



# Environmental factors regulate occupancy of free-ranging dogs on a sub-Antarctic island, Chile

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**Abstract** Domestic dogs (*Canis familiaris*) are the most common carnivore species in natural ecosystems worldwide. They are of considerable concern for wildlife conservation, particularly in the absence of predators. However, we are only beginning to understand the ecology of free-ranging dogs, and even less is known in sub-Antarctic environments. Here, we used camera-trap data to assess space use of free-ranging dogs on a sub-Antarctic island in the Cape Horn Biosphere Reserve, southern Chile, which lacks native terrestrial carnivores. We predicted free-ranging dogs to be associated with human settlements, trails, and roads and to prefer open habitats over forest for the ease of movement. We obtained 67 independent dog records of 62 individuals over 3909 camera-trap days from 200 sites. Single-species single-season

occupancy models revealed that both rural/village dogs, as well as putative feral dogs chose peatbogs over forest, but their preference for settlements and roads was less pronounced and inconsistent among dog categories. Our findings revealed evidence for a reproducing feral dog population on Navarino Island that may be sustained by recruits from rural/village dogs, as identical sites were visited by both dog categories. However, due to a higher occupancy with proximity to human dwellings, the dependence of feral dogs on human resources remain uncontested. In light of the penetration of dogs into pristine sub-Antarctic habitats and their possible impacts on native vulnerable prey, we recommend the implementation of responsible pet-ownership regulations, as well as ethically-approved control actions for feral dogs to protect one of the planet's last wilderness areas.

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## Introduction

Domestic dogs (*Canis familiaris*) are currently the most abundant carnivore species on earth (Gompper 2014) and can be found on all continents except Antarctica (Hughes and Macdonald 2013). From leashed to feral dogs at the extremes, they live along a gradient of varying conditions of confinement and dependence upon humans (Vanak and Gompper 2009). As subsidized predators, dog populations often outnumber those of wild carnivores (Gompper 2014). The high densities of dogs, together with their often unrestricted mobility, explain the high vulnerability of wildlife to domestic dogs. Indeed, recent assessments state that the global impacts of dogs on wildlife, with currently 188 vertebrate species potentially threatened, have been grossly underestimated (Doherty et al. 2017). Free-ranging dogs negatively impact wildlife through predation, harassment, competition, hybridization, and disease transmission (reviewed by Young et al. 2011; Hughes and Macdonald 2013; Twardek et al. 2017). More subtly, dogs also can trigger behavioral changes in native species, such as shifts in activity patterns (Zapata-Ríos and Branch 2018; Mella-Méndez et al. 2019) or space use (Silva-Rodríguez and Sieving 2012).

While impacts of free-ranging dogs on wildlife have been the research focus recently, knowledge on their habitat use is still relatively scarce and inconsistent: Studies revealed that free-ranging dogs were positively associated with human-modified rural landscapes (e.g., farmed land and bare-ground, Vanak and Gompper 2010; pasture habitat, Sepúlveda et al. 2015; open habitat, Dos Santos et al. 2018), moved along roads (Moreira-Arce et al. 2015; Sepúlveda et al. 2015; Warembourg et al. 2020), and stayed close to human houses (Vanak and Gompper 2010; Woodroffe and Donnelly 2011; Silva-Rodríguez and Sieving 2012; Ruiz-Izaguirre et al. 2015). This suggests that forests might represent a barrier to movement, thus triggering a selective wandering behavior in dogs (Sepúlveda et al. 2015). However, dogs were also found on the edges of protected areas (Srbek-Araujo

and Chiarello 2008; Lacerda et al. 2009; Marks and Duncan 2009), foraging in riparian habitats (Meek 1999), and even within forested habitat (Paschoal et al. 2012; Ribeiro et al. 2019; Zanin et al. 2019). The free-ranging dogs targeted in these studies comprise overall owned or unowned, rural or urban free-ranging dogs or village dogs (*sensu* Vanak and Gompper 2009). For feral dogs the picture is even less clear. Following Vanak and Gompper (2009), feral dogs are completely wild dogs surviving without human-derived subsidy. Free-ranging dogs used habitats according to their availability in a National Park in Ecuador located in the high Andes (Zapata-Ríos and Branch 2018). Dogs under a less-strict definition, i.e., living in a free state with no direct food or shelter intentionally supplied by humans (Causey and Cude 1980), selected lower road density, higher woodland density, and garbage dumps (Boitani et al. 2017). Community dumps were also visited by feral dogs in the United States (Scott and Causey 1973; Daniels and Bekoff 1989; Green and Gipson 1994).

Studying carnivores' space use is a challenge as they typically forage over large areas, occur at low densities, and exhibit elusive behavior. Camera-trapping is an increasingly-used, noninvasive survey method to study carnivores (O'Connell et al. 2011). Data derived from camera-traps can be analyzed through occupancy modelling, which allows to account for imperfect detection, low detection probabilities, and missing observations (Mackenzie et al. 2006). Hence, occupancy studies have been applied to a wide range of elusive carnivores, such as kodkod cat (*Leopardus guigna*, Fleschutz et al. 2016), sun bears (*Helarctos malayanus*, Linkie et al. 2007), or red slender loris (*Loris tardigradus*, MacKenzie and Reardon 2013). Free-ranging dogs also have been studied via occupancy to collect information on abundance (Paschoal et al. 2016), habitat use (Marks and Duncan 2009), edge effects for protected areas (Srbek-Araujo and Chiarello 2008; Paschoal et al. 2012), and impacts on wildlife (Silva-Rodríguez and Sieving 2012; Parsons et al. 2016; Mella-Méndez et al. 2019).

In Chile, human–dog ratios in the rural areas are up to four times higher than the global estimate (Gompper 2014). Recent studies have intensively described conflicts with endangered wildlife such as huemul (*Hippocamelus bisulcus*), pudu (*Pudu puda*), and kodkod cat (Corti et al. 2010; Silva-Rodríguez and

Sieving 2012; Sepúlveda et al. 2014), along with a lacking awareness of these conflicts by local people (Schüttler et al. 2018; Villatoro et al. 2018). None of these dog populations were feral; the only exception to evidence of truly feral dogs thus far has been described in the southernmost portion of Chile (Schüttler et al. 2018). Here, on sub-Antarctic Navarino Island, located within the Cape Horn Biosphere Reserve (CHBR), invasive wild and domestic mammalian species outnumber their native counterparts (Anderson et al. 2006). Free-ranging dogs, represent an extensive conservation concern in this wilderness setting, due to the absence of native terrestrial predators, and their possibly-severe impacts on avian (Schüttler et al. 2009, 2018) and southernmost guanaco (*Lama guanicoe*) populations. Importantly, guanacos are considered in danger of local extinction (González 2010).

In this study, we aimed to assess the occupancy of free-ranging dogs in relation to anthropogenic and environmental factors within a gradient from human presence to almost pristine sub-Antarctic environment. To our knowledge, this is the first assessment of space use by unconfined dogs in a sub-Antarctic wilderness setting. We predicted free-ranging dogs to be associated with human settlements, and trails and roads (e.g., Vanak and Gompper 2010; Woodroffe and Donnelly 2011; Silva-Rodríguez and Sieving 2012; Moreira-Arce et al. 2015; Sepúlveda et al. 2015; Parsons et al. 2016) to gain access to wild habitats. We further predicted preference of open habitats such as pastures and shrublands over forest (e.g., Vanak and Gompper 2010; Sepúlveda et al. 2015, but see Paschoal et al. 2012; Ribeiro et al. 2019) for the ease of movement and richness of prey (e.g., livestock and waterbirds; Scott and Causey 1973; Schüttler et al. 2009). Finally, we compared the use of space of two categories of free-ranging dogs, rural and village dogs (hereafter rural/village dogs) and putative feral dogs (hereafter feral dogs, sensu Vanak and Gompper 2009) following a classification based upon a photographic census. If feral dogs were truly feral on Navarino Island (i.e., independent of human subsidy) and avoiding human contact (Boitani et al. 2017), they should avoid human dwellings. We close with management recommendations for conserving this sub-Antarctic wilderness at the southern tip of the Americas.

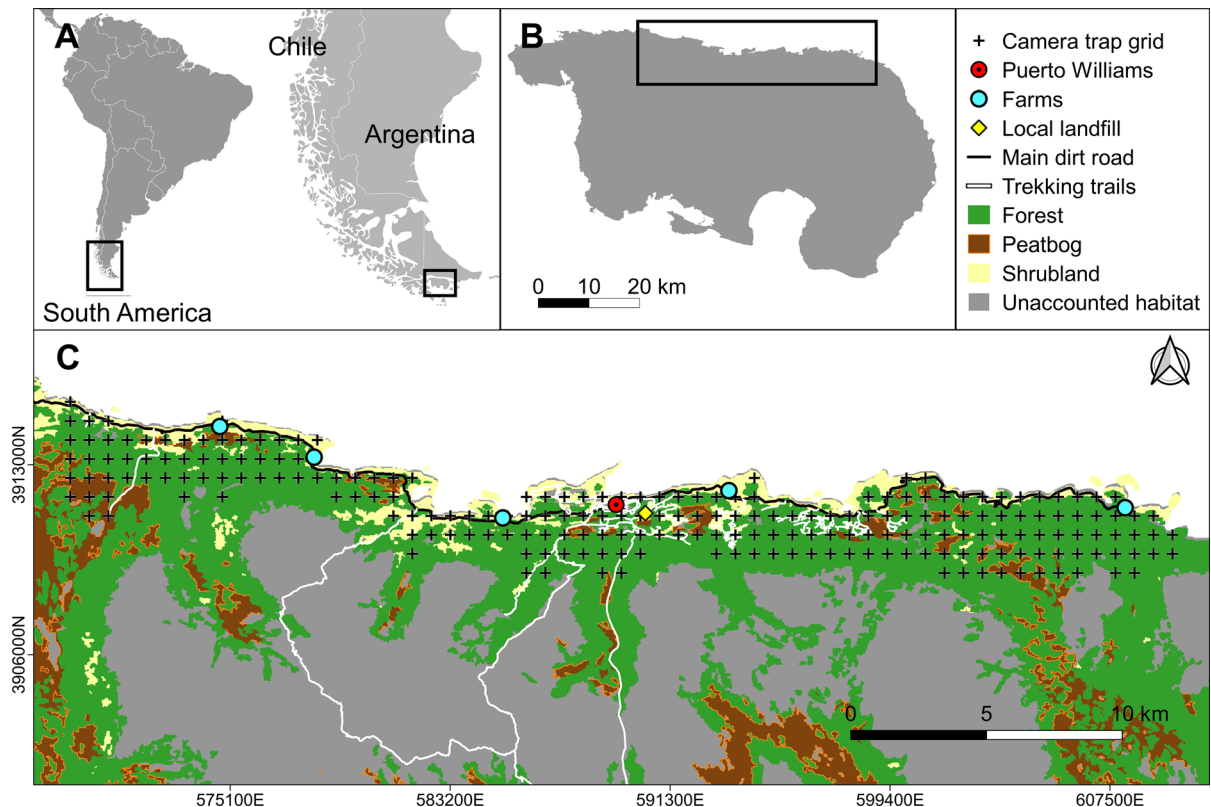
## Methods

### Study area

Our study was carried out on Navarino Island (2528 km<sup>2</sup>), located within the CHBR, southern Chile (Fig. 1). The archipelagic CHBR exists within the Magellanic sub-Antarctic ecoregion (Rozzi et al. 2012), and consists of forests of southern beeches (*Nothofagus* spp.) and Winter's bark (*Drimys winteri*), Magellanic tundra, or peatbogs (*Sphagnum* spp.), high-Andean habitats, glaciers, and shrublands (Pisano 1977). The terrestrial vertebrate community on Navarino is rich in birds (> 150 spp., Couve et al. 2016), but depauperate in native mammals (two rodent species, two bat species, and the guanaco, Anderson et al. 2006); amphibians and reptiles are absent. The only terrestrial carnivores are invasive American mink (*Neovison vison*) and free-ranging cats (*Felis catus*) and dogs. The human population within the reserve is concentrated in Puerto Williams (~ 2100 inhabitants) on the northern coast of Navarino. Additionally, a small fishing town (Puerto Toro) exists on the eastern coast of the island, as well as eight rural farms. Local people earn income on artisanal fishery, small-scale livestock farming, and tourism. To date, the infrastructure is limited to a dirt road along the northern coast of Navarino, some logging trails, and three trekking routes. Beyond the town and infrastructure, pristine sub-Antarctic habitat predominates. Currently, the island is facing a massive increase in the flux of visitors, as well as economic stimuli by the Chilean government, such as the construction of docks for cruise liners, increase in air traffic, parceling and settling of land, and new roads (total ~ 190 km, IMCH 2015). These activities will have consequences for the access of free-ranging dogs to natural areas.

### Sampling design

We studied the presence of dogs across 200 0.7 × 0.7 km (62.4 km<sup>2</sup>) grid squares around Puerto Williams, which covered varying habitat types and degrees of human infrastructure (Fig. 1). Due to logistic constraints, the 220 cells (to correct for inaccessible sites we added an additional 10% to the sample size) did not surpass 300 m.a.s.l., neither did they exceed four km south from the northern coast. As home ranges of free-ranging dogs have been described



**Fig. 1** Study area and sampling sites for camera-trapping on Navarino Island, southern Chile (a, b). Cameras were installed at 200 sites, at 0.7 km intervals, restricted to < 300 m.a.s.l.,

and < 4 km from the coast (c). Coloring refers to the main habitats on Navarino (see legend for details)

to vary between 0.4 (Dürr et al. 2017) and 20.6 km<sup>2</sup> (Atickem et al. 2010), we ensured site independency by checking whether the same individual appeared in different camera-traps during one sampling occasion (i.e., one day). This did not occur. In the case of non-identifiable dogs, we at least assured that dogs with similar phenotypic traits were not registered during the same day. The grid was designed with QGIS (Version 2.18.7, QGIS Development Team 2017).

#### Camera-trap sampling

We installed a total of fifty remote cameras (Bushnell Outdoor Products, Overland Park, USA) in four subsequent rotations of 20 days each during a closed-season between October 2016 and February 2017, during which we assumed that colonization and/or extinction processes did not occur. Camera-traps were installed in a < 100 m radius around the center of each grid cell depending on the vegetation;

coordinates were recorded using a GPS device (GARMIN Oregon<sup>®</sup> 650). Camera-traps were tied to trees at an approximate height of 50 cm above ground (e.g., Moreira-Arce et al. 2015). To improve detection probability, an olfactory attractant (perforated tuna can) was nailed to a branch or root 2-5 m from the camera focus (Thorn et al. 2009). During the first rotation, camera-traps were set to capture three photos per trigger every 30 s, but for the subsequent rotations, the interval time was reduced to one s to assure the maximum of triggered photos. As species detectability is prone to be influenced by the immediate surrounding of the camera (Kolowski and Forrester 2017), we recorded understory density and the number and density of game trails in a 10 m-radius around the camera. From the 20-day exposure period of each camera, we constructed binary detection histories using one day as a sampling unit. We then combined two consecutive sampling occasions to improve the 0:1 ratio (e.g., Paschoal et al. 2016). That way,  $n = 45$

of the 91 missing observations (due to technical problems) were also deleted. Permits to work on private lands and those administered by the Chilean navy were acquired in advance.

### Classification of free-ranging dogs

To distinguish between camera-trapped rural/village and feral dogs, we used a photographic catalogue of village dogs from Puerto Williams (four-season-census) and of owned rural dogs along the northern coast of Navarino from 2015 to 2016 (Schüttler et al., unpublished data). This catalogue was updated by the first author in parallel to the camera survey. Feral dogs were classified as those absent in the photographic catalogue, but without knowing whether those dogs were truly feral (i.e., surviving without any human food provisioning, following the definition of Vanak and Gompper 2009). The classification into rural/village dogs, feral dogs, and unidentified dogs was carried out by three independent reviewers. Dogs could not be identified when pictures only showed a portion of the dog or when morphological patterns could not be clearly distinguished. Where opinions dissented, photos were discussed until achieving consensus.

### Cartography

We measured landscape metrics within circular 500 m buffers around each camera-trap (e.g., Moreira-Arce et al. 2015). Based upon land use (year 2016) and Google Earth™ (Google Inc. 2017) satellite images, we derived the following three habitat categories: (i) forest (i.e., deciduous, evergreen, mixed, and semi-dense), (ii) peatbogs (i.e., peatbogs, succession bog, and transition bog), and (iii) shrubland (i.e., coastal, pastures, and shrubland). Roads and trails were GPS-tracked in the field, or in Google Earth™, and edited using BaseCamp® (Garmin Ltd. 2017). All geoprocessing was done in QGIS (QGIS Development Team 2017) using the projection WGS 1984 zone 19S.

### Occupancy modelling

First, we explored the anthropogenic and environmental parameters (Table 1) following Zuur et al. (2009). If the parameters showed correlation coefficients  $> 0.71$ , we kept the variable with higher

biological importance, accuracy, and ease of interpretation (i.e., distance from landfill was excluded from models due to a high correlation with distance from town; number of game trails was excluded while keeping game trail density). Overdispersion was assessed via Variance Inflation Factors (VIF, Burnham and Anderson 2002), accepting values between  $1 \leq c \leq 4$ . Metric variables were transformed to z-scores as they were measured in different units. For further analyses, detection histories were classified into the following three groups: model set 1: free-ranging dogs (i.e., all dogs including unidentified dogs), model set 2: rural/village dogs, and model set 3: feral dogs. We used these three model sets as we could not include dog category as a covariate into the overall model set 1 due to the high number of unclassified dogs ( $n = 21$ ) in relation to the overall sample size ( $n = 62$ ).

We fitted single-species single-season occupancy models with a logistic link structure (Mackenzie et al. 2006) following a two-step approach (e.g., Soto and Palomares 2015; Fleschutz et al. 2016). Firstly, we selected which covariates (Table 1) best predicted detection probability ( $\hat{p}$ ) using Akaike's Information Criterion (AIC, Burnham and Anderson 2002) while occupancy was held constant. Secondly, these best covariates on  $\hat{p}$  were used to fit occupancy ( $\hat{\psi}$ ) models.

For modelling, we included interactions between the variables Habitat and Elevation as well as Distance from town and Distance from farm. All possible covariate combinations for detection probability and occupancy were analyzed through data dredging for model sets 1 and 2. For model set 3, presence sample size was too low and required starting values. Therefore, all possible combinations for detection probability modelling were done manually, while for occupancy modelling the dredge function was used without the covariate Rotation. To assess model fit, we added Rotation to the best three models afterwards. For model selection, we used AIC-ranking while models with  $\Delta AIC \leq 2$  were considered to have substantial statistical support (Burnham and Anderson 2002). We calculated the importance of each covariate by summing up AIC weights ( $\omega AIC$ ) for each test predictor across models. Estimated beta coefficients ( $\hat{\beta}$ ) for the confidence model set ( $\Delta AIC \leq 2$ ) were used to investigate the magnitude and directionality ( $\pm$ ) of the effect of the given covariate on  $\hat{\psi}$  or  $\hat{p}$ . Occupancy models and multi-model inference were



**Table 1** Summary of predictor variables for occupancy and detection probability for modelling occupancy of free-ranging dogs in southern Chile

Predictor variables	Abbreviation	Description
<i>Occupancy</i>		
Anthropogenic factors		
Distance from farm	d.farm	Euclidean distance (m) from nearest farm
Distance from landfill*	d.landfill	Euclidean distance (m) from center of the landfill
Distance from road/trail	d.road	Euclidean distance (m) from nearest road or trail
Distance from town	d.town	Euclidean distance (m) from center of Puerto Williams
Road/trail density	road.dens	Total road and trail length within 500 m buffer (ha)
Environmental factors		
Elevation	elevation	Altitude above sea level (m)
Habitat	habitat	Predominant habitat type within 500 m buffer
Detection probability		
Game trail density	trail.dens	Density of game trails within 10 m radius around camera-trap (steps/m <sup>2</sup> )
Julian date	date	Time specific variable (start date 01/01/2016)
Number of game trails*	n.trails	Number of animal trails within 10 m radius around camera-trap (number/m <sup>2</sup> )
Rotation	survey	Four consecutive rotations of 20 days each
Understory density	ustory.dens	Understory density visibility index (0-10)

\*Variables not included in occupancy modelling due to collinearity

run in R (R Core Team 2017) using packages Unmarked and MuMIn (Fiske and Chandler 2015; Bartón 2017).

## Results

A total of 3909 camera-trap days recorded 62 different dogs in 27 of the 200 sampled sites. Thus, naïve occupancy was 0.14 (i.e., the proportion of sites with detection). From 62 dog records, 26 individuals were free-ranging rural/village dogs (among which 19 were identified as owned dogs), 15 individuals were putative feral dogs, and 21 dogs remained without classification (33.9%; Fig. 2).

### Model set 1: free-ranging dogs

Detection probability of the first model set (all data) ranged between 0.12 and 0.33 (Table 2). The most important predictors with the highest importance were Julian date ( $\omega_i = 1.0$ ), Rotation ( $\omega_i = 1.0$ ), and Game trail density ( $\omega_i = 0.45$ ). Understory density was less important ( $\omega_i = 0.28$ ). Model selection revealed a decreasing detection towards the end of the survey, a

positive effect of the rotational camera-trap placement towards latter surveys, and a slightly-improved detection probability with denser game trails (Fig. 3) These variables (second-best ranked model) were used for subsequent occupancy modelling.

The most important covariates for occupancy (range: 0.19–1.0) were Habitat ( $\omega_i = 1.0$ ), Elevation ( $\omega_i = 1.0$ ), Distance from road/trail ( $\omega_i = 0.74$ ), Distance from town ( $\omega_i = 0.56$ ), Distance from farm ( $\omega_i = 0.56$ ), and the interaction between Habitat and Elevation ( $\omega_i = 0.53$ ) (Table 3), while the interaction between Distance from town and Distance from farm was less important ( $\omega_i = 0.37$ ). Dogs preferred peatbogs over forests and shrublands. Lower elevations were selected in forest or shrubland habitats, whereby elevation was less relevant in peatbogs. Free-ranging dogs preferred sites farther from roads and trails (preferences shown in Fig. 4). Finally, dogs were found more frequently in proximity to Puerto Williams or to farms, but seem to avoid sites far away from both farms and the town.



**Fig. 2** Free-ranging dogs in various categories photographed by camera-traps in varying habitat types in southern Chile. These include **a** village dog in peatbog habitat, **b** feral dog with

pup in forested habitat, **c** feral dog in shrubland, and **d** owned village dogs with collar in forested habitat

### Model set 2: rural/village dogs

Detection probability of rural/village dogs ranged between 0.02 and 0.48 (Table 2). In line with the modelling results of the complete data set, most important predictors were Rotation ( $\omega_i = 0.95$ ) and Julian date ( $\omega_i = 0.90$ ), but followed by Understory density ( $\omega_i = 0.50$ ) and Game trail density ( $\omega_i = 0.49$ ). In contrast to model set 1, rural/village dogs were better detected in sites with fewer game trails and a denser understory (Fig. 3). All these variables were selected for occupancy modelling (second best-ranked model).

The most important covariates for occupancy (estimated in 1.0) were Elevation ( $\omega_i = 1.0$ ), Habitat ( $\omega_i = 0.99$ ), Distance from farm ( $\omega_i = 0.97$ ), Distance from road/trail ( $\omega_i = 0.94$ ), and the interaction

between Habitat and Elevation ( $\omega_i = 0.60$ ; Table 3). Again, dogs preferred peatbogs over forests and shrublands and lower elevations in forests, as well as sites farther from roads and trails. Rural/village dog occupancy was also higher closer to Puerto Williams and farther from farms (Fig. 5).

### Model set 3: feral dogs

We anticipate that feral dog models are probably biased by overfitting due to the sparse data ( $n = 15$ ) and results can only be understood as a possible trend (Stockwell and Peterson 2008; Schuette et al. 2013). Detection probabilities were estimated in 1.0 (Table 2). As in model set 2, the most important predictors were Rotation ( $\omega_i = 1.0$ ), Julian date ( $\omega_i = 0.99$ ), and Game trail density ( $\omega_i = 0.75$ ).

**Table 2** Summary of model estimates ( $\Delta\text{AIC} \leq 2$ ) of occupancy ( $\hat{\psi}$ ) and detection probability ( $\hat{p}$ ) of free-ranging dogs (overall data), rural/village dogs, and feral dogs in southern Chile with occupancy held constant in all models (first-step modelling)

Model set	$k$	AIC	$\Delta\text{AIC}$	$\omega_i$	$\hat{\psi}$ (SE)	$\hat{p}$ (SE)
<i>1 Free-ranging dogs</i>						
$\psi(\cdot), p(\text{date} + \text{survey})$	6	421.4	0.00	0.39	0.23 (0.05)	0.24 (0.04)
$\psi(\cdot), p(\text{date} + \text{survey} + \text{trail.dens})$	7	421.7	0.34	0.33	0.24 (0.05)	0.33 (0.06)
$\psi(\cdot), p(\text{date} + \text{survey} + \text{ustory.dens})$	7	423.2	1.87	0.15	0.23 (0.05)	0.12 (0.03)
<i>2 Rural/village dogs</i>						
$\psi(\cdot), p(\text{date} + \text{survey})$	6	222.1	0.00	0.26	0.25 (0.09)	0.12 (0.05)
$\psi(\cdot), p(\text{date} + \text{survey} + \text{trail.dens} + \text{ustory.dens})$	8	222.4	0.27	0.23	0.24 (0.08)	0.08 (0.03)
$\psi(\cdot), p(\text{date} + \text{survey} + \text{ustory.dens})$	7	222.5	0.32	0.22	0.27 (0.09)	0.48 (0.25)
$\psi(\cdot), p(\text{date} + \text{survey} + \text{trail.dens})$	7	223.2	1.05	0.15	0.22 (0.08)	0.02 (0.02)
<i>3 Feral dogs</i>						
$\psi(\cdot), p(\text{date} + \text{survey} + \text{trail.dens})$	7	222.6	0.00	0.54	0.22 (0.07)	1.00 (0.28)
$\psi(\cdot), p(\text{date} + \text{survey} + \text{trail.dens} + \text{ustory.dens})$	8	224.6	1.96	0.20	0.22 (0.07)	1.00 (0.33)

$k$ : number of parameters per model;  $\Delta\text{AIC}$ : the difference from the lowest AIC value;  $\omega_i$ : model weight; SE: standard error

Understory density was less important ( $\omega_i = 0.29$ ). All three model sets showed decreasing detection towards the end of the survey and a positive effect of the rotational camera-trap placement towards latter surveys. However, higher game trail density and lower understory density positively influenced the detection of feral dogs (contrasting from rural/village dogs; Fig. 3). For subsequent occupancy models, we chose the four variables of the second-best ranked model (Rotation, Julian date, Game trail density, and Understory density).

Occupancy of feral dogs was low (0.01) and best predicted by Habitat ( $\omega_i = 1.0$ ), Distance from farm ( $\omega_i = 1.0$ ), Distance from town ( $\omega_i = 1.0$ ), the interaction between Distance from farm and Distance from town ( $\omega_i = 1.0$ ), Elevation ( $\omega_i = 1.0$ ), and the interaction between Habitat and Elevation ( $\omega_i = 0.98$ ; Table 3). Feral dogs also preferred peatbogs over forest and shrublands and lower elevations in forests. Feral dogs more likely occupied sites either very close to Puerto Williams or very far from town, but in the surroundings of farms (Fig. 5).

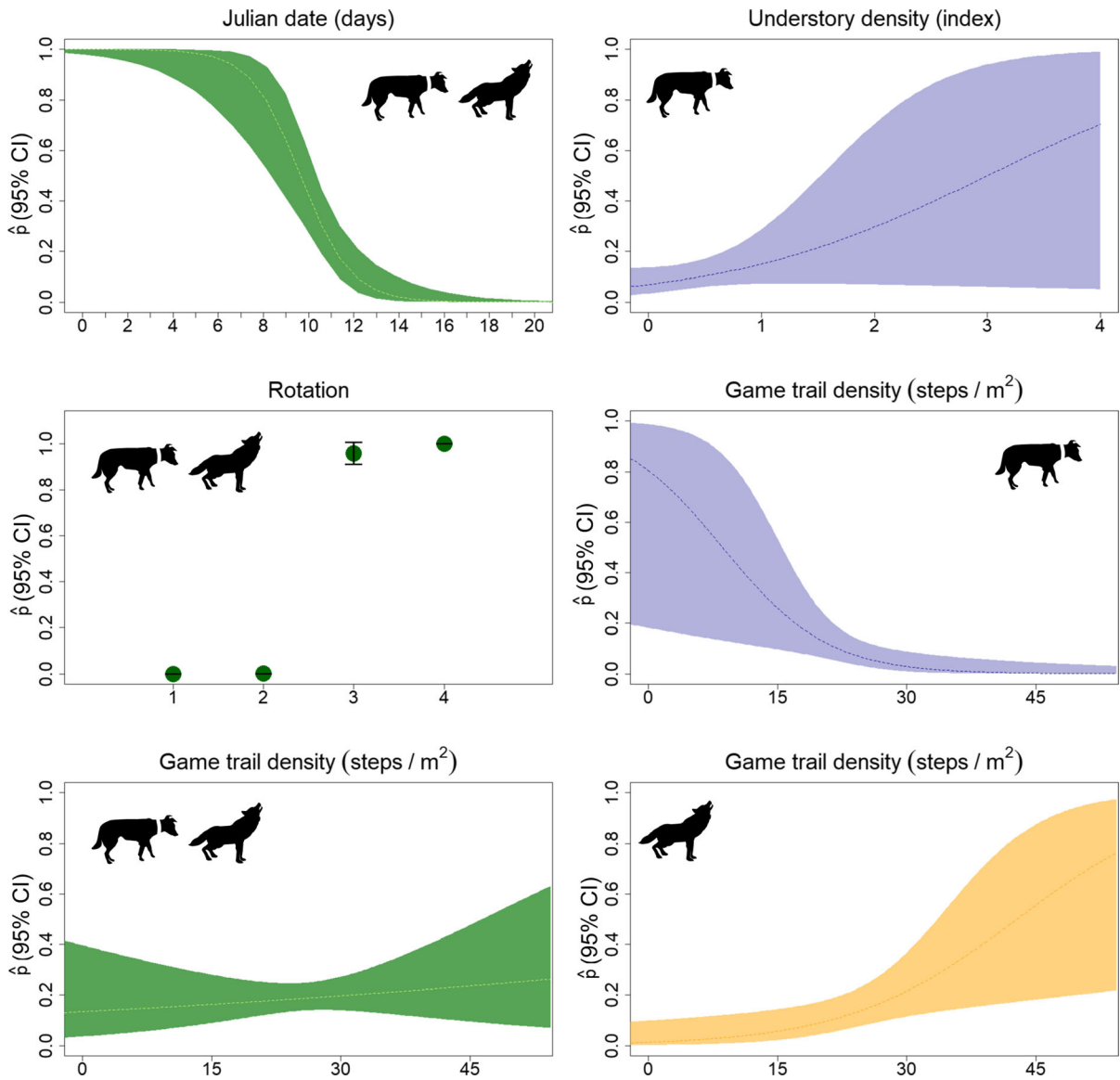
## Discussion

Our study contributes to our knowledge on space use of free-ranging dogs, stressing the sub-Antarctic environment. In contrast to our predictions, we found

that environmental predictors were more important in occupancy models than anthropogenic predictors. Their preference for human settlements and roads was less pronounced and inconsistent among dog categories with feral dogs occupying sites either close to town or close to farms. As predicted, both rural/village, and feral dogs chose peatbogs (*Sphagnum* spp.)—an open habitat—over forest and shrubland as well as lower elevations in forest/shrubland habitats.

These results confirm that free-ranging dogs show selective behavior in heterogeneous landscapes (as proposed by Sepúlveda et al. 2015), versus more generalist habitat-use patterns (e.g., Woodroffe and Donnelly 2011; Zapata-Ríos and Branch 2018). There is a lack of research on peatbog use by free-ranging dogs, but a relatively consistent finding is that free-ranging dogs choose open habitats over forest (e.g., Lacerda et al. 2009; Vanak and Gompper 2010). Shrublands, grasslands, savannas, pastures, and also peatbogs, are habitats facilitating movement, and may therefore preferably be used by dogs for forays, for example, for better orientation, or rapid mobilization. Peatbogs in particular may be important for dogs in our study system because these habitats contain many possible prey items such as cattle (prey items in dog diet, Schüttler et al. 2018; dogs feeding on carcasses, Atickem et al. 2010) or ground-nesting waterfowl (nest predation of upland geese, *Chloephaga picta*, by dogs, Schüttler et al. 2009), but also the American





**Fig. 3** Estimates of detection probability ( $\hat{p}$ ) with 95% confidence intervals (CIs) plotted against relevant detection variables for free-ranging dogs of model set 1 (green), rural/village dogs of model set 2 (purple), and feral dogs of model set 3 (orange)

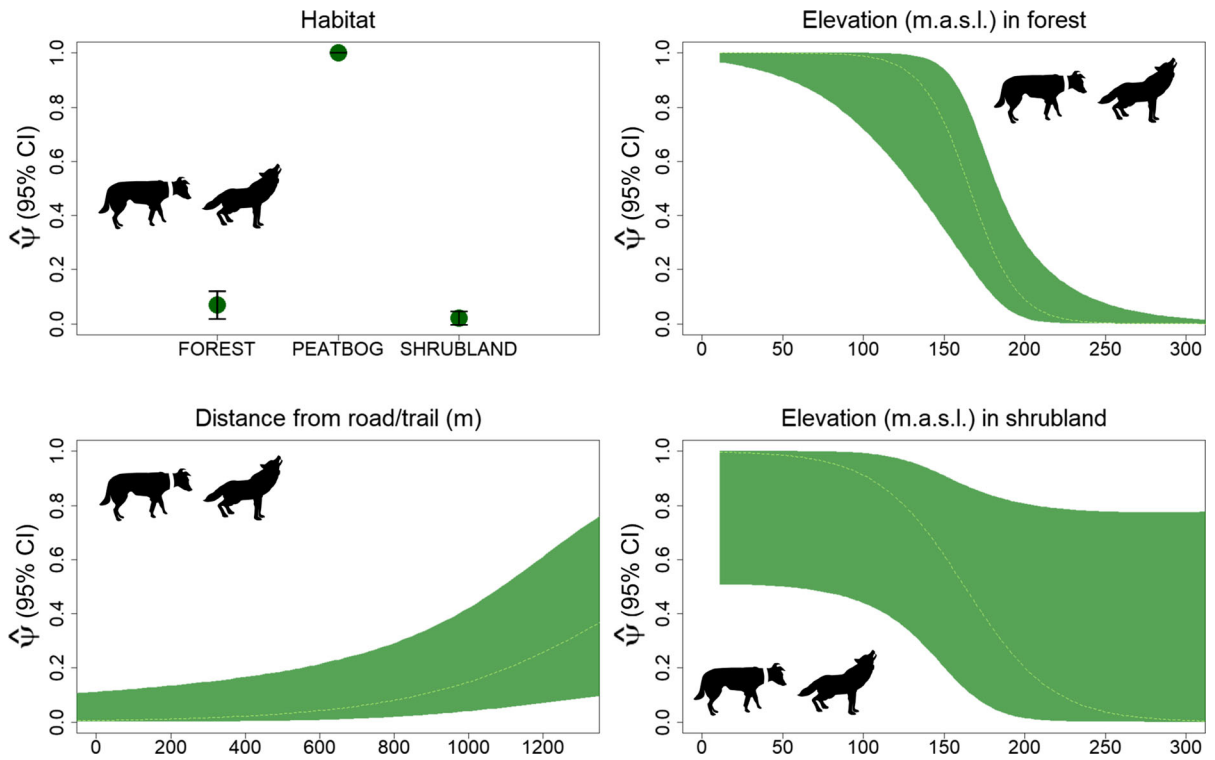
beaver (*Castor canadensis*), an invasive species present on the island since 1962 (Sielfeld and Venegas 1980), which can be found in peatlands due to the availability of water (Henn et al. 2016). In the present study, cattle were photographed by camera-traps on Navarino in 88% of 27 shrubland sites and in 81% of 10 peatbog sites, but only in 36% of 163 forest sites. Further, upland geese typically are associated with all types of inland water bodies (Couve et al. 2016).

Regarding anthropogenic variables, our results indicate that their effect on occupancy depended upon dog category. Please note again that the feral dog models, however, have to be treated with caution as they were probably overfitted. Several studies described proximity to human households as a predictor for the distribution of free-ranging rural or village dogs (Woodroffe and Donnelly 2011; Ruiz-Izagirre et al. 2015; Soto and Palomares 2015). In our study, the occupancy of rural/village dogs was also

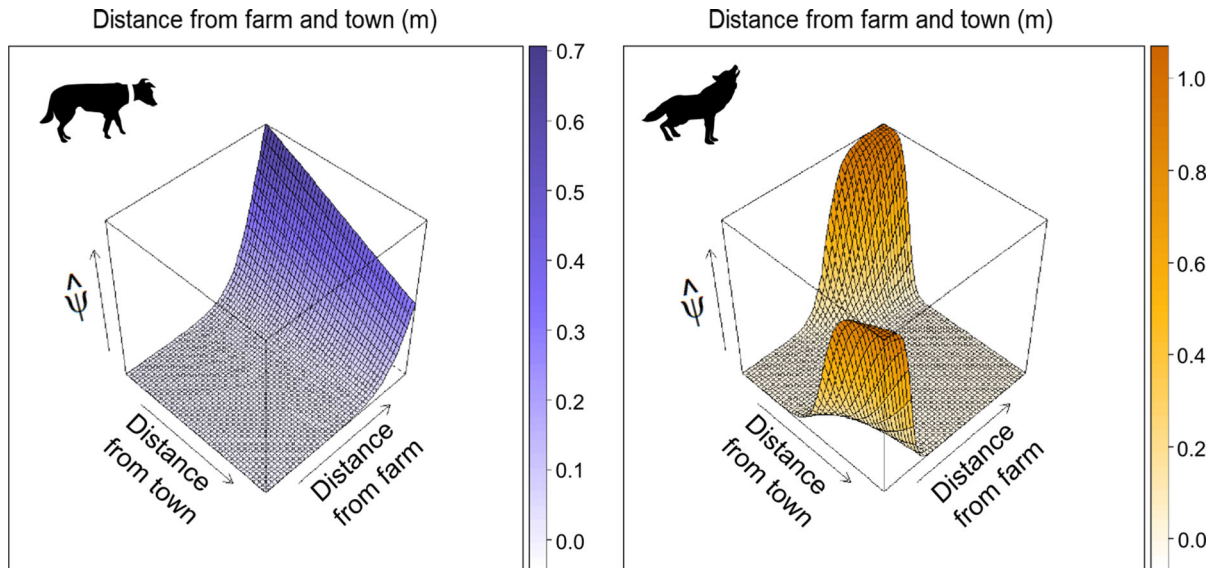
**Table 3** Summary of model estimates ( $\Delta AIC \leq 2$ ) of occupancy ( $\hat{\psi}$ ) and detection probability ( $\hat{p}$ ) of free-ranging dogs (overall data), rural/village dogs, and feral dogs in southern Chile with pre-selected detection probabilities taken from the first-step models

Model set	$k$	AIC	$\Delta AIC$	$\omega_i$	$\hat{\psi}$ (SE)	$\hat{p}$ (SE)
<i>1 Free-ranging dogs</i>						
$\psi(\text{d.farm} + \text{d.road} + \text{d.town} + \text{elevation} + \text{habitat} + \text{d.farm:d.town} + \text{elevation:habitat}), p(\text{date} + \text{survey} + \text{trail.dens})$	16	395.5	0.00	0.12	0.96 (0.03)	0.15 (0.08)
$\psi(\text{d.farm} + \text{d.road} + \text{d.town} + \text{elevation} + \text{habitat} + \text{d.farm:d.town}), p(\text{date} + \text{survey} + \text{trail.dens})$	14	396.0	0.57	0.09	0.86 (0.11)	0.99 (0.01)
$\psi(\text{d.road} + \text{elevation} + \text{habitat} + \text{elevation:habitat}), p(\text{date} + \text{survey} + \text{trail.dens})$	13	396.1	0.63	0.09	1.00 (0.01)	0.99 (0.02)
$\psi(\text{d.road} + \text{elevation} + \text{habitat}), p(\text{date} + \text{survey} + \text{trail.dens})$	11	396.7	1.27	0.06	0.37 (0.13)	1.00 (0.01)
$\psi(\text{d.farm} + \text{d.road} + \text{d.town} + \text{elevation} + \text{habitat} + \text{road.dens} + \text{d.farm:d.town} + \text{elevation:habitat}), p(\text{date} + \text{survey} + \text{trail.dens})$	17	396.9	1.41	0.06	0.19 (0.10)	0.98 (0.02)
$\psi(\text{elevation} + \text{habitat}), p(\text{date} + \text{survey} + \text{trail.dens})$	10	397.3	1.87	0.05	0.20 (0.08)	0.97 (0.03)
<i>2 Rural/village dogs</i>						
$\psi(+\text{d.farm} + \text{d.road} + \text{elevation} + \text{habitat} + \text{elevation:habitat}), p(\text{date} + \text{survey} + \text{trail.dens} + \text{ustory.dens})$	15	200.5	0.00	0.26	1.00 (0.01)	0.61 (0.23)
$\psi(\text{d.farm} + \text{d.road} + \text{elevation} + \text{habitat}), p(\text{date} + \text{survey} + \text{trail.dens} + \text{ustory.dens})$	13	200.9	0.48	0.21	1.00 (0.01)	0.89 (0.15)
$\psi(\text{d.farm} + \text{d.road} + \text{elevation} + \text{habitat} + \text{road.dens} + \text{elevation:habitat}), p(\text{date} + \text{survey} + \text{trail.dens} + \text{ustory.dens})$	16	202.4	1.89	0.10	1.00 (0.01)	0.65 (0.23)
$\psi(\text{d.farm} + \text{d.road} + \text{d.town} + \text{elevation} + \text{habitat} + \text{elevation:habitat}), p(\text{date} + \text{survey} + \text{trail.dens} + \text{ustory.dens})$	16	202.5	2.00	0.10	1.00 (0.01)	0.48 (0.22)
<i>3 Feral dogs</i>						
$\psi(\text{d.farm} + \text{d.town} + \text{elevation} + \text{habitat} + \text{d.farm:d.town} + \text{elevation:habitat}), p(\text{date} + \text{trail.dens} + \text{survey} + \text{ustory.dens})$	16	209.1	0.00	0.71	0.01 (0.01)	0.01 (0.55)
$\psi(\text{d.farm} + \text{d.town} + \text{elevation} + \text{habitat} + \text{road.dens} + \text{d.farm:d.town} + \text{elevation:habitat}), p(\text{date} + \text{trail.dens} + \text{survey} + \text{ustory.dens})$	17	211.1	1.99	0.26	0.01 (0.02)	0.02 (0.04)

$k$ : number of parameters per model;  $\Delta AIC$ : the difference from the lowest AIC value;  $\omega_i$ : model weight; SE: standard error



**Fig. 4** Estimates of site occupancy ( $\hat{\psi}$ ) with 95% confidence intervals (CIs) plotted against relevant occupancy variables for free-ranging dogs of model set 1



**Fig. 5** Estimates of site occupancy ( $\hat{\psi}$ ) plotted against the interaction between Distance from farm and Distance from town for rural/village dogs of model set 2 (purple) and feral dogs of model set 3 (orange)

higher close to Puerto Williams (20 dogs were village dogs, while only six dogs were rural), but negatively related to the distance from farms. Apparently, the majority of dog stayed relatively close to human stimuli such as food, shelter, or human bonds. However, 50% of rural/village dogs were photographed in packs of 2–4 individuals and distances reached up to 16.5 km from the town, indicating that some rural/village dogs probably exhibit group dynamics, hunting instinct (Wierzbowska et al. 2016), or interaction with feral dogs (see below). Neither roads nor trails were positively related to rural/village dogs, although other studies indicated movement along roads (Moreira-Arce et al. 2015; Sepúlveda et al. 2015; Warembourg et al. 2020). This may be associated with the overall traversable character of the landscape on Navarino Island, where the understory in old-growth forests is poorly developed (Pisano 1977), and the few fences do not represent a true barrier. In total, the 21 identified village dogs represented 16% of all free-ranging village dogs in Puerto Williams (estimated  $n = 21/132$ , Schüttler unpublished data). Hence, only a proportion of unrestricted dogs exhibited foraging behavior and only 52% (estimated  $n = 11/21$ , Schüttler unpublished data) dogs travelled  $> 1.5$  km from town. This is similar to findings from other studies (Ruiz-Izaguirre et al. 2015; Sepúlveda et al. 2015), and strengthens the pattern that only a proportion of owned or unowned village dogs move away from human dwellings. A further research need is an understanding of which factors (i.e., related to husbandry; for example, food provision, see Silva-Rodriguez and Sieving 2011, dog-owner bond, dog personality, etc.) characterize these dogs, as they come into contact with wildlife.

With regard to putative feral dogs, our study empirically supports earlier findings from questionnaire data (Schüttler et al. 2018) that propose the existence of a feral dog population on Navarino Island. We identified 14 dogs as absent from the photographic catalogue of rural and village dogs. Although the identification of animals from photos is error-prone (Yoshizaki et al. 2010; Foster and Harmsen 2012), we think our classification is reliable, as three independent reviewers followed a conservative approach (21 dogs remained unclassified). On one photographic sequence we also identified a feral dog with a lactating pup (Fig. 2), confirming locals' observations of pup sightings outside town (52 participants in Schüttler et al. 2018); this most

likely indicates reproduction in feral dogs. However, as feral dogs are highly social animals and generally live in packs (Daniels and Bekoff 1989), we should have registered more dogs in packs (only 13% of feral dogs in groups in the camera focus). According to our results, feral dogs had a higher probability of occupying sites either closer to farms and farther from the town (median distance from farm: 2 km, range: 0.2–5.5 km), or closer to the town and farther from farms (median distance from town: 13.3 km, range: 0.7–19.4 km) (Fig. 5). As the parameter Distance from town was strongly correlated with Distance from landfill, it is probable that some dogs searched for food there (e.g., Boitani et al. 2017; Sarkar et al. 2019), and/or in the surrounding of farms. Feral dog populations are hardly self-sustaining, as they have rapid population turnover driven by high juvenile mortality (Butler and Bingham 2000). Therefore, they apparently depend upon recruits to maintain their population sizes (Daniels and Bekoff 1989; Boitani et al. 2017). In our study system, in seven occasions, rural/village and feral dogs shared sites at different times, both near (700 m), and far from (14.8 km) town. Thus, the over-lapping home ranges of both dog categories point to an interaction, perhaps cooperative hunting, or mating for recruitment. In summary, our results indicate that feral dogs on Navarino Island are probably not truly feral (i.e., independent of human resources, following the stricter definition of Vanak and Gompper 2009). More research is needed to better understand the ecology of the feral dog population on Navarino Island through, for example, GPS monitoring (e.g., Claridge et al. 2009), animal-borne cameras (e.g., Gerencsér et al. 2013) or Unmanned Aerial Vehicles (Warembourg et al. 2020).

Free-ranging dogs penetrated pristine sub-Antarctic habitats within the Cape Horn Biosphere Reserve reaching far beyond the anthropogenic edge of human settlements. As those free-ranging dogs are top predators in an ecosystem that lacks native, terrestrial predators, our findings have important conservation implications. Although only a proportion of owned, unrestricted dogs ( $n = 19/39$ , Schüttler et al. 2018) were registered in our camera-traps, we recommend working with local authorities on regulations and education for responsible pet-ownership (e.g., Soto and Palomares 2015); this also should reduce the number of abandoned, unowned village dogs, and recruits for feral dogs. Such a campaign should be accompanied by raising awareness of the negative



impacts of unconfined dogs on wildlife, which commonly are hardly recognized (Schüttler et al. 2018; Villatoro et al. 2018). Feral dogs, on the other hand, which likely rely heavily on wild prey, might pose a threat to the southernmost population of guanacos, which is considered in danger of local extinction (González 2010), and avian prey such as upland geese or flightless steamer ducks (*Tachyeres pteneres*, Schüttler et al. 2009). Therefore, those dogs should be removed in the future (how is a legal matter yet to be defined), while our results indicate that peatbogs could be target habitats. Here, it would be ideal to follow a community-level management approach (see Crego et al. 2016) that considers the invasive species community as a whole to avoid possible meso-predator (Courchamp et al. 1999) or herbivore release effects (Barnett 1986). As the management of invasive species is an increasingly relevant and conflictive issue in society (Estévez et al. 2015; Crowley et al. 2017), each management action should consider ethical consensus principles (e.g., Dubois et al. 2017), in particular when domestic species are involved.

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#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Research involving animals** The present research involved free-ranging dog presence data obtained through camera-traps, and only included the monitoring of animals in an indirect way, without direct contact.

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