Spatial and temporal plasticity in free-ranging dogs in sub-Antarctic Chile

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ABSTRACT

Free-ranging owned dogs are a conservation concern worldwide, but knowledge on their movement ecology is only recently increasing. To examine unsupervised dog movements into wilderness, we attached Global Positioning System devices to 33 village and four rural dogs on a sub-Antarctic island in Chile during the four seasons of a year (n = 86115 locations). This corresponded to a quarter of the local free-ranging dog population based on a photographic mark-recapture survey. The longest maximum distance to the owner's home was 20.4 km. The median home range size ranged between 15.8 (spring) and 24.4 ha (summer), but with great individual variation (1.6 ha - 148.8 km^2). Nine individuals had home ranges > 100 ha in at least one seasonal monitoring; seven individuals performed excursions spending 1–6 nights in pristine nature, and two individuals accompanied tourists on trekking trips lasting 3–6 days. Remarkably, village dogs were quite active at night (40.7% of the locations). Top-ranked habitats in the compositional analysis of habitat use of village dogs were forest and infrastructure. However, coasts were also important at second order and peatbog at third order habitat selection. Our study revealed a high temporal and spatial plasticity of dog movement in sub-Antarctic ecosystems, likely interacting with wildlife. We conclude that future research should address predictors of problematic animals, which have been treated as "outliers" in many studies. In Chile, the control of legislation and education beyond the mere owner should be improved wherever dogs occur near sensitive wilderness areas.

1. Introduction

Estimated in almost a billion individuals, domestic dogs (*Canis familiaris*) are the most abundant carnivore species worldwide (Gompper, 2014). In other words, there is one dog for eight people on earth - under different outdoor conditions. Leashed dogs have limited access to nature, free-ranging owned or abandoned dogs have partial or full access, and feral dogs occur in nature without human help (Boitani et al., 2017). All dogs, but particularly those without restriction, can cause conflicts with wildlife through predation, competition, disease transmission, and hybridization (reviewed in Doherty et al., 2016; Hughes and Macdonald, 2013; Twardek et al., 2017; Young et al., 2011, who also reviewed the positive effects of dogs in conservation). More subtle impacts are disturbance of wildlife by dogs resulting in higher vigilance levels (Vanak et al., 2009), shift in activity patterns (Zapata-Ríos and Branch, 2016), or reduced foraging times (Suraci et al., 2016). Most dogs are subsidized predators (Gompper, 2014), and as such they reach

remarkably high population densities (e.g., 2.5–10.3 rural dogs/km^2 in Tanzania, Lembo et al., 2008), outnumbering native carnivores (e.g., 3–85 times more abundant in Brazil, Paschoal et al., 2016). The high densities of dogs, together with their often-unrestricted mobility, explain why domestic dogs are among the group of invasive mammalian predators with the most pervasive impacts on vertebrates (188 spp., Doherty et al., 2017).

In the context of conservation, movement ecology is an emerging discipline holding a promise for enhancing wildlife management planning (Allen and Singh, 2016). A better understanding of an animal's space use can inform about the causes and patterns of movement and how these are linked to environmental change (conceptual framework in Nathan et al., 2008). In fact, if movement data for endangered mobile species is available, it is generally reflected in species status assessments (Fraser et al., 2018). The rapid recent technological progress in accuracy and resolution of tracking data allows a quasi-continuous record of how, where, and why animals move (Kays et al., 2015). Along with the

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development of rigorous analytical methods to maximize the extraction of information contained in autocorrelated data (e.g., Fleming et al., 2015), the range of scientific questions answered by tracking data is steadily growing. In the field of biological invasions, tackling the causes, patterns, and consequences of movement of invasive species is central to adequately design control actions (Nathan et al., 2008) and reveal the links to the dynamics of human movement and affiliated pets (Jeltsch et al., 2013).

A better understanding of the movements of free-ranging dogs for conservation is particularly relevant in parts of the world where these roam freely, which is true in many countries in Africa, Asia, and South America (Reece, 2005; Warembourg et al., 2021). Fortunately, during the last decade dog movements have been increasingly tracked, for example in Chad, to determine whether hunting activities of owners influenced the space use of dogs (Wilson-Aggarwal et al., 2021); in China, to evaluate exposure to canine distemper virus in wild pandas (Jin et al., 2017); and in Peru, to assess movement patterns across urban landscapes for rabies control (Raynor et al., 2020). One general pattern is that most dogs stay close to their owner's home: Half of the fixes were recorded < 100 m from home in Mexico (Ruiz-Izaguirre et al., 2015) and 80% within 200 m from home in Chile (Sepúlveda et al., 2015). However, maximum distances of individual dogs reached as far as 10.4 km in Chile (Pérez et al., 2018) and even 30 km in Australia (Meek, 1999). Similarly, home range estimations (95% kernel isopleths) varied among the tracked dogs of each study, ranging for example between 1–97 ha in Kenya (Muinde et al., 2021) and 31–1161 ha in Australia (van Bommel and Johnson, 2014). Also, the dogs' habitat use differed from study to study: foraging habitat along rivers (Meek, 1999), at beaches (Ruiz-Izaguirre et al., 2015), in agroforests (Dos Santos et al., 2018), in pasture habitats (Sepúlveda et al., 2015), and in crop fields (Parsons et al., 2016). Night forays in free-ranging dogs (van Bommel and Johnson, 2014; Ruiz-Izaguirre et al., 2015), but also diurnal activity patterns (Sepúlveda et al., 2015) have been described. Finally, seasonal space use has been studied to a lesser degree (e.g., van Bommel and Johnson, 2014; Wilson-Aggarwal et al., 2021).

In Chile, there is one dog for every four people (Gompper, 2014), while 31–50% of town dogs (Acosta-Jamett et al., 2010; Schüttler et al., 2018) and 67–92% of rural dogs are allowed to roam free (Acosta-Jamett et al., 2010; Sepúlveda et al., 2014; Silva-Rodríguez and Sieving, 2012). During the past years, studies on the Chilean dog-wildlife-society problem have increased. Researchers have addressed the impacts of free-ranging dogs on livestock (Montecino-Latorre and San Martín, 2018), endangered wildlife (Beltrami et al., 2021; Silva-Rodríguez and Sieving, 2012), and human-associated factors of dog movement (Saavedra-Aracena et al., 2021; Villatoro et al., 2016). In parallel, the Chilean government has increased its awareness of the dog problem. In 2017, a new Chilean law (Nr. 21.020) aimed at regulating responsible pet ownership, instructing the dog's confinement to the owner's property; meanwhile, the situation of feral dogs remains unsolved. An attempt to include feral dogs into the Hunting Law in 2015 failed two months later (Decrees Nr. 65 and 6), among other aspects, due to the definition of feral dogs. They were defined as dogs in packs at a distance > 400 m of a settlement or isolated rural home, irrespective of the possible presence of roaming owned dogs.

Our aim was to contribute knowledge on the movement ecology of free-ranging dogs, from a little-known part of the world perspective. We performed this study in the context of conservation, examining dog foraging movements in a sensitive wilderness setting to inform management policies. Specifically, we focused on assessing dog (1) ranging distances to the owner's home, (2) home range estimation during the four seasons of the year, (3) diel activity patterns, and (4) habitat use. This study provides a first insight into how dogs move through sub-Antarctic wilderness. The discussion of the results shows the global relevance of dog confinement wherever dogs roam free next to wildlife and highlights the need to strengthen research on the causes of individual variability.

2. Methods

2.1. Ethical approval

We obtained signed informed consent from each participant by reading together the aims and procedure of the study, anonymous data storage, access to the results, lack of risks, and benefits from participating (i.e., a 3-kg bag of dog food was provided to each dog owner). The Scientific Ethical Committee of the University of Magallanes, Chile, certified ethical approval of the instrument (Certificate 03/30/2016).

2.2. Study area

Our study was carried out in southernmost Chile (55°S), on Navarino Island (~2500 km², Fig. 1). This region belongs to the Magellanic sub-Antarctic ecoregion (Rozzi et al., 2012), classified as an archipelago with low human impact (Jacobson et al., 2019), which is covered by southern beech forests (*Nothofagus* spp.), peatbogs (*Sphagnum* spp.), Andean habitats above the tree line, and shrublands. The climate is cool and under oceanic influence (-2 °C to +10 °C variation over the year); water bodies are largely ice-bound in the winter (Tuhkanen et al., 1990). The 2200 inhabitants live concentrated in the town of Puerto Williams. Their income is based on artisanal fishery, tourism, and small-scale livestock farming. Terrestrial infrastructure is limited to the northern coast of Navarino, some logging trails, and trekking routes, whereas most of the island is pristine sub-Antarctic wilderness. However, new maritime infrastructure, new roads, and land parceling and settling will likely increase the access of people and free-ranging dogs to wilderness in the near future.

Following a survey based on questionnaires, around one third of owned dogs roam free on Navarino Island (31%, Schüttler et al., 2018) and camera-trap data points to the existence of feral dogs (Contardo et al., 2020). Free-ranging dogs represent a major conservation concern, because (1) no native terrestrial predators exist and hence, dogs take the role as a new guild of apex predators (along with domestic cats *Felis catus* and American mink *Neovison vison* as medium-sized introduced predators, Schüttler et al., 2019), and (2) they might severely impact the southernmost population of guanacos (*Lama guanicoe*), considered at local extinction risk by González (2010). Silva Rochefort and Root-Bernstein (2021) propose that native camelids in Chile are particularly vulnerable to predation by dogs as they may have evolved in the absence of pack-hunting cursorial predators.

2.3. Dog censuses

For one year, we conducted seasonal censuses of free-ranging dogs in the streets of Puerto Williams (May 2015, September 2015, November 2015, and March 2016). During each census, we walked through all the streets of the village taking photos of all dogs without restriction of movement, including dogs resting in courtyards with open access to a street. This was repeated at different times during the four days of each census. As some dogs had similar physical aspects, to assure the correct identification of individuals, three independent reviewers revised the photographic catalog and differences were discussed until reaching consensus.

2.4. Dog-owner recruitment

We recruited 35 dog owners in Puerto Williams by revising photos of the photographic catalog of the dog census together with the Municipality's veterinarian and selected those free-ranging dogs from which roaming behavior was believed; limited to one adult (≥ 1 year) dog per owner. We then approached the dog owners and asked them whether they would participate in our study. In the rural area, we asked all six farmers located on the northern coast of Navarino Island who owned dogs to participate in the study. Only two dog owners in Puerto Williams
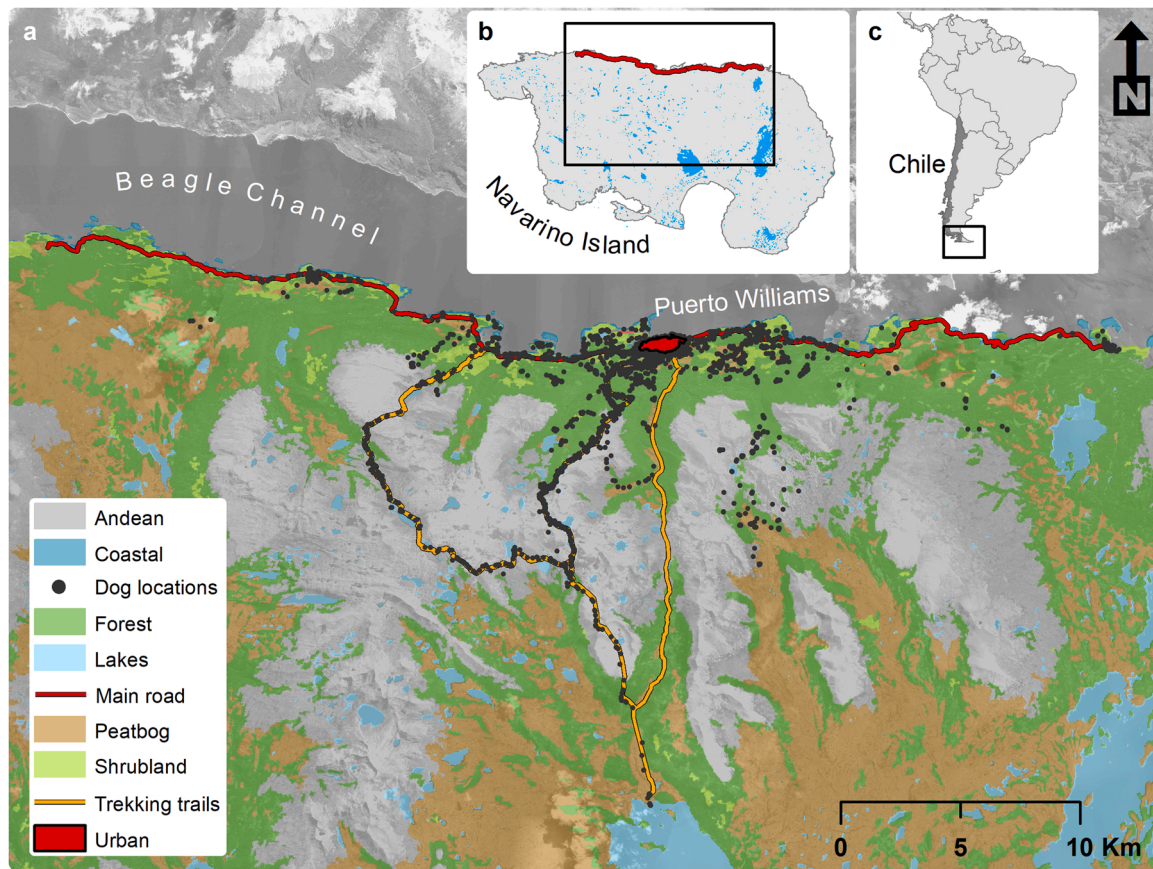
Fig. 1. Study area showing the principal ecosystems and tracking data (n = 86115) of 37 free-ranging dogs with unsupervised movements (a) on Navarino Island (b) in southern Chile (c).

refused to participate in the study, whereas all rural households participated. During the one-year-long study in 2016/2017, four owners (2 urban/2 rural) refused to participate in the second/third seasonal monitoring (reasons given were risks of injury due to the collar). Upon recruitment and in a face-to-face approach, we asked owners to answer a questionnaire containing 22 questions on the dog's age, sex, husbandry, and hunting behavior, as well as the dog-owner relationship and basic personal data of the owner. To be able to distinguish between forays of unaccompanied dogs' excursions and those together with the owner, the owners were given a 3-weeks calendar in which they were asked to make notes on the dates and places outside the village they visited together with their monitored dog. Finally, the town veterinarian performed an in-situ health check (general inspection and 9-point body condition score following Laflamme, 1997). The data of the summer surveys of 12 of these dogs have been used in Saavedra-Aracena et al. (2021) to address the influence of the dog-owner bond on dog movement.

2.5. GPS-tracking

We equipped a total of 41 dogs (35 village dogs and 6 rural dogs) with commercial Global Positioning System (GPS) devices (Igot-U GT-600, Mobile Action, Taiwan, 37 g) in sealed leather bags strapped to adjustable animal collars around the neck. The weight of the GPS device was always below 0.5% of the animal's weight and all devices were retained after completing the seasonal surveys to recharge the batteries. Movement data was collected at 10-min intervals, only when an animal was moving, during a 3-week period in the four seasons of the year (between February 2016 and March 2017). With four dogs we could not continue to work (two lost their collars during the first survey, one dog got lost and one dog changed owner). In nine occasions, dogs lost their GPS collars (but in five occasions these were found and returned by local

people), in only one occasion the data could not be retrieved from the GPS unit. We repeated the monitoring in seven occasions, either when the GPS got lost or when only some days were recorded. In summary, we were able to collect the complete seasonal data for 26 village dogs and for two rural dogs. Once the 3-week period was completed, the GPS device from each dog was retrieved and the locations were checked together with the owner on a digital map on a computer screen, unless the owner declined to do so. We asked each owner whether during the monitoring period the dog had accompanied trips (by car or walks together with the owner) outside the village. Any car trip (depicted as a route) was cross-checked with the owner and excluded from the analysis. That way, we filtered the data to use only presumably unaccompanied locations of the dogs.

2.6. Data accuracy

To estimate the accuracy of the GPS locations, we performed static and mobile tests (Cargnelutti et al., 2006; Camp et al., 2016). We compared the fixes of the Igot-U GPS devices with the position described by a portable highly sensitive GPS receiver (Garmin GPSmap® 60CSx). For the static tests, we placed a GPS tag ~50 cm above ground to simulate the height of a dog and recorded the fixes every 10 min for 24 h. A total of 9 static tests were performed inside houses, in the forest, and in peatbog habitats. For the mobile tests, we performed three 1-hour walks with a leashed dog carrying a GPS device maintaining a distance < 5 m from the GPS receiver carried on the side. We then calculated the errors by computing the differences between the readings on the GPS device and receiver. The accuracy of the static tests was greatest for peatbog (average error 13.2 m, range 1–117.5 m, n = 447), followed by forest (15.7, 0.7–85.3, n = 414), and least inside houses (29.5, 0.5–1055.2, n = 317), whereas the mobile tests had an average error of

6.2 m (0.2–27.3, n = 15). We found that fixes with a difference > 50 m between the GPS device and receiver (3.9%, n = 1208) presented abnormal elevation parameters recorded by the GPS device. We finally excluded those fixes with abnormal elevation parameters and with inconsistent chronological history. Of 93092 fixes we discarded 2907 (3.1% of the data) due to erroneous recording and 4070 locations which were either replicates or from accompanied movements (final n = 86115).

2.7. Data analysis

The population size of free-ranging dogs in Puerto Williams was estimated with closed capture models in program MARK (White and Burnham, 1999). We used three model types, constant capture and recapture probability, time varying, and behavioral response to capture. Best models were those with lowest values of the Akaike Information Criterion adjusted for small sample size (AICc, Burnham and Anderson, 2002).

We used the software @trip PC (Mobile Action, Taiwan) to download the locations and then analyzed the data in the R Environment (R Core Team, 2021). We calculated the linear distances from each dog's location to its home and used descriptive statistics to describe them. Home ranges were calculated through continuous time movement modeling (Calabrese et al., 2016) using the *ctmm* package in program R. When we visually evidenced range residence in the variograms of each dog's seasonal monitoring, we fitted isotropic and anisotropic versions of Ornstein-Uhlenbeck (OU) and OU Foraging (OUF) processes, which assume autocorrelation in the data. We also fitted models under the independent identically distributed (IID) data assumption. After AICc model selection, the best model was used to estimate home ranges via autocorrelated kernel density estimation (95% AKDE, Fleming et al., 2015), whereas the IID model was used to provide the traditional 95% KDE home range estimation. To adjust for over-estimation, for three dogs with multiple overnight excursions we used the low value of the 95% confidence intervals of the 95% AKDE estimate. The aquatic habitat of the Beagle Channel was treated as a physical barrier. Therefore, we created a buffer of 243 m from the coastline, beyond which we deleted the home range area (calculated by taking the farthest location of a swimming dog, 236.8 m, and adding the GPS error of 6.2 m). We applied a Friedman test to compare home range sizes between seasons and subsequently paired Wilcoxon signed rank tests with Bonferroni corrections. To assign activity during day versus nighttime we calculated daily sunlight times using R-package *suncalc*. We used two-sample tests for equality of proportions with Bonferroni corrections to compare whether the proportions of locations at day or at night were significantly different in seven types of habitats (Andean, coast, forest, infrastructure, lakes, peatbog, and shrubland).

Finally, we used compositional analysis to determine habitat use (Aebischer et al., 1993). This analysis compares proportional habitat use versus availability through log-ratio transformation and evaluates the significance of nonrandom habitat use by using randomization tests (at p < 0.05). Based on the matrix of the mean differences between the used and available log-ratios, habitats are then ranked from most to least preferred (the times a habitat is used more than another in the ranking matrix), but ranks can be interchangeable when habitats are not significantly more used. Habitat selection was considered at two levels: (i) home range use within the study area or second order selection and (ii) habitat use within the home range or third order selection (Johnson, 1980). For this analysis, we defined the study area as the area covered by the 95% AKDE estimates of all 33 village dogs adjusted for over-estimation as described above. The home ranges were the individual AKDE estimates and the single locations within the home ranges were used for third order selection. We determined second order habitat selection for all village dogs for each season, while we used a subset of nine village dogs with > 5% of their locations outside the urban area for third order selection, again for each season. Rural dogs were only four individuals, while for

compositional analysis a minimum of six individuals are needed (Aebischer et al., 1993); therefore, as a reference, we only provide percentages of locations per habitat pooled across all seasons. Following the recommendations of Aebischer et al. (1993) in R-package *adehabitatHS* zero values in the available habitat matrix were replaced by 0.01 and statistical significance in these matrices were determined by weighted mean lambdas instead of usual lambdas. We performed this analysis for five habitat types excluding all locations within the urban area (n = 75422): coastal, forest, infrastructure, peatbogs, and pastures and shrubland, hereafter shrubland (n = 3990). Coastal included coastal habitat and the buffer of 243 m from the coastline, and infrastructure referred to roads, trails, and rural infrastructure (i.e., landfill, industrial areas, rural houses). Poorly used Andean habitats (n = 656 locations of 4 dogs) and lakes (n = 101 locations of 5 dogs) were excluded from the analysis to reduce the number of null cells in the matrices (see Aebischer et al., 1993). Due to this fact, the final sample sizes of the eight analyses (4 seasons for 2nd and 3rd order analyses each) vary. We used ArcMap 10.4 (ESRI, Redlands, USA) and the projection WGS 84/UTM zone 19S for geoprocessing and mapping. The land cover classification (30 m resolution, year 2016) was updated by visual inspection in Google Earth TM (Version 7.1.2.2600). For the background of our figures, we downloaded satellite images from Bing Maps (3 m resolution) available through SAS Planet (Version 171130).

3. Results

Dog owners had a mean age of 43.5 years (range 22–70), 56.8% were female. The highest education levels were 35.2% technical or university formation, 32.4% high school, and 32.4% less than high school. The mean number of dogs per household was 2.5 (range 1–7).

3.1. Dog background

Most of the 37 participating dogs (summary of characteristics in Table 1) received basic standard care; 70.3% were sterilized and 89.2% received parasite treatment. Only 21.6% of the dogs were fed mainly with leftovers. However, when asking the owners what the dog had eaten the day before, the fraction of leftovers was higher (37.8%). Over half of the dogs (54.1%) had ideal weight (body condition scores BCI 4 and 5, Laflamme, 1997), and only 16.2% was underweight (BCI 1–3). The questionnaires also gave insights into dog-animal interactions: 24.3% of the dogs brought prey home when returning from roaming (mainly birds and body parts of livestock, both categories 36.4% each) and 86.5% were observed harassing other animals, mostly livestock (48.1%), followed by birds (22.2%), and other dogs (20.4%).

Table 1
Characteristics of 37 free-ranging GPS-tracked dogs in southern Chile. The data is based on dog owner questionnaires and a health check by a veterinarian.

| Parameter	Value
Number of village/rural dogs	33/4
Born on Navarino Island (%)	89.2
Dogs owned for company (% village dogs)	87.9
Males/females (%)	54.1/45.9
Mean age of dogs in years (SD, range)	4.5 ± 2.4 (1.3–10)
Uncastrated/unsterilized dogs (%)	29.7
Dogs vaccinated against rabies (%)	45.9
Dogs with parasite treatment (%)	89.2
Dogs receiving pet food (pellet) and/or meat (%)	48.7
Dogs receiving leftovers (%)	21.6
Dogs receiving a mix of the above (%)	29.7
Dogs fed in more than one household (%)	56.8
Mean body condition score of dogs (SD, range)	5 ± 1.7 (1–9)
Dogs free-ranging during day and night (%)	75.7
Dogs free-ranging during day only (%)	24.3
Dogs having brought home prey (%)	24.3
Dogs observed harassing animals (%)	86.5

3.2. Dog census

The mean number of free-ranging dogs in the village estimated through capture-recapture models was 131.8 ± 2 individuals (95% Confidence Interval 129.8–139) for summer, 140.7 ± 6.1 individuals (133.5–159.6) for autumn, 131 ± 3 individuals (127.4–140.1) for winter, and 126.2 ± 1.4 individuals (125.2–132.4) for spring. For spring the best model accounted for temporal variation in the capture and recapture probabilities, for autumn for differences in the encounter probability, and for summer and winter the best models had no behavioral or temporal variations.

3.3. Movement ecology

In total, we collected tracking data of 37 free-ranging dogs (33

village dogs, 4 rural dogs) with unsupervised movements (n = 86115) with a mean of 647.5 ± 290.6 locations (median = 611, range = 102–1495) during 133 seasonal 3-week monitoring sessions with a mean duration of 17.9 ± 5.6 days (19, 4–34). The devices failed to collect data during 3.4 ± 3.8 days (2, 0–17) over the sessions. Considering the mean number of individuals counted over the year, we monitored 24.9% of the free-ranging village dog population.

The mean distance to the dogs′ homes was 601.8 ± 2074.4 m (median = 41.7 m, range = 0–19.1 km, n = 23025) during summer, 268 ± 971.7 m (40 m, 0–20.4 km, n = 21289) during autumn, 192.5 ± 688.5 m (36.2 m, 0–11.2 km, n = 20154) during winter, and 259.4 ± 891.7 m (32.7 m, 0–11.2 km, n = 21647) during spring. Maximum distances to the owners′ homes were > 500 m for all dogs, but one, during at least one of the four seasons, 32 dogs (86.5%) had maximum distances > 1 km, eight dogs (21.6%) > 5 km, and five dogs (13.5%) > 10 km. The longest distance
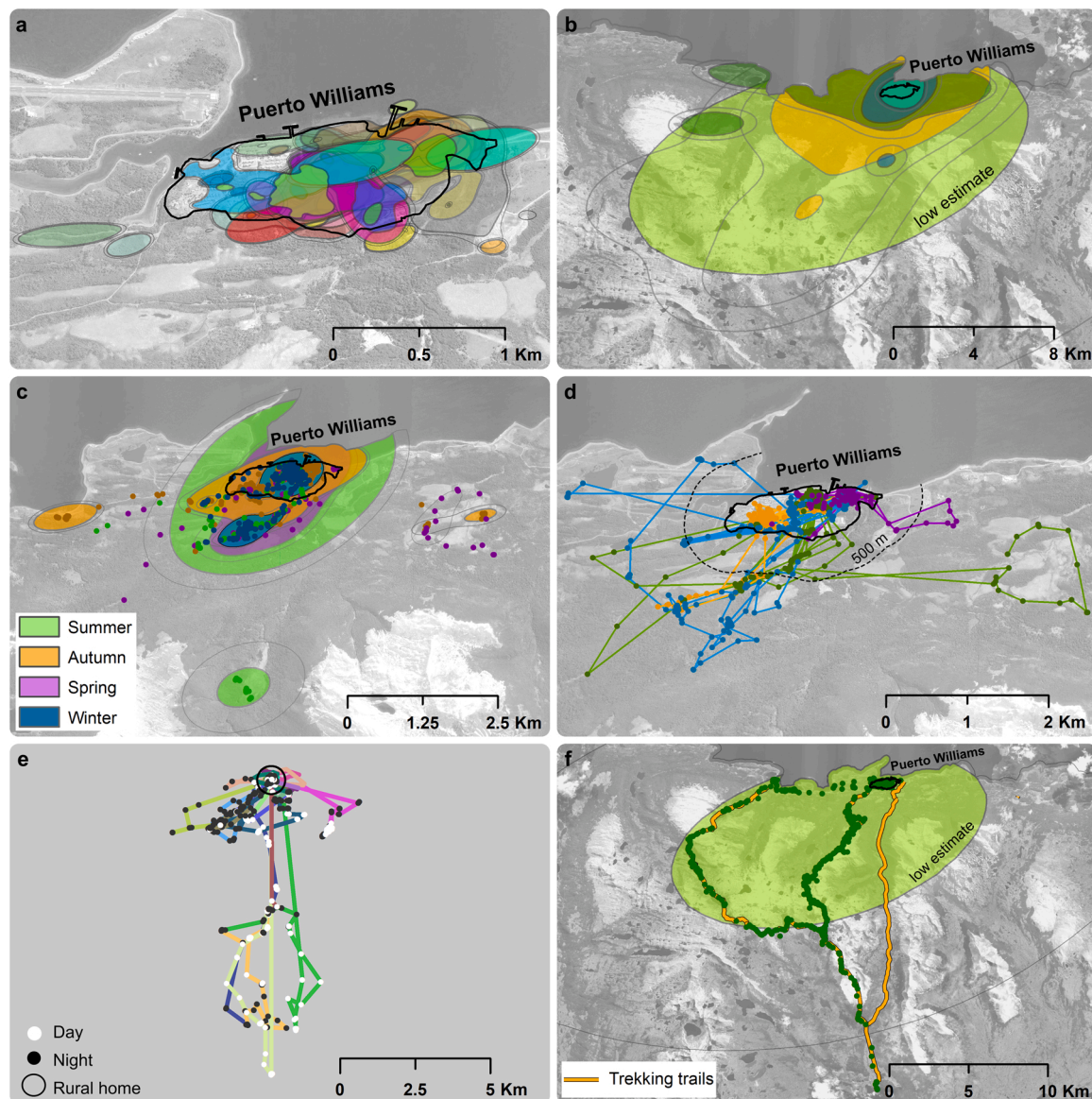
Fig. 2. Tracking data (points), 95% AKDE home ranges (shapes) and daily movements (lines) of free-ranging dogs (unsupervised movements) on Navarino Island in southern Chile. (a) Tracking data of 25 village dogs with home ranges ≤ 100 ha during summer; (b) Relocation data of five village dogs (P1, P2, P3, P4, P5) with home ranges > 100 ha during summer; (c) Seasonal relocation data and home ranges for one village dog (P1); (d) Daily excursions of four village dogs (P1, P2, P6, P7, in different colors) > 500 m from the urban area during one season each; (e) Overnight excursions (colors representing different dates) of a rural dog (P8) during autumn including day and nighttime locations (spatial data anonymized to avoid that rural owner can be identified); (f) Village dog (P4) following a trekking trail during summer. Gray lines indicate low and high values of the 95% confidence intervals of the 95% AKDE estimate (one individual is represented with its low value to adjust for over-estimation).

(20.4 km) was traveled by a village dog during the day to an area without infrastructure nor trails and predominated by peatbogs.

Mean home range size of dogs during summer was 710.4 ± 2706.4 ha (median = 21, range = 1.6–14879.1, n = 32), during autumn 292.1 ± 1065.5 ha (24.4, 5.1–5922.4, n = 36), during winter 174.5 ± 617.4 ha (16.2, 2–3378.7, n = 34), and during spring 220.8 ± 882.8 ha (15.8, 1.9–4845.8, n = 30). Nine different dogs (8 village, 1 rural) had home ranges > 100 ha in at least one seasonal monitoring (2299.1 ± 3521.5, 690, 116.5–14879.1, n = 19) and four individuals repeatedly (during 3 or 4 seasonal monitoring sessions). When checking whether home ranges were different among seasons, the overall comparison was significant ($X^2(3) = 13$, p = 0.005, n = 28), but with a small effect size (Kendall's W = 0.16, on a scale from 0 to 1 = large effect). Significantly larger home ranges only occurred in autumn versus winter (paired Wilcoxon signed rank test, V = 350, p = 0.003, n = 28), not among other seasons. Finally, AKDE home range estimates were 0.8–2 times bigger than the conventional KDE estimates (AKDE 53.6 ± 250.8 ha, median = 16.2, range = 1.6–2466.3, n = 107, and KDE 39.3 ± 175.5 ha, 14.8, 1.7–1779, n = 107). Fig. 2(a-c) illustrates these findings for selected dogs.

Having a closer look on excursions, we found that six village dogs and one rural dog spent at least one night outside the urban area during all seasons. Considering only village dogs performing daily excursions > 500 m away from the urban limit, almost half of them (16 or 48.5%) were engaged in at least one excursion during the sampling period, nine dogs (27.3%) veered away more than twice (mean 3.4 ± 2.8, range 1–9 times). The locations of two village dogs followed complete trekking trails with a duration of 3–6 days during summer of which owners confirmed they followed tourists. Only three individuals were recorded on the local landfill, but one of them went on repeated occasions. Fig. 2 (d-f) highlights selected data on excursions.

Regarding the dogs' activity patterns, we distinguished between locations recorded during daytime, defined as the time between sunrise and sunset, and at night. Rural dogs were equally active during day (49.8%) and night (50.2%, n = 4747 locations), but village dogs tended to be slightly more active during the day (59.4%, n = 80169). Village dogs had 40.7% of their locations during the night in the urban area (n = 75422) and 38.3% in nature (n = 4747, Fig. 3). When comparing

the number of locations in seven habitats (Andean, coastal, forest, infrastructure, lakes, peatbog, shrubland) during the day (n = 3645) dogs used significantly more infrastructure and coastal habitat than at night (n = 2528; two-sample tests for equality of proportions of locations, $X^2 = 12.1$, p = 0.004 and $X^2 = 40.2$, p < 0.001, respectively), whereas in forest and peatbogs dogs were significantly more active during the night ($X^2 = 29.5$, p < 0.001 and $X^2 = 11.7$, p = 0.004, respectively). The number of locations during the day compared to those at night had no statistical differences in Andean habitat, lakes, and shrubland.

Among the 80169 locations of the 33 village dogs only 5.9% were recorded outside the urban radius. Of those, almost half were recorded in forest (49.1%), followed by infrastructure (15.7%), Andean habitat (13.8%), coastal (7.1%), shrubland (6.2%), peatbog (6%), and lakes (2.1%). Second order habitat selection (i.e., home ranges within the study area) was nonrandom for all four seasons (Wilks' lambdas $\lambda \leq 0.38$, p < 0.002, Fig. 4). For summer, habitat of village dogs was ranked (most to least preferred) infrastructure > forest > coastal > peatbogs > shrubland and for the other three seasons forest > coastal > infrastructure > peatbogs > shrubland. However, between the three top-ranked habitat types the intensity of habitat selection was similar, but these were significantly more used than the remaining habitat types, being shrubland the least preferred overall (Fig. 4). Third order habitat selection (i.e., locations within home ranges) of village dogs with > 5% locations outside the urban area was significant for summer and autumn only at p = 0.1 level ($\lambda \leq 0.14$) and clearly random for winter and spring seasons ($\lambda \leq 0.13$, p > 0.1, Fig. 5). Infrastructure and peatbogs were most preferred habitats during summer and autumn; for summer, also forest habitat was among the top-ranked habitat, whereas coastal habitat was the least ranked habitat type for all four seasons. The four rural dogs had 47.6% of their locations in shrubland, 30.1% in forest, 8.3% in peatbog, 6.7% in Andean habitat, 3.9% in coastal, and 3.5% in roads/trails (n = 1471); rural infrastructure (n = 4473) was excluded as this area represented their homes.

4. Discussion

This study describes the movement ecology of 37 owned dogs
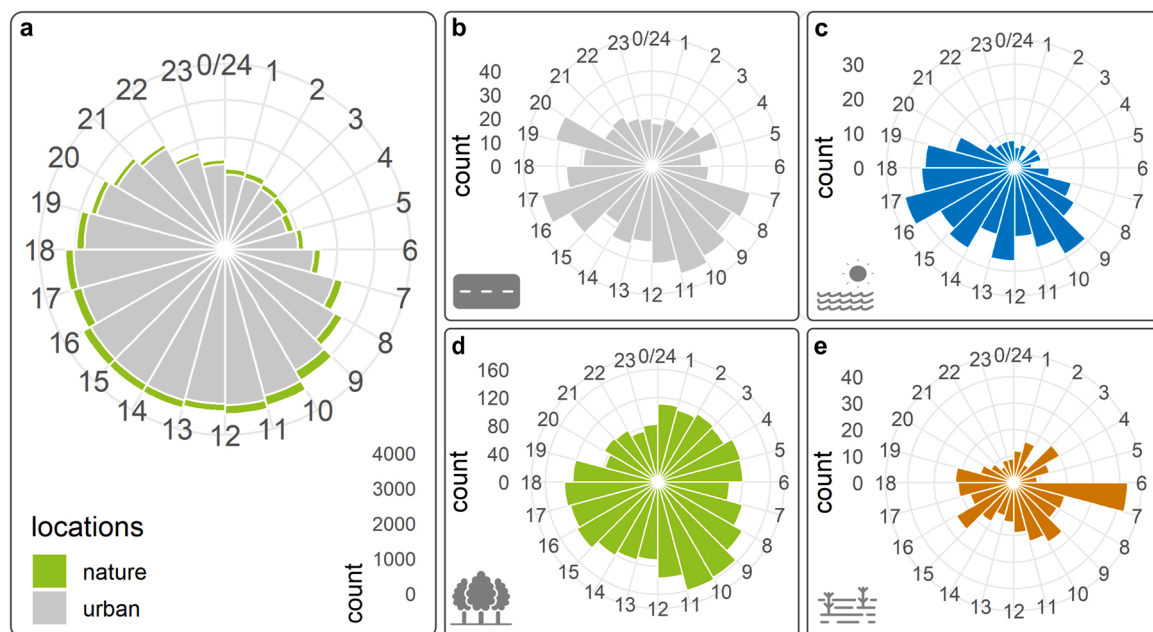
Fig. 3. Daily activity of 33 free-ranging village dogs during 24 h in southern Chile in natural versus the urban area, without day/night difference (a, n = 80169 locations). Activity of village (33) and rural (4) dogs in habitats outside the urban area/rural homes, in infrastructure (b, n = 748 of 28 dogs), coastal habitat (c, n = 394 of 32 dogs), forest (d, n = 2772 of 33 dogs), and peatbog (e, n = 407 of 16 dogs).
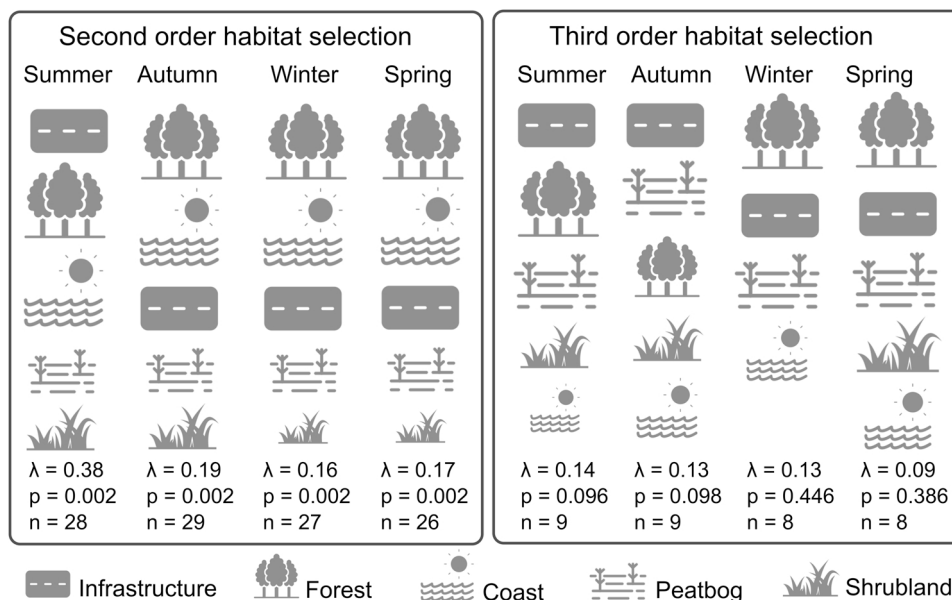
Fig. 4. Habitat selection of village dogs outside the urban area in southern Chile. Second order habitat selection was analyzed for all village dogs and third order habitat selection for dogs with > 5% of their locations outside the urban area. Different sizes of icons mean significantly different ranks. Shrubland was deleted from the third order winter habitat selection as availability was only given for one animal. λ = Wilks' lambda, p = p-value, n = number of individuals.

allowed to roam free unsupervised on a sub-Antarctic island in southern Chile. As expected, dogs generally stayed close to the owners' homes, with median and mean distances to their homes of 33–42 m and 193–602 m, respectively, depending on the season. However, 86.5% of the dogs had maximum distances > 1 km. This is more distant compared to other studies, which detail that, for example, 36% of rural dogs were engaged in 77% of 51 forays > 200 m away from home (Sepúlveda et al., 2015) or finding a village dog at ≥ 1 km from their home had less than a 10% chance (Ruiz-Izaguirre et al., 2015). Our study also revealed that almost half of the tracked dogs (48.5%) roamed beyond a radius of 500 m from the town limit, which shows how problematic the distinction between free-ranging owned and feral dogs for legislation is. Indeed, this was one of the reasons for the failed law intent in Chile (Degree Nr. 6, 2015). The maximum distance traveled in this study (southernmost Chile, 20.4 km) was more than usually reported: 1.5 km in Tibet (Vaniscotte et al., 2011), 2 km in Kyrgyzstan (van Kesteren et al., 2013), ~4 km in Mexico (Ruiz-Izaguirre et al., 2015), 4.3 km in south-central Chile (Sepúlveda et al., 2015), 4.5 km in Tanzania (Parsons et al., 2016), 10.4 km in southern Chile (Pérez et al., 2018), and 17 km in Australia (Sparkes et al., 2014). Only in an earlier study in our study area (Saavedra-Aracena et al., 2021) a dog veered as far as 28.4 km and in Meek et al. (1999), Australia, distances of up to 30 km were common in two of 10 free-ranging dogs. The wider roaming of dogs in our study may be explained by the fact that we did not select dogs randomly, but focused on dogs from which was believed (but not evidenced) they roamed. This shows how important it is that movement research discloses the selection procedure of dogs. At the same time, a random selection procedure cannot always be achieved due to the refusal of owners to participate (Sepúlveda et al., 2015) or because of handling difficulties of certain dogs (e.g., van Kesteren et al., 2013).

Although the general pattern of staying close or relatively close to home has been acknowledged by several authors (e.g., van Kesteren et al., 2013, Sepúlveda et al., 2015), in most studies there were some dogs behaving as exceptions from the rule, as we can see from the different maximum distances. Data from those dogs are often called "outliers" (Pérez et al., 2018) or "not representative" (Ruiz-Izaguirre et al., 2015), and not seldom excluded from analysis (e.g., Sparkes et al., 2014). Outliers as influential values can dominate the results. Particularly in regression-type analyses (e.g., defining predictors of movement),

they are not easy to deal with and although transforming the data or choosing probability distributions which allow a greater variation for means might be an option, outliers are often removed (Zuur et al., 2009). Generalization is a problem when studying free-ranging dogs, as, apparently, those dogs with an extreme movement behavior are of special conservation concern. Fortunately, some studies quantitatively describe the behavior of "extreme" dogs. Those were, for example, 9.3% (8 dogs out of 86) with more than 25% of their locations in the rural area (Pérez et al., 2018), 4.3% (1 out of 23) using water channels to travel up to 14 km away from home (Raynor et al., 2020), 6.9% (4 out of 58) with home ranges > 10 ha and 1.7% (1 out of 58) with home ranges > 100 ha (Molloy et al., 2017), and 13.5% (5 out of 37) with excursions > 10 km away from town (this study).

In contrary to maximum distances traveled that might only reflect "exploratory forays" (Sparkes et al., 2014), home ranges are more representative for movement patterns. However, studies are difficult to compare as the methodologies differ in relation to the number of dogs monitored, the sampling effort, the home range estimator, etc. (Table 2). Studies conducted during the last decade reported home ranges of up to 21 km^2 (Pérez et al., 2018), others up to 10 ha (Vaniscotte et al., 2011), whereas median values of the 95% extent were generally below 10 ha (Table 2). Compared to those studies, we report the largest median home range (24.4 ha, summer estimate) and largest upper range (149 km^2). The latter corresponded to an individual dog on trekking routes lasting for several days, which could have been excluded from home range analysis as a type of extraordinary behavior. However, as already mentioned, we believe that extreme movement in free-ranging dogs is of special interest and should be carefully reported. In our study, two dogs accompanied tourists on 3–6-day trekking trips into sub-Antarctic wilderness, highlighting the role of tourism as a possible driver of dog movement where the access of dogs is not controlled.

Beyond this special case, some authors (e.g., Meek, 1999; Sparkes et al., 2014) suggest that the variability in home range sizes could be explained by the Resource Dispersion Hypothesis (Macdonald, 1983), i. e., dogs needing to extend their forays where resources are poor, similar to wild carnivores (e.g., Ethiopian wolves *Canis simensis,* Tallents et al., 2012; foxes *Vulpes vulpes,* Bino et al., 2010). Other reasons for roaming far are biological, husbandry-related, and environmental factors. However, studies are not concordant in their findings. Some found that male

Table 2

Selection of 10 dog movement studies during the last decade, highlighting the variability in methodologies and results. R = rural dogs, U = urban dogs, V = village dogs. AKDE = Autocorrelated Kernel Density Estimation, BRB = Biased Random Bridge method, CHP = Hull Polygon method, MCP = Maximum Convex Polygon, T-LoCoH = Time Localized Convex Hulls. Dashes indicate that size was not reported. In this study, median home range size was based on summer data, in Raynor et al. (2020) on water channel usage, only.

GPS-tracked dogs (n, type)	Sampling effort in days, median or mean ± SD (range)	95% home range in ha, median (range)	Site	Reference
37 V, R	19 (4–34)	24.4 (1.6–14879, AKDE)	Chile	This study
73 U, R	5.1 (1–6.3)	9.3 (4.1–14.3, kernel)	Kenya	Muinde et al. (2021)
100 R	2.5 (1.2–4.7)	7.7 (1.1–103, kernel)	Chad	Warembourg et al. (2021)
23 U	- (4–28)	1.8 (0–370, T-LoCoH)	Peru	Raynor et al. (2020)
86 V	3–11	0.04 (0.1–2097, MCP)	Chile	Pérez et al. (2018)
135 V	2–16	4.5 (0.9–40.5, kernel)	Australia	Dürr et al. (2017)
58 R	1 (0.9–4.3)	3.1 (0.9–131, BRB)	Australia	Molloy et al. (2017)
12 R	115 ± 11 (9–174)	- (31–1161, kernel)	Australia	van Bommel and Johnson (2014)
37 V	0.8 ± 0.4 (0.06–2)	2.3 (-, CHP)	Kyrgyzstan	van Kesteren et al. (2013)
87 V	- (1–4)	- (0–10, MCP)	Tibet	Vaniscotte et al. (2011)

(Dürr et al., 2017; Sparkes et al., 2014; Vaniscotte et al., 2011), intact dogs (Dürr et al., 2017; Molloy et al., 2017; but see Garde et al., 2015), younger (Pérez et al., 2018, but see Muinde et al., 2021), and malnourished dogs (Molloy et al., 2017; Ruiz-Izaguirre et al., 2015, but see Pérez et al., 2018) roamed further. Others report that during the dry season dogs had more extended movement patterns than during the wet season (Maher et al., 2019; Wilson-Aggarwal et al., 2021). Recently, Saavedra-Aracena et al. (2021) in addition to the more classical predictors, addressed the influence of the owner's bond on roaming behavior. The focus of our study was on movement ecology, not predictors, but we believe that further studies are needed to better understand predictors of movement, including novel aspects until now not addressed, such as personality.

Even if only a small percentage of dogs roam far from home, this is still relevant for conservation policies, particularly next to protected areas. A single dog can severely affect prey populations (e.g., surplus killing of kiwis *Apteryx australis*, Taborsky, 1988). Moreover, due to the often-high population density of dogs (Gompper, 2014) a small percentage of far-roaming dogs is still a considerable number of carnivores for the ecosystem and thus very impactful. For example, in our study, nine dogs (27%) of the 33 village dogs had > 5% of their locations in natural areas. Considering the results of the street dog census (126–141 free-roaming village dogs in total, depending on the season), an extrapolated 34–38 individuals could enter natural areas frequently. Taking only into account the two dogs following tourists over several days into wilderness, an extrapolated 8–9 individuals out of the total population could behave similarly. Finally, invasive predators pose a severe threat to native fauna in insular ecosystems (Doherty et al., 2016) as on islands, where prey often lack behavioral or evolutive defense strategies (Banks and Dickman, 2007). This is the case in our study system, where native species have been long isolated from mammalian predators (Schüttler et al., 2009).

Activity patterns indicated an almost even pattern of diurnal (59% of locations) and nocturnal (41%) movements. In southern Chile, 80% of forays > 200 m away from home took place during the day (Sepúlveda et al., 2015); in Brazil, Madagascar, and Australia free-ranging dogs were also photographed predominantly during the day (Silva et al., 2018; Sparkes et al., 2016). Yet, crepuscular activity was observed in feral dogs in Ecuador (Zapata-Ríos and Branch, 2016) and nocturnal habits in wild-living dogs in Australia (Sparkes et al., 2016). A reason for the apparent difference in activity patterns between free-ranging versus feral dogs might be that in free-ranging dogs human and dog activity are often related (Dos Santos et al., 2018; Wilson-Aggarwal et al., 2021). Social activity (e.g., following a person, playing with a person, jumping) was one of the main behaviors shown by free-ranging village dogs in southern Chile (Garde et al., 2015). In fact, dogs preferred to be petted by unfamiliar persons over food in India (Bhattacharjee et al., 2017), and the presence of dogs at sandy beaches was associated with beach-goers, not necessarily owners (Cortés et al., 2021). This

dog-human link could explain why in our study dogs used infrastructure and coastal habitat more during the day - where likely more human activity takes place -, in contrast to forest or peatbog habitat more frequented during the night.

Finally, our study found preference for forest, infrastructure, and coastal habitat across the seasons, and avoidance of shrubland. Hence, dogs were not habitat specialists, but used a mix of man-made and natural habitats available. A preference for forest in free-ranging dogs has been acknowledged previously (Dos Santos et al., 2018; Ribeiro et al., 2018), although this would depend on the density of the understory of the forest (Sepúlveda et al., 2015). In our study area, old-growth forests have poorly developed understory and therefore, may not represent a barrier for movement or prey concealment (Contardo et al., 2020). Coasts might be interesting to dogs in our study area as those habitats harbor plenty of coastal birds. The presence of dogs at beaches has been associated to the harassment of shorebirds (Cortés et al., 2021), scavenging of carcasses (Schlacher et al., 2015), and nest predation of geese (Schüttler et al., 2009) and sea turtles (Ruiz-Izaguirre et al., 2015). But dogs made also use of road and trails, as earlier described (Sepúlveda et al., 2015; Warembourg et al., 2020). On a finer scale, individuals (n = 9) preferred peatbogs, as earlier revealed by camera-trap data (Contardo et al., 2020), highlighting those ecosystems as areas deserving special conservation efforts.

5. Conclusion

Our findings reveal a relatively high spatial (movement patterns, habitat use) and temporal (seasonal, daily) plasticity in free-ranging owned dogs moving through pristine sub-Antarctic environments. Although we could not directly address the impacts of dogs, this plasticity gives dogs access to a wide range of recognized interactions with wildlife. Although most dogs stayed relatively close to their homes, our study showed that excursions into natural areas were not only limited to "extreme dogs." These dogs are the one that should receive a higher attention in future research, particularly with respect to predictors of movement and their impact on wildlife. The findings of our study also show the need of legislation to restrict the movement of dogs. Pet ownership strategies must acknowledge that dogs are active during the night, mainly in the absence of human presence. On the other hand, also people who are not owners of dogs must be educated when visiting sensible natural settings as they can be drivers of dog movement. Free-ranging dogs are social animals often owned for company and if owners take advantage of this fact and acknowledge their responsibility, wildlife will benefit.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

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