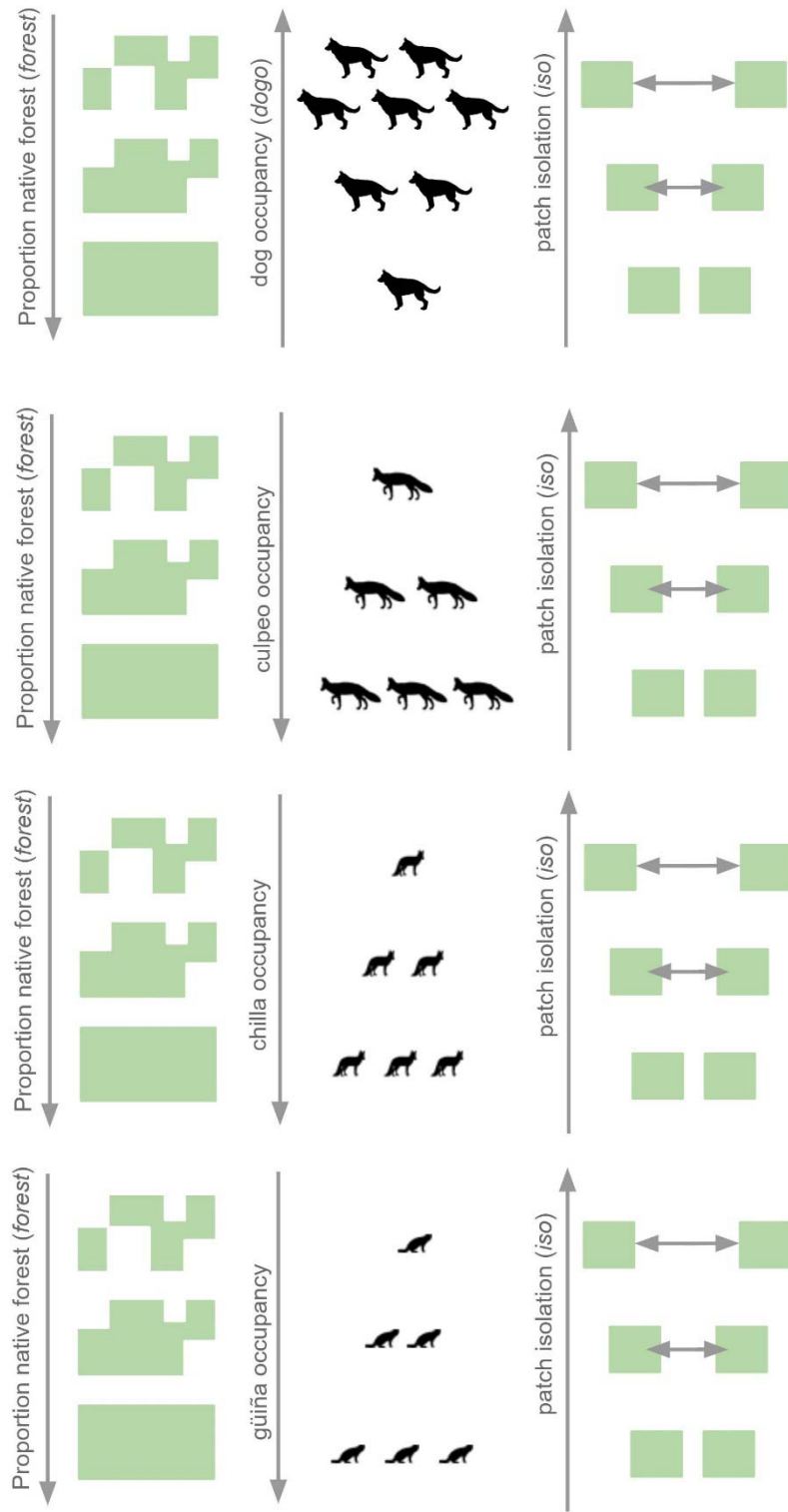
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Figure 1.



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Figure 2.



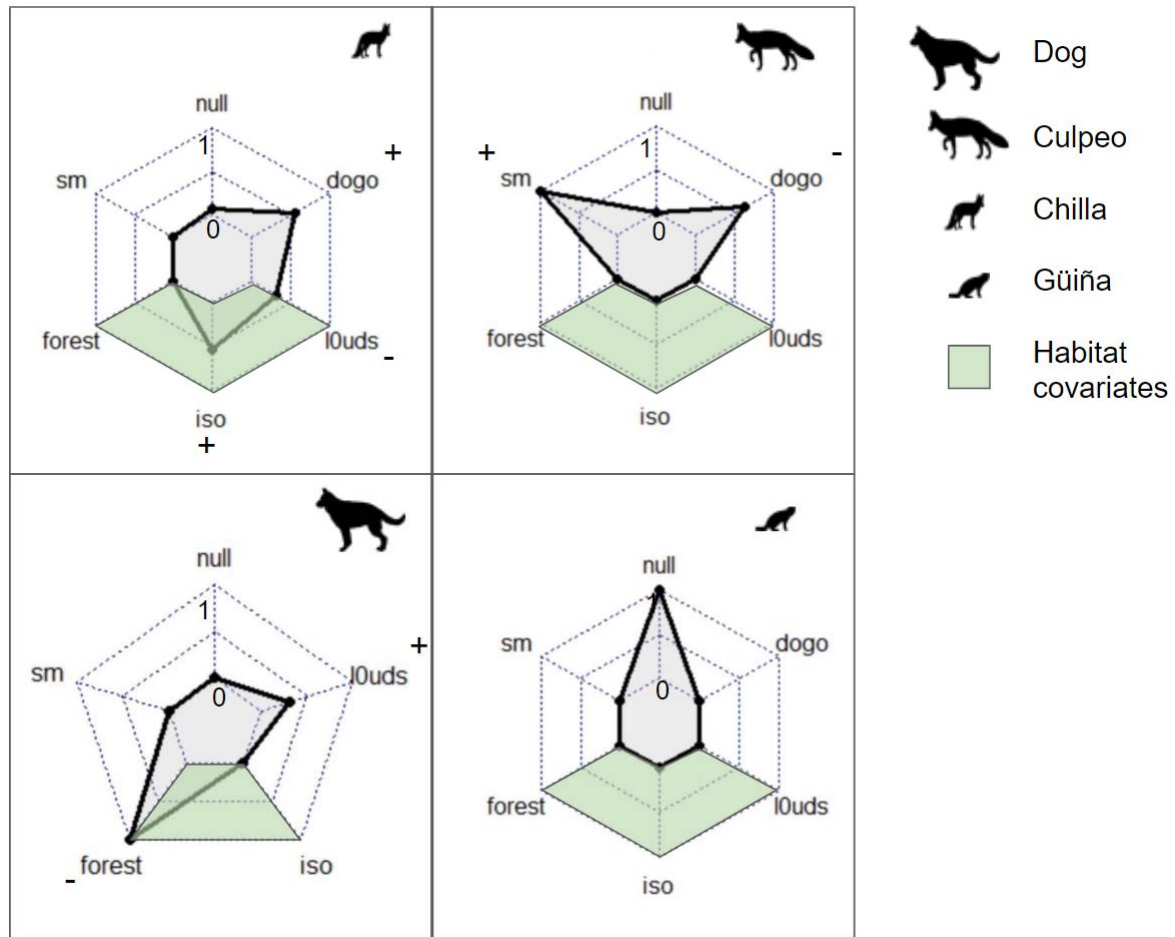
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Figure 3.



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Figure 4.



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Table 1. Top occupancy models for every species (occupancy(Ψ), detection(p)). QAICc was used instead of AICc in model ranking for güiña occupancy to account for overdispersion of the global model.

Table 1.

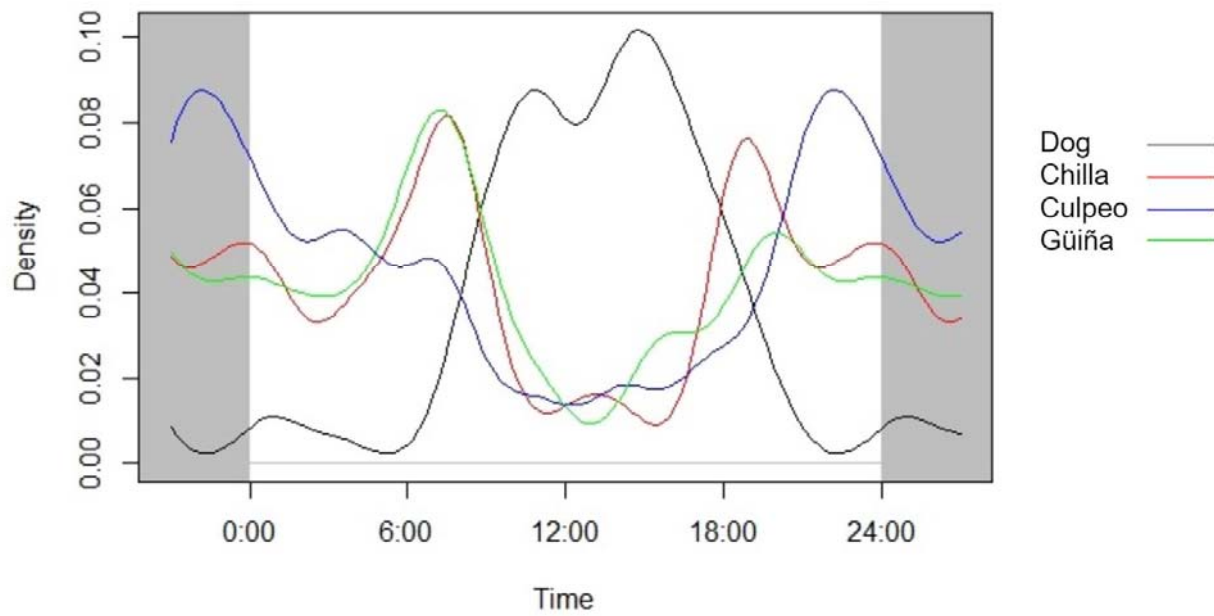
Species	Top models	AICc	Δ AICc*	w_i
Chilla	p(dogo, 10uds) Ψ (iso)	429.809	0	0.175
	p(dogo, 10uds, cam) Ψ (iso)	430.289	0.480	0.138
	p(dogo, 10uds) Ψ (dogo)	430.613	0.804	0.117
	p(dogo, 10uds) Ψ (dogo, 10uds)	430.782	0.974	0.108
	p(dogo, 10uds, cam) Ψ (dogo)	430.948	1.139	0.099
	p(dogo, 10uds) Ψ (iso, dogo)	431.139	1.331	0.090
	p(dogo, 10uds, cam) Ψ (dogo, 10uds)	431.511	1.702	0.075
	p(dogo, 10uds) Ψ (iso, 10uds)	431.736	1.927	0.067
	p(dogo, 10uds) Ψ (~1)	431.738	1.929	0.067
	p(dogo, 10uds) Ψ (iso, dogo, 10uds)	431.792	1.982	0.065
	Culpeo	p(dogo, cam, 10uds) Ψ (dogo, sm)	124.932	0
p(dogo, 10uds) Ψ (dogo, sm)		126.238	1.306	0.142
p(dogo, cam, 10uds) Ψ (sm)		126.280	1.348	0.139
p(dogo, cam) Ψ (dogo, sm)		126.598	1.666	0.119
p(dogo, trap, 10uds) Ψ (sm)		126.734	1.802	0.111
p(dogo, 10uds) Ψ (sm)		126.753	1.821	0.110
p(dogo, cam, trap) Ψ (dogo, sm)		126.802	1.870	0.107
Dog	p(10uds, trap) Ψ (forest)	272.000	0	0.370
	p(10uds, trap, cam) Ψ (forest)	272.306	0.306	0.318
	p(10uds, trap) Ψ (forest, 10uds)	273.704	1.704	0.158
	p(10uds, trap, cam) Ψ (forest, 10uds)	273.757	1.757	0.154
Güiña	p(~1) Ψ (~1)	6.830	0	0.101

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Supplementary Material

Figure S1. 24-hour activity patterns of all four study species. Dogs are distinct from native species in having a clearly diurnal activity pattern.

Figure S1.



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Figure S2. The effect of a simulated increase in dog occupancy across the landscape on the beta coefficient and 95% confidence interval for the *dogo* covariate in the culpeo occupancy model. *represents a significant beta coefficient.

Figure S2.

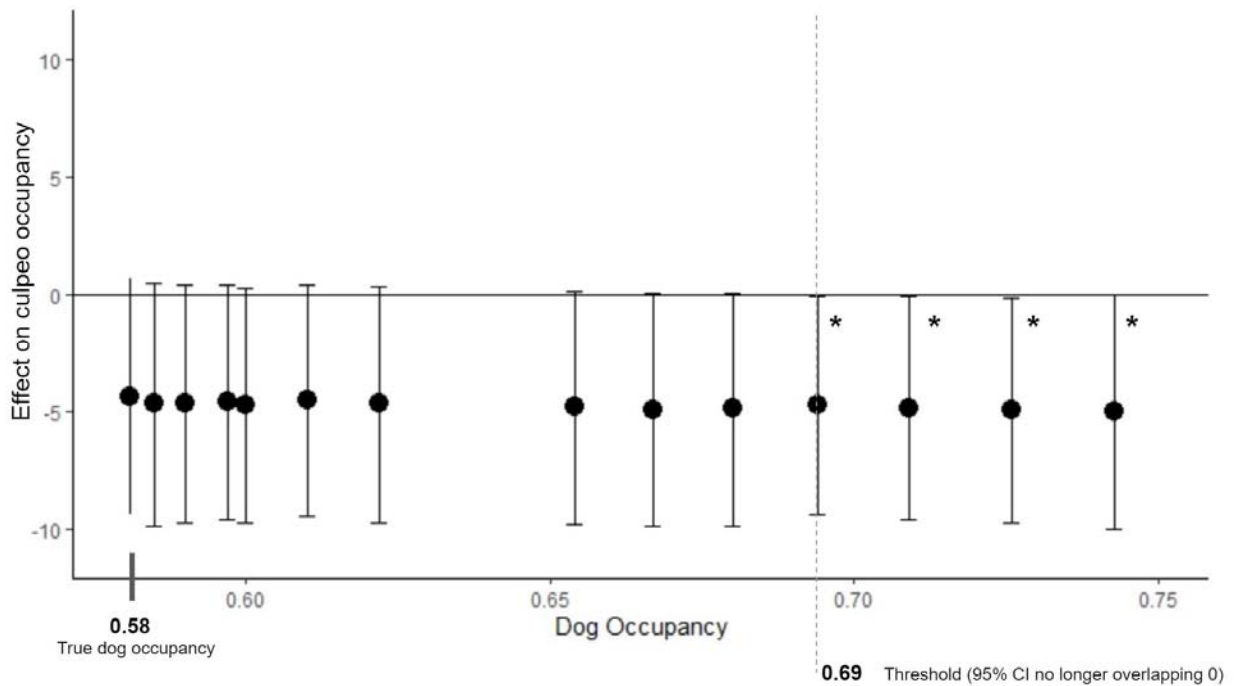


Table S1. Overlap coefficients (Δ) and Mardia-Watson-Wheeler test for homogeneity of means for every pairwise combination of the study species. Δ_4 was used for every comparison except for those pairs containing the culpeo, where Δ_1 was used to account for lower number of triggers.

Table S1.

Comparison	Δ Overlap (95% CI)	W statistic	<i>p</i> -value
Chilla-Dog	0.40 (0.25-0.44)	83.62	<0.001
Culpeo-Dog	0.35 (0.22-0.48)	42.96	<0.001
Guigna-Dog	0.43 (0.30-0.56)	47.84	0.001
Chilla-Culpeo	0.78 (0.66-0.89)	5.02	0.08
Chilla-Guina	0.89 (0.80-0.97)	0.47	0.79
Guina-Culpeo	0.78 (0.75-1.03)	4.79	0.09