

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

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### **Conflict of interest**

The authors do not have any conflicts of interest to declare.

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### **Biosketch**

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RM explores how anthropogenic pressures alter species interactions. More specifically, he is interested in how fragmentation alters native carnivore movement (short time scales) and occupancy (longer time scale), and how this translates to the community level.

JEJ examines the population and community ecology of mammals and birds with conservation concern in southern South America and Texas. More recently he added the impacts of exotic mammals on local biotas, dispersal ecology and the biogeography of tardigrades.

<http://jaimeejimenez.com>

NCH explores the antagonisms in nature, focusing on competition, predation, and parasitism in mammalian systems. She links these research themes with anthropogenic pressures such as human-wildlife interactions to inform the conservation of large carnivores.

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8 Patch characteristics and domestic dogs differentially affect carnivore space use in fragmented  
9 landscapes in Southern Chile

10 **Abstract**

11 **Aim**

12 In an increasingly anthropogenic world, species face multiple interacting threats. Habitat  
13 fragmentation and domestic dogs are two perturbations threatening terrestrial mammals globally.  
14 Our aim was to determine if (1) the spatial use of domestic dogs increases with habitat  
15 destruction and (2) whether domestic dogs and habitat destruction drive the spatial use of native  
16 carnivores in a heavily degraded agricultural landscape.

17 **Location**

18 Central valley/Andean foothills transition of Los Lagos, Chile.

19 **Methods**

20 We implemented a camera trap survey in a fragmented landscape comprised of native forest  
21 patches amidst a matrix of pastureland. We used single-species occupancy models to assess the  
22 impact of domestic dogs and habitat destruction on three mesocarnivores – the foxes, culpeo  
23 (*Lycalopex culpaeus*) and chilla (*Lycalopex griseus*) and the wild cat güiña (*Leopardus guigna*).  
24 Additionally, we compared temporal overlap of all study species (including domestic dogs).

25 **Results**

26 Detection rates for both the foxes increased with domestic dog occupancy, while factors driving  
27 occupancy differed for each of the native species. We found that a 12% projected increase in  
28 domestic dog occupancy negatively impacted the spatial use of the culpeo. Habitat loss and  
29 fragmentation were positive drivers for chilla and domestic dog occupancy. The güiña did not  
30 respond to fragmentation and other habitat covariates or domestic dog occupancy. All native  
31 carnivore species were primarily nocturnal, while the domestic dog was almost entirely diurnal.

## 32 **Main Conclusions**

33 We highlight that domestic dog occupancy was positively correlated with habitat loss. Native  
34 species showed varied tolerance to domestic dog occupancy, and no negative response to habitat  
35 destruction. Future conditions of increased fragmentation and habitat loss will likely increase the  
36 potential contact between domestic dogs and native carnivores.

37

38 Keywords: *Canis lupus familiaris*, fragmentation, invasive species, landscape, *Leopardus*,  
39 *Lycalopex*, occupancy

## 40 **1. Introduction**

41 Fragmentation and habitat loss remain a global threat to biodiversity, increasing isolation  
42 between habitat patches, with emergent consequences from edge effects (Haddad et al. 2015;  
43 Pfeifer et al. 2017). Globally, 70% of forests are within 1 kilometer of an edge and are becoming  
44 increasingly fragmented, which has resulted in abundances for over 85% of vertebrates being  
45 impacted by edge effects (Haddad et al. 2015; Pfeifer et al. 2017; Montibeller et al. 2020). The  
46 negative effects of fragmentation remain highly debated given inconsistent impacts across  
47 species and ecological interactions (Fahrig 2013; Rielly-Carroll & Freestone 2017; Fletcher et al.  
48 2018; Fahrig et al. 2019; Harrison & Banks-Leite 2020). While species may be able to inhabit  
49 edge habitats, they may be excluded via biotic factors such as competition or predation (Michel  
50 et al. 2016). Additionally, fragmentation may interact with other factors such as habitat loss, fire  
51 prevalence, and hunting, challenging ascertain of individual drivers that alter species or  
52 interactions (Cochrane 2001; Peres 2001; Bennett & Saunders 2010; Bartlett et al. 2016).

53 Domestic dogs (*Canis lupus familiaris*, hereafter referred to as ‘dogs’) represent another global  
54 threat to biodiversity as the most abundant carnivore worldwide with a global population

55 estimated at 700 million (Hughes & Macdonald 2013; Gompper 2013). Therefore, dogs are a  
56 widespread invasive species that can commonly exploit fragmented landscapes as they more  
57 easily permeate from areas of human residence (Oehler & Litvaitis 1996; Broadbent et al. 2008;  
58 Paschoal et al. 2018). Dogs commonly harass and kill native carnivores, compete for prey  
59 species, and transmit pathogens to wild populations (Laurenson et al. 1998; Vanak & Gompper  
60 2009; Doherty et al. 2017). These disturbances can alter activity patterns and reduce relative  
61 abundance of native carnivores. For example, carnivores in Madagascar exhibited spatial  
62 avoidance when dogs were present, and were more likely to be replaced by dogs in degraded  
63 forests near human settlement (Farris et al. 2016, 2017). Similarly, chilla fox (*Lycalopex griseus*)  
64 visits to scent stations in Southern Chile were negatively correlated with dog presence, and  
65 telemetry data showed that foxes rested in a habitat type that was not preferred by dogs (Silva-  
66 Rodríguez et al. 2010a). In general, how dog-wildlife interactions are facilitated by habitat  
67 fragmentation and concurrent loss (hereafter referred to as habitat ‘destruction’) is largely  
68 unstudied. Furthermore it is also unknown whether habitat destruction and dogs have similar,  
69 opposing, or synergistic impacts on carnivores. Given the pervasiveness of both dogs and habitat  
70 destruction as major disturbances, it is surprising that few studies have measured and compared  
71 their simultaneous effects on native species.

72 Predicting the effects of habitat destruction on native carnivores, especially in  
73 conjunction with dogs, is difficult because our expectations for mesocarnivore response to these  
74 two threats (destruction and dogs) may not align. Based on intraguild predation theory, we would  
75 expect smaller carnivores such as mesocarnivores to be particularly susceptible to harassment by  
76 dogs modulated by body size (Donadio & Buskirk 2006). In contrast, for fragmentation and  
77 edge effects, a component of habitat destruction, large-bodied mammalian carnivores are  
78 particularly susceptible due to their relatively small population sizes, slow growth rates and  
79 extended habitat requirements and corresponding home ranges (Schipper et al. 2008). In general,  
80 the impacts of habitat destruction on carnivores are harder to predict because many aspects of  
81 their ecology such as prey availability and habitat quality are also impacted. Mammals vary in  
82 their sensitivity to fragmentation and in their adaptive responses to fragmentation (Crooks 2002;  
83 Janecka et al. 2016; Smith et al. 2019; Palmeirim et al. 2020). For example, a disturbance from  
84 fragmentation may shuffle species distributions and facilitate the invasion of nonnative  
85 competitors or other species (Crooks 2002; Echeverría et al. 2007; Jessen et al. 2018). Overall,

86 the impacts of fragmentation are even less clear for mesocarnivores, many of which are  
87 generalists and have smaller home ranges than their larger counterparts, and thus, may be more  
88 resistant to or even benefit from fragmentation (but see Crooks et al. 2017; Rocha et al. 2020).  
89 Similar to fragmentation, our expectations for the effect of habitat loss on carnivores are not  
90 straightforward, and the importance of habitat type may be superseded by intraguild dynamics  
91 (Randa & Yunger 2006). For example, Massara et al. (2016) found that the occupancy of  
92 generalist mesocarnivores was negatively correlated to reserve size throughout the remnant  
93 patches of the Atlantic Forest in Brazil, while in an urban-rural gradient in the US, Randa &  
94 Yunger (2006) found that raccoon occupancy increased with residential/urban habitat rather than  
95 forest.

96 In the Valdivian temperate forests biodiversity hotspot of Chile, both habitat destruction  
97 and the presence of dogs are widespread and potentially devastating endemic species (Myers et  
98 al. 2000). These forests are being rapidly lost and converted to exotic plantations and  
99 pasturelands (Echeverría et al. 2008; 2012). Protected areas are insufficient for meeting goals to  
100 maintain the biodiversity value of these forests because protected areas are restricted to the  
101 inland Andes rather than to the endemic-rich coastal areas (Smith-Ramírez 2004). The central  
102 valley, which formerly connected the coastal and montane sections as contiguous forest, has  
103 been heavily deforested and is now dominated by cow pastures and exotic plantations (Smith-  
104 Ramirez et al. 2010). Today, only small patches of native forests remain as available wildlife  
105 habitat that are interspersed throughout this landscape that is privately-owned and managed (Fig.  
106 1). Free-ranging dogs pose a major threat to the persistence of at least two mammal species of  
107 conservation concern, the pudu (*Pudu puda*, IUCN status of Vulnerable) and the Darwin's fox  
108 (*Lycalopex fulvipes*, IUCN status of Endangered) (Silva-Rodríguez et al. 2010b, 2016).

109 Here, we model the effects of habitat destruction, the presence of dogs, and their  
110 interactions on the spatial use of carnivores. Specifically, we surveyed privately-owned forest  
111 patches that were outside of protected areas or forestry company ownership using remotely-  
112 triggered cameras. We expected habitat destruction metrics to be more important than dog space  
113 use in explaining the occupancy of forest specialists (e.g., güiña, *Leopardus guigna*). In contrast,  
114 we also expected that in these largely altered landscapes dog occupancy would be the major  
115 driver of native canid spatial use, due to the immediate threat they present, and induced fear

116 effects (Palomares & Caro 1999; Vanak et al. 2009; Vanak & Gompper 2010). We hypothesized  
117 that increasing patch isolation and reducing the proportion of forest would be important drivers  
118 of dog occupancy, providing evidence that their presence is facilitated by fragmentation (Fig. 2).  
119 Our work will enhance our understanding of native carnivore occurrence in the later stages of  
120 human-altered landscapes and reconcile the relative contributions of interacting threats from  
121 fragmentation and dog presence.

122

## 123 **2. Methods**

### 124 2.1 Study area

125 From mid-May 2019 through the end of August 2019, we surveyed the carnivore community in  
126 the Los Lagos region of Chile, near the city of Osorno, between Lago Rupanco and Lago  
127 Llanquihue (40° 76' to 41° 21' S, 72° 54' to 72° 97' W, Fig. 1). This area is characterized by  
128 Valdivian temperate rain forest (mean daily temperature ranging from 3-23°C for the year) with  
129 a cold, rainy winter season between May and September (1346 mm annual rainfall) and warm  
130 temperate summers (en.climate-data.org). The landscape, formerly dominated by native forest,  
131 was at the time of the study dominated by pastures that were used primarily for cattle as well as  
132 plantations of pine (*Pinus radiata*) and eucalyptus (*Eucalyptus* sp.) with small remnant stands of  
133 native forest. The study area was relatively flat and sandwiched between a large protected area  
134 (Parque Nacional Vicente Rosales) on the eastern edge and the Osorno metropolitan area on the  
135 western edge. Native forest patches were mostly made up of degraded strips along the edges of  
136 pastures comprised of a mix of *Lophozonia obliqua*, *Nothofagus dombeyi*, *Persea lingue*, and  
137 *Laurelia sempervirens* with a bamboo understory (*Chusquea quila*).

138

### 139 2.2 Camera trap survey

140 We deployed 50 remotely-triggered cameras (Reconyx© PC 850, 850C, 900, 900C) in forest  
141 patches throughout the study area from June to August 2019 (the austral winter), aiming for  
142 maximum coverage of areas where we obtained permission. We affixed cameras to trees  
143 (minimum diameter 0.25 m) with cable locks and placed 0.5 m off the ground. We used signs of  
144 animal activity such as game trails and scat to determine the specific micro-site location of

145 camera placement, to maximize detections. Cameras were placed at least 0.5 km apart from each  
146 other, and efforts were made to place within the core of each patch if minimum spacing allowed.  
147 Each camera was baited with canned mackerel placed inside a bottle with a perforated cap, wired  
148 down to keep animals from accessing or removing the bait. Camera settings included: high  
149 sensitivity, one-second lapse between three pictures in a trigger, rapidfire (no quiet period  
150 between triggers).

151 At the end of the survey period, we retrieved images from the cameras and identified  
152 them by a single observer to the species level. After image identification, we applied a 30-minute  
153 quiet period to ensure independence of species detections (Wang et al. 2015; Suraci et al. 2016).  
154 These images and the associated site-level environmental variables (explained below) were used  
155 to estimate individual species occupancy. We used Moran's I in ArcPro (vers. 2.3.1) and did not  
156 find evidence of spatial autocorrelation. The 'camtrapR' package was used to organize camera  
157 trap images and extract data for modeling (Niedballa et al. 2016), implemented in Program R  
158 vers. 3.6.2 (R Core Team 2019).

## 159 2.3 Occupancy modeling

160 Using single-species single-season occupancy models (MacKenzie et al. 2003), we evaluated the  
161 impacts of habitat degradation on the occupancy ( $\Psi$ ) and detectability ( $p$ ) of dogs, and evaluated  
162 the impacts of habitat degradation and dog occupancy (dogo) on the occupancy and detectability  
163 of three focal native species: the chilla (*Lycalopex griseus*), culpeo (*Lycalopex fulvipes*), and  
164 güiña (Fig. 3). Covariates for habitat degradation included proportion of native forest (forest) and  
165 patch isolation (iso), as well as a measure of understory (10uds). We also included small  
166 mammal trap success (sm) as a coarse measure of prey availability. We first separated species  
167 detections into 7-day observation periods (Wang et al. 2015). We then modeled detection  
168 probabilities for each species holding occupancy constant, to account for non-detection. Finally,  
169 we used the best detection models to model the occupancy for each species.

### 170 2.3.1 Detection covariates

171 We modeled detection probabilities with covariates that could increase or decrease the likelihood  
172 of an animal being captured on camera if it occupied the vicinity. We measured understory cover  
173 using a point-intercept method, with the understory height measured every meter for 10m in the  
174 four cardinal directions surrounding each camera (Karl et al. 2017). We then aggregated values



175 for the understory cover into three categories: 0m (no understory), 0.25m, and 0.5m. Understory  
176 at 10m (10uds) is an average of all understory measurements taken every meter within a 10-  
177 meter radius of the camera tree (40 measurements per camera site). Understory was not included  
178 in the detection model for the culpeo, as inclusion prevented convergence of the global model.  
179 We first modeled occupancy of dogs using habitat covariates (10uds, forest, iso, sm), and then  
180 included the resulting site level estimates as the dogo covariate for native species models (Fig.  
181 3). Patches were digitized in ArcPro (vers. 2.3.1) using high resolution satellite imagery from  
182 2018 (Maxar Vivid, 0.5m resolution, 5m accuracy) to obtain forest, iso, and edge estimates. The  
183 iso covariate was measured as the mean border-to-border distance to the nearest patch within a 1-  
184 km radius of each camera. The edge covariate was measured as the mean ratio of patch perimeter  
185 size to patch area for all patches within a 1-km radius of each camera. However, edge was  
186 excluded from the final global model, as it was highly correlated with both forest and iso  
187 covariates ( $p < 0.01$ ). We estimated sm as a metric of prey availability, using the total number of  
188 all independent lagomorph, rodent, and shrew opossum triggers per camera standardized by the  
189 number of trap nights. Camera type (cam) was included to distinguish between white-flash  
190 cameras and infrared cameras. Lastly, trap nights (trap), the number of nights an individual  
191 camera was operational to collect species detections, were included to determine if sampling  
192 effort affected detection rates. Covariates were compared using Pearson's R, with a cutoff  
193 threshold of  $R > 0.5$  or  $p < 0.05$ .

### 194 2.3.2 Occupancy covariates

195 Occupancy for each species was modeled with dogo and habitat covariates (10uds, forest, iso,  
196 sm); edge was highly correlated with forest and omitted from the model. To test whether the  
197 impact of dogs on carnivores was facilitated by lack of understory, we included an interaction  
198 term between dogo and 10uds.

### 199 2.3.3 Model evaluation

200 The dog global model included mean understory height within 10m (10uds), camera type, and  
201 trap night (cam, trap) covariates for detection, while occupancy covariates included understory  
202 (10uds), prey (sm), proportion forest (forest) and patch isolation (iso). Native species global  
203 models used the same covariates as the dog model, with the addition of dog occupancy (dogo)  
204 for detection, and an interaction term for dog occupancy and understory (dogo\*10uds) for

205 occupancy. All detection and occupancy covariates were tested for correlation by site using  
206 Pearson's R. Model ranking was carried out using Akaike Information Criterion, corrected for  
207 small sample sizes (AICc), or quasi-AICc (QAICc) if the global model was overdispersed ( $\hat{c} > 1.2$ ),  
208 with the top model being defined as the one with the lowest AICc or QAICc score.  
209 Goodness of fit was tested for all top models ( $< 2 \Delta AICc$  units or  $\Delta QAICc$  units of the highest  
210 rank model) using a Chi-square statistic. All occupancy modeling was completed in the  
211 'unmarked' package (Fiske & Chandler 2011) in Program R vers. 3.6.2 (R Core Team 2019).

#### 212 2.3.4. Threshold response to dogs

213 We interpreted the  $\beta$  coefficient of dogo and confidence intervals not overlapping zero when  
214 occurring in top models to conclude significant effects of dogs on carnivore occupancy. When  
215 the top models included dogo as a covariate with a non-significant negative coefficient, we  
216 determined the threshold level of dog occupancy required for dogo to become a significant  
217 negative driver on carnivore occupancy. We incrementally increased the value of the dogo to the  
218 maximum occupancy value (1), a single camera at a time. The order was determined by ranking  
219 cameras from highest to lowest dogo value.

#### 220 2.4 Temporal use

221 As sympatric carnivores may be more likely exhibit temporal instead of spatial partitioning to  
222 promote coexistence (Santos et al. 2019), we estimated pairwise temporal overlaps for all  
223 species, and compared the overlap of native carnivore pairs with the overlap of native  
224 carnivores-dog pairs. We plotted the temporal activity distributions of each species and  
225 determined the degree of overlap between pairs ( $\Delta$ ) with 95% confidence intervals generated by  
226 10,000 parametric bootstrap iterations.  $\Delta$  values range from 0 indicating completely distinct and  
227 non-overlapping temporal activity to 1 indicating complete overlap between the comparison  
228 groups.  $\Delta_1$  was used for comparisons when one of the sample groups had less than 50 triggers;  
229 otherwise  $\Delta_4$  was used to estimate temporal overlap between species pairs (Ridout & Linkie  
230 2009). We then used the Mardia-Watson-Wheeler test to determine if the temporal patterns  
231 varied significantly between individual species, which compares two sets of circular data and  
232 determines if there is homogeneity in the means or variances. We implemented the temporal  
233 analyses using the 'overlap' and 'circular' packages in Program R (Ridout & Linkie 2009,  
234 Agostinelli & Lund 2017).

235

### 236 3. Results

237 We detected all three carnivore species over a total effort of 3500 trap-nights. Naïve occupancy  
238 estimates for the güiña (n=56 independent triggers), chilla (n = 225), and culpeo (n=39) were  
239 0.51, 0.59, and 0.16 respectively. Dogs were fairly common (n=64) found at 20/49 camera sites  
240 (naïve  $\psi = 0.41$ ). Additional native carnivores that were detected, although rare, included the  
241 chingue (*Conepatus chinga*, n=13) and the puma (*Puma concolor*, n=4). We also detected two  
242 additional introduced species: the mink (*Neovison vison*, n=20) and domestic cat (*Felis catus*,  
243 n=21). Darwin's fox (*Lycalopex fulvipes*) was not detected during our camera survey in the area,  
244 though it has been found in the area previously (personal communication J. E. Jiménez).

#### 245 3.1 Detection of carnivores

246 Our study area was comprised of an understory that ranged from completely open to thickets of  
247 dense vegetation with specific camera sites comprising no understory to over two meters in  
248 height. As such, we expected detection to vary by understory, depending on species preference  
249 on microsite selection for dense vegetation, and the ability of the understory to reduce the  
250 visibility range for a camera trap. For the chilla ( $\beta = -6.16$ , SE = 1.38) and dog ( $\beta = -7.44$ , SE =  
251 1.84), understory was a strong driver of detection probability, decreasing the detectability for  
252 both species (Table 2). For both chilla ( $\beta = 1.77$ , SE = 0.37) and culpeo ( $\beta = 3.23$ , SE = 0.834),  
253 dog occupancy increased detectability. The null model best described güiña detection; that is, no  
254 effect of covariates improved model fit.

#### 255 3.2 Occupancy of carnivores

256 Overall, modeling occupancy with covariates and accounting for imperfect detection improved  
257 our understanding of carnivore space use. Chillas had the highest overall occupancy ( $\psi = 0.67$ ),  
258 while culpeos had the overall lowest occupancy, but nearly doubled from the naïve estimate ( $\psi =$   
259 0.36). Güiña was the only species for which the null model was the best model, and the  
260 occupancy estimate was thus the same as the naïve estimate ( $\psi = 0.51$ ). In comparison to the  
261 native carnivores, dog occupancy was higher than the culpeo and güiña, but lower than that of  
262 the chilla ( $\psi = 0.58$ ).

263 Factors driving occupancy of carnivores varied by species (Fig. 4, Table 1). Despite the  
264 importance of understory for species detection, it did not appear in the best model for any  
265 species. It was however a negative driver of chilla occupancy in 4/10 top models which had  
266 comparable weight to the best model (Table 1). Given the reliance of mammalian carnivores on  
267 prey, unexpectedly, small mammal trap success was important only for the occupancy of the  
268 culpeo ( $\beta = 1.05$ ,  $SE = 0.53$ ).

269 Our work contrasted the ecological consequences of habitat destruction (loss and  
270 fragmentation), and dog occurrence on the space use of carnivores (Table 1, 2). Habitat metrics  
271 were important drivers of chilla and dog occupancy but did not appear in the model sets for  
272 culpeo or güiña. For example, patch isolation was in the top two models for the chilla ( $\beta = 0.09$ ,  
273  $SE = 0.04$ ), and was positively correlated with occupancy. Proportion of forest did not appear to  
274 be important for occupancy of any native species. It was however important for dogs ( $\beta = -26.06$ ,  
275  $SE = 12.1$ ), with increasing proportion of forest decreasing dog occupancy. Dog occupancy  
276 appeared in 4/5 top models for culpeo (including the best model) and was important for model fit  
277 for the culpeo but was not a significant driver of culpeo occupancy ( $\beta = -4.19$ ,  $SE = 2.74$ ).

278 Similarly, results varied in quantifying responses of native carnivore occupancy to dog  
279 presence. For chilla, dog occupancy was not in the best chilla model but appeared as a positive  
280 driver in 6/10 top models, which had comparable weight to the best model (Table 1). The dog  
281 occupancy covariate was not influential, positive or negative, on occupancy for güiña. Culpeo  
282 was the only species with dog occupancy in the top model with a negative (non-significant)  $\beta$   
283 coefficient. The dog landscape level occupancy from the top model was 0.58. Increasing dog  
284 occupancy to 0.65 (an increase of 12.1%) resulted in dog occupancy becoming a significant  
285 negative driver of culpeo occupancy (Fig. S1.1, see Appendix S1).

286 We found no evidence for the interaction of dog occupancy and understory affecting  
287 occupancy for native mesocarnivore species occupancy. Overall, we conclude that landscape  
288 characteristics via metrics of increasing fragmentation have similar positive effects for both  
289 generalist native carnivores and for dogs (Fig. 4).

### 290 3.4 Temporal activity

291 We evaluated temporal activity patterns of all our study species to determine if there was  
292 evidence for temporal avoidance with dogs (Fig. S1.2, see Appendix S1). Activity patterns for  
293 the three native carnivores was largely restricted to the nocturnal and crepuscular hours. Overlap  
294 among the native carnivores was high ( $\Delta$  ranging 0.78 – 0.89) and did not vary significantly  
295 among pairs (Table 3: p values: 0.08-0.79). In contrast, dog activity was almost entirely diurnal,  
296 resulting in significantly different activity patterns from native species ( $\Delta$  ranging 0.35-0.43;  $p <$   
297 0.001). Furthermore, 95% confidence intervals for  $\Delta$  dog-native species pairs and for  $\Delta$  native-  
298 native species pairs did not overlap in a single case, indicating that native species overlapped  
299 significantly more with other native species than they did with dogs.

300

#### 301 **4. Discussion**

302 The threats that mammals face from habitat loss and fragmentation are especially relevant in the  
303 context of the temperate rainforests of central Chile, which have included rapid deforestation and  
304 fragmentation in the past 50 years (Echeverría et al. 2006; Nahuelhual et al. 2012; Uribe et al.  
305 2020). An additional human-related threat is the presence of dogs, which antagonize native  
306 species and preferentially use the matrix that separates the remaining patches (Silva-Rodríguez et  
307 al. 2010a). Using single species models, we investigated the impacts of these two phenomena  
308 (habitat destruction and dogs) on the occupancy of three native carnivores (foxes – chilla and  
309 culpeo; cat – güiña), in remnant forest patches within an agricultural matrix. Our results varied  
310 by species, indicating that components of habitat destruction have opposing effects for the two  
311 foxes, as do dogs. For dogs, we found evidence that occupancy increases with habitat loss. Time  
312 use of all native species was concentrated during the nocturnal period, in stark contrast to the  
313 diurnal time use of the dog. Our results provide the necessary baseline to understand dogs and  
314 habitat destruction metrics as drivers of native species occupancy and could be further expanded  
315 to multispecies models to examine species interactions.

316 For the species included in this study, at first glance our results suggest that landscape  
317 degradation does not pose an immediate concern. For the chilla, the positive correlation between  
318 patch isolation and occupancy is likely a reflection of the ecology of the fox, which primarily  
319 forages in the open fields that comprise the matrix between patches (Silva-Rodríguez et al.  
320 2010a). However, this species also utilizes interior habitat of these patches as a refuge and thus,

321 would likely have negative consequences if patches fell below a threshold size (Silva-Rodríguez  
322 et al. 2010a). Our results for culpeos and güiñas, which did not show any response to either  
323 habitat loss or patch isolation could indicate that: a) these species are plastic in their habitat  
324 requirements; b) fragmentation and habitat loss have not reached a sufficient threshold to elicit a  
325 response; c) there is a time lagged ‘extinction debt’, or d) these species are tracking spatial  
326 patterns of prey, predator, or competitor species instead (Hanski & Ovaskainen 2002; Ryall &  
327 Fahrig 2006; Swift & Hannon 2010; Halley et al. 2016). The model results for the culpeo  
328 suggested this latter mechanism, as they were positively driven by prey availability, and dog  
329 occupancy was consistent in the top models having a negative coefficient (though note that  
330 neither covariate was significant using a significance level of  $\alpha=0.05$ ) While landscape  
331 characteristics did not appear as a negative driver in any native species models, the inverse  
332 relationship between dog occupancy and proportion of forest indicates as habitat loss increases in  
333 this region native species will have less refuge habitat to avoid exposure to domestic dogs  
334 (Torres & Prado 2010; Paschoal et al. 2018).

335 We expected dogs to influence native carnivore occupancy because of their documented  
336 impact on small carnivores through interference and exploitation competition, and the increased  
337 mortality risk they pose as disease reservoirs (Laurenson et al. 1998; Rhodes et al. 1998; Sillero-  
338 Zubiri et al. 2004; Vanak & Gompper 2009, 2010). Dogs have been linked to the decline of the  
339 pudu, a potential prey item for the two fox species in this study (Silva-Rodríguez & Sieving  
340 2012). Despite the threat that a dog encounter presents, dog occupancy did not clearly present a  
341 negative driver of native species occupancy, and only featured as a non-significant negative  
342 covariate for culpeo top models. While this partially fit our expectation that native canids would  
343 more likely have antagonistic interactions with dogs and exhibit avoidance, we expected the  
344 smaller chilla fox to have greater sensitivity to dog presence (Donadio & Buskirk 2006; Vanak &  
345 Gompper 2009). Previous studies corroborate this expectation as dogs enforce interference  
346 competition to alter space use and have been observed harassing and killing chilla (Silva-  
347 Rodríguez et al. 2010a). A lack of a negative response from chillas to dogs using our occupancy  
348 framework could indicate that foxes were avoiding dogs at finer spatial or temporal scales, or  
349 that dog density was not sufficiently high to elicit a spatial avoidance (Zapata-Ríos & Branch  
350 2018; Qi et al. 2020). Indeed, our analysis of activity patterns suggests temporal partitioning as a  
351 mechanism for avoidance of dogs (Kronfeld-Schor & Dayan 2003; Schuette et al. 2013). In

352 contrast to chillas, culpeos did indicate a potential response to dogs at a landscape level, and  
353 showed no response to habitat loss and fragmentation. Our result for culpeo occupancy was  
354 consistent with that of Zapata-Ríos & Branch (2018), despite differences in the landscape  
355 histories between our formerly contiguously forested site, and their historically patchy Andes  
356 site. Congruent with the dog occupancy estimates ( $\bar{\Psi} = 0.66$ , range: 0.53 - 0.73) from Zapata-Ríos  
357 & Branch (2018), it took a projected 12% increase in dog occupancy in our study site for it to  
358 have a significant negative effect on culpeo occupancy.

359 While dogs had opposite effects on the occupancies of the fox species, they increased  
360 detection for both the culpeo and the chilla. Movement data for canids highlight quicker speeds  
361 through riskier areas, which would likely impact detection rates (Péron et al. 2017; Broadley et  
362 al. 2019). Thus, increased detection for the fox species may reflect a finer scale response to the  
363 risk posed by dogs, rather than a broader change in spatial use (Broekhuis et al. 2013). This  
364 interpretation, along with mismatched time use, would reconcile the open habitat preferences of  
365 the chilla fox with its increased susceptibility to dog antagonism based on size (Donadio &  
366 Buskirk 2006).

367 Fragmentation can facilitate the spread of invasive species through numerous pathways,  
368 such as roads increasing the occurrence of dogs (Loss et al. 2013; Moreira-Arce et al. 2015). Yet,  
369 few occupancy studies have looked at the impacts of both dogs and habitat loss and  
370 fragmentation on native carnivores. Dogs are typically considered human associated, though they  
371 may travel considerable distances and thus, can impact the larger landscape (Young et al. 2011,  
372 Gompper 2014). Furthermore, their space use, while tied to human impacts on the landscape, are  
373 more nuanced than simply being a result of nearby human habitation. In a North American  
374 system for example, dog occupancy has been found to increase with proportion forest (Morin et  
375 al. 2018), in contrast with our results that dog occupancy decreased marginally with proportion  
376 of forest. However, Morin et al. (2018) also found that pastures and grasslands were an even  
377 stronger positive predictor of dog occupancy; the land type that was the inverse of our measured  
378 metric for proportion forest. Whether the interaction between dogs and proportion forest impacts  
379 native carnivores can be intuitively answered when we see that dog occupancy can be a negative  
380 driver of culpeo occupancy if it surpasses a threshold. In ‘working’ landscapes this is particularly  
381 relevant as habitat loss and dog occupancy will likely continue to increase over time. Our

382 occupancy results suggest that the spatial use of both fox species (indirectly in the case of the  
383 culpeo, through dog occupancy) is tied to fragmentation and habitat loss. Furthermore, habitat  
384 destruction in the landscape increases the exposure of both foxes to the threat of a dog encounter  
385 (Farris et al. 2017, 2020). In the currently remaining forest stands that we surveyed, the largely  
386 nocturnal temporal use of native species provides a likely avoidance mechanism (Gerber et al.  
387 2012; Shores et al. 2019).

388 Our study gives us insight into the drivers of native carnivore space use in ‘working’  
389 landscapes rather than the protected areas that represent ideal and untouched habitats. By  
390 situating our study on privately-owned smallholder lands, we also have the unique opportunity to  
391 inform the conservation of species in these increasingly anthropogenic landscapes through local  
392 education efforts (Gramza et al. 2016). The remnant patches in these private lands may be  
393 particularly important for the persistence of native carnivores in the landscape, and in general  
394 agricultural landscapes may hold considerable biodiversity and conservation value (Kremen &  
395 Merenlender 2018; Lindenmayer 2019; Wintle et al. 2019). Many landowners do not have access  
396 to camera traps, and thus are unlikely to encounter elusive carnivores that are present even in  
397 small patches of forest along the edges of their pasturelands. While voluntary strategies for  
398 conservation have greater social acceptance than prescribed management action, they are not  
399 possible without landowners first having the knowledge of what species are on their land (Kamal  
400 et al. 2015). By partnering with landowners, scientists and managers can facilitate species  
401 conservation in these important landscapes, which are not typically considered conservation  
402 targets (Naugle et al. 2020). This partnership may yield dividends in collaboratively designing  
403 management solutions for dogs (Ford-Thompson et al. 2012). The management of domestic  
404 animals can be a source of intense debate, especially in regards to animals typically considered  
405 as pets (Wald et al. 2013). The impacts of dogs on wildlife is underestimated; conservation  
406 practitioners can learn from the intense controversy generated by the management of feral cats  
407 by involving local stakeholders, and by bringing a strong understanding of what factors drive the  
408 impacts of dogs (Loyd & Miller 2010; Doherty et al. 2017).

#### 409 **Data availability/accessibility**

410 The data that support the findings of this study are openly available in Dryad at  
411 doi:10.5061/dryad.3xsj3txfv.



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### 659 **Biosketch**

660 RM explores how anthropogenic pressures alter species interactions. More specifically, he is  
661 interested in how fragmentation alters native carnivore movement (short time scales) and  
662 occupancy (longer time scale), and how this translates to the community level.

663 JEJ examines the population and community ecology of mammals and birds with conservation  
664 concern in southern South America and Texas. More recently he added the impacts of exotic  
665 mammals on local biotas, dispersal ecology and the biogeography of  
666 tardigrades. <http://jaimeejimenez.com>

667 NCH explores the antagonisms in nature, focusing on competition, predation, and parasitism in  
668 mammalian systems. She links these research themes with anthropogenic pressures such as  
669 human-wildlife interactions to inform the conservation of large carnivores.

670

### 671 **Table and figure legends**

672 Figure 1. (a) Study area located in the Los Lagos Region of south-eastern Chile. (b) Landscape  
673 level distribution of camera deployment throughout patches of native forest straddling the  
674 Osorno Volcano. The borders of the box for (b) roughly delineate a ~6km dairy farm, with the  
675 cameras placed within the patches of native forest that are interspersed throughout cow pastures.

676 Figure 2. Projected facilitation of dog occupancy by habitat loss and fragmentation with  
677 expectation that decreasing proportion of native forest and increasing patch isolation would  
678 promote higher dog occupancy. Expectations for native carnivore response to fragmentation

679 were opposite those of dogs, with native carnivore occupancy expected to decrease with  
680 decreasing forest and increasing patch isolation.

681 Figure 3. Focal carnivores in this study for size comparison of the three native species relative to  
682 and dogs: the güiña (1.5-3kg), chilla (2.5-5.5kg), dog (10-25kg), and culpeo (5-13.5kg) from  
683 top left clockwise. Note that the upper weight range of the culpeo likely represents more  
684 southern parts of the range than the study area; they are relatively bigger than chillas, and smaller  
685 than dogs. Photo credit: R. Malhotra and NC Harris, Applied Wildlife Ecology Lab.

686 Figure 4. Relative importance of each covariate on species occupancy based on summed model  
687 weights for top model sets ( $< 2 \Delta AICc/QAICc$ ). dogo: dog occupancy; cam: camera type; 10uds:  
688 average understory height within 10m; iso: average distance between patches; forest: proportion  
689 native forest; sm: small mammal trap success. Beta coefficients for each covariate were averaged  
690 across the top model set. (a) dog occupancy and patch isolation were positively correlated with  
691 chilla occupancy, while understory was negatively correlated; (b) small mammal trap success  
692 was positively correlated with culpeo occupancy, while dog occupancy was negatively  
693 correlated; (c) proportion of native forest was negatively correlated with dog occupancy, while  
694 understory was positively correlated; (d) güiña occupancy was best described by the null model.

695 Table 1. Top occupancy ( $\Psi$ ) and detection ( $p$ ) models for native carnivore and dogs ranked by  
696 AICc, with model weights ( $w$ ) provided. \*QAICc was used instead of AICc in model ranking for  
697 güiña occupancy to account for overdispersion of the global model. dogo: dog occupancy; cam:  
698 camera type; 10uds: average understory height within 10m; iso: average distance between  
699 patches; forest: proportion native forest; sm: small mammal trap success.

700 Table 2. Untransformed  $\beta$  coefficients with 95% confidence intervals for the top model for each  
701 species.

702 Table 3. Overlap coefficients ( $\Delta$ ) and Mardia-Watson-Wheeler test for homogeneity of means for  
703 every pairwise combination of the study species.  $\Delta_4$  was used for every comparison except for  
704 those pairs containing the culpeo, where  $\Delta_1$  was used to account for lower number of triggers.

705 Figure S1.1. The effect of a simulated increase in dog occupancy across the landscape on the  
706 beta coefficient and 95% confidence interval for the dogo covariate in the culpeo occupancy  
707 model. \*represents a significant beta coefficient.

708 Figure S1.2. 24-hour activity patterns of all four study species. Dogs are distinct from native  
709 species in having a clearly diurnal activity pattern.

Species	Top models	AICc	$\Delta$ AICc*	w
Chilla	$\Psi(\text{iso}) p(\text{dogo}, 10\text{uds})$	429.809	0	0.175
	$\Psi(\text{iso}) p(\text{dogo}, 10\text{uds}, \text{cam})$	430.289	0.480	0.138
	$\Psi(\text{dogo}) p(\text{dogo}, 10\text{uds})$	430.613	0.804	0.117
	$\Psi(\text{dogo}, 10\text{uds}) p(\text{dogo}, 10\text{uds})$	430.782	0.974	0.108
	$\Psi(\text{dogo}) p(\text{dogo}, 10\text{uds}, \text{cam})$	430.948	1.139	0.099
	$\Psi(\text{iso}, \text{dogo}) p(\text{dogo}, 10\text{uds})$	431.139	1.331	0.090
	$\Psi(\text{dogo}, 10\text{uds}) p(\text{dogo}, 10\text{uds}, \text{cam})$	431.511	1.702	0.075
	$\Psi(\text{iso}, 10\text{uds}) p(\text{dogo}, 10\text{uds})$	431.736	1.927	0.067
	$\Psi(\sim 1) p(\text{dogo}, 10\text{uds})$	431.738	1.929	0.067
	$\Psi(\text{iso}, \text{dogo}, 10\text{uds}) p(\text{dogo}, 10\text{uds})$	431.792	1.982	0.065
Culpeo	$\Psi(\text{dogo}, \text{sm}) p(\text{dogo}, \text{cam}, 10\text{uds})$	124.932	0	0.273
	$\Psi(\text{dogo}, \text{sm}) p(\text{dogo}, 10\text{uds})$	126.238	1.306	0.142
	$\Psi(\text{sm}) p(\text{dogo}, \text{cam}, 10\text{uds})$	126.280	1.348	0.139
	$\Psi(\text{dogo}, \text{sm}) p(\text{dogo}, \text{cam})$	126.598	1.666	0.119
	$\Psi(\text{sm}) p(\text{dogo}, \text{trap}, 10\text{uds})$	126.734	1.802	0.111
	$\Psi(\text{sm}) p(\text{dogo}, 10\text{uds})$	126.753	1.821	0.110
	$\Psi(\text{dogo}, \text{sm}) p(\text{dogo}, \text{cam}, \text{trap})$	126.802	1.870	0.107
Dog	$\Psi(\text{forest}) p(10\text{uds}, \text{trap})$	272.000	0	0.370
	$\Psi(\text{forest}) p(10\text{uds}, \text{trap}, \text{cam})$	272.306	0.306	0.318
	$\Psi(\text{forest}, 10\text{uds}) p(10\text{uds}, \text{trap})$	273.704	1.704	0.158
	$\Psi(\text{forest}, 10\text{uds}) p(10\text{uds}, \text{trap}, \text{cam})$	273.757	1.757	0.154
Güiña	$\Psi(\sim 1) p(\sim 1)$	6.830	0	0.101

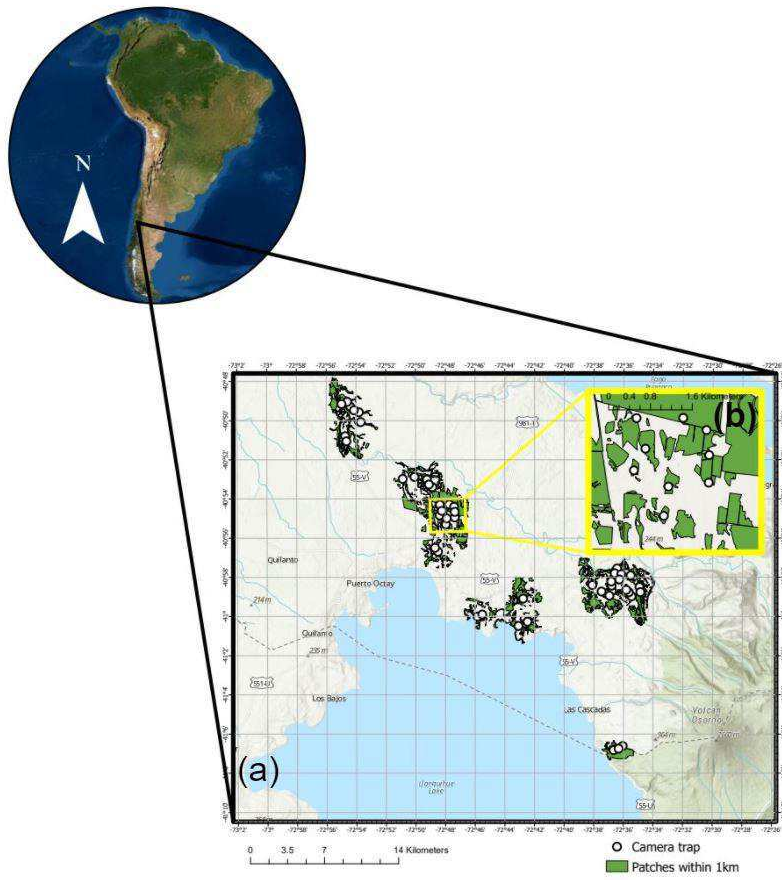
Table 1. Top occupancy ( $\Psi$ ) and detection ( $p$ ) models for native carnivore and dogs ranked by AICc, with model weights ( $w$ ) provided. \*QAICc was used instead of AICc in model ranking for güiña occupancy to account for overdispersion of the global model. dogo: dog occupancy; cam: camera type; 10uds: average understory height within 10m; iso: average distance between patches; forest: proportion native forest; sm: small mammal trap success.

Species	$\Psi$ covariates					p covariates			
	Forest	Patch isolation	Understory	Small mammal	Dog occupancy	Trapnights	Camera type	Understory	Dog occupancy
Chilla	-	0.09 (0.00 – 0.17)	-	-	-	-	-	<b>-6.16</b> (-8.85 – -3.46)	<b>1.77</b> (1.05 – 2.49)
Culpeo	-	-	-	1.00 (-0.11 – 2.11)	-4.32 (-9.65 – 1.01)	-	<b>1.60</b> (.48 – 2.73)	-	<b>3.18</b> (1.50 – 4.85)
Dog	-23.06 (-46.83 – -0.71)	-	-	-	-	<b>-0.12</b> (-0.23 – -0.01)	-	<b>-7.45</b> (-11.05 – -3.84)	-
Güiña	-	-	-	-	-	-	-	-	-

Table 2. Untransformed  $\beta$  coefficients with 95% confidence intervals for the top model for each species.

<b>Comparison</b>	<b><math>\Delta</math> Overlap (95% CI)</b>	<b>W statistic</b>	<b>p-value</b>
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

Table 3. Overlap coefficients ( $\Delta$ ) and Mardia-Watson-Wheeler test for homogeneity of means for every pairwise combination of the study species.  $\Delta_4$  was used for every comparison except for those pairs containing the culpeo, where  $\Delta_1$  was used to account for lower number of triggers.



Eri, NASA, NGA, USGS,  
Earthstar Geographics, Esri,  
HERE, Garmin, METI/NASA,  
USGS

