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Do dog-human bonds influence movements of free-ranging dogs in wilderness?

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Abstract

Domestic dogs have a close and mutualistic relationship with humans. When unconfined, they usually stay close to the owner's home, but some undertake intensive forays in nature with negative impacts on wildlife. Predictors for such problematic dogs in previous research concentrated on dog characteristics and husbandry. Here we additionally explored which aspects of the dog-human bond influenced the movements of free-ranging village dogs in southern Chile. Using an interdisciplinary framework, we assessed the strength of this relationship through (i) attachment behaviours performed during the Strange Situation Procedure (SSP, dog's perception of the relationship) and (ii) the Monash Dog-Owner Relationship Scale questionnaire (MDORS, owner's perception) in 41 dog-owner dyads while remotely monitoring the dogs' movements using GPS tracking (n= 36394 locations). We found that 39% of dogs had > 5% of their locations in natural areas, but only three individuals exhibited overnight excursions. Home range size (1.8 – 4227 ha) and mean distances to the owner's home (0 – 28.4 km) varied greatly among individuals. Through generalized linear models we identified that dogs had larger home ranges, moved farther away from home or accessed nature more (i.e., they exhibited more intensive forays) when they explored more, greeted their owners intensively, and expressed more passive behaviours in the presence of their owners (SSP). However, the MDORS questionnaire was a poor predictor of home range, distance to home and access to nature. When considering

the dogs' background, older dogs, males, and dogs that got missing more frequently exhibited more intensive forays. Compared to SSP results in confined dogs, we suggest that owners of free-ranging dogs do not play an important role as an attachment figure. We conclude that the dog-owner bond indeed influences roaming behaviour in dogs. This highlights the necessity of wildlife management strategies considering the cultural context. In specific terms, we recommend to foster the knowledge of the importance of bonds between dogs and their owners in educational campaigns on responsible dog ownership, along with biological (age, sex) and behavioural characteristics (exploration, getting missing). That way, awareness campaigns can focus on owners of possible problematic dogs.

Key words

Behavioural ecology, *Canis familiaris*, Chile, Monash Dog Owner Relationship Scale, Strange Situation Procedure, wildlife management

1. Introduction

Dogs (*Canis familiaris*) are the first domesticated species by humans (33000 years before present, Wang et al. 2016). This long relationship has led to manifold roles for dogs in human societies, from company to guardian, hunting, search, rescue or guide dogs (Lord et al. 2016; Arahori et al. 2017). Not only do the roles of dogs in human societies differ, but also their husbandry. In industrialized countries dogs are often in-door family members with highest care and health standards, whereas in other cultures they are often less confined and under lower subsistence conditions (Jackman and Rowan 2007; MacDonald and Carr 2017). Yet, dog husbandry not only depends on a country's economic level, but above all - on culture. In a cross-cultural analysis of human-pet dynamics covering 60 societies, Gray and Young (2011) revealed dogs were actually most often used in hunting and least for entertainment, whereas positive treatments such as grooming occurred less than negative interactions (e.g., physical abuse). In most societies, dogs roamed outdoors, next often indoors, and lastly outdoors with people; and they slept equally outside and inside.

During the last decade, the consequences of unrestricted dog movements has gained increased attention in the field of Conservation Biology (Young et al. 2011; Hughes and Macdonald 2013; Twardek et al. 2017). The impacts of free-ranging dogs in natural ecosystems from most to least reported are predation, disturbance, transmission of diseases, competition, and hybridization with wildlife (Doherty et al. 2017). This trend may be increasing as dog populations increase with human populations worldwide, currently reaching 987 million dogs (Gompper 2014).

Free-ranging dogs are urban, village, rural – with a gradient in dependency on humans – or feral dogs, which are completely wild and independent of human subsidy (Vanak and Gompper 2009). As stated above, in many regions of the planet, owned dogs are allowed to roam free and they do not refrain from impacting wildlife (Gompper 2014). Owned dogs may veer away as far as 10 – 20 km from their homes (Molloy et al. 2017; Pérez et al. 2018) but most stay within their vicinity (< 250 m, Vaniscotte et al. 2011; Sepúlveda et al. 2015). A range of factors can influence the movement of free-ranging dogs, e.g., dog characteristics (Dürr et al. 2017), provision of food (Ruiz-Izaguirre et al. 2015, Molloy et al. 2017), and the presence of owners (Dos Santos et al. 2018). However, to our knowledge the potential effects of dog-owner bonds on dogs' movements have not been addressed.

Dogs have remarkable social skills which allow them to develop a close and mutualistic relationship with humans (Miklósi and Topál 2013; Payne et al. 2015; Lea and Osthaus 2018). This bond, or attachment, is defined as "the relatively long-enduring tie in which a partner is important as a unique individual and is interchangeable with none other", where partner is an attachment figure (Ainsworth 1989:711). According to Bowlby (1969), attachment is applicable to all mammals and involves specific behaviours related to the attachment figure such as maintaining proximity, distress at separation and attachment figure as a secure base to explore the environment, finding security and comfort in it, if necessary. These behaviours are the result of evolutionary processes, adopted to improve survival by maintaining proximity with their conspecifics, especially with the mother (Bowlby 1969; Ainsworth 1989). Importantly, attachment and dependency are different constructs (empirical evidence in Kungl et al. 2019). The Strange Situation Procedure (SSP) is a method to assess attachment from infants to their mothers by putting them in a stressful situation by meeting a stranger in a new environment (Ainsworth and Bell 1970). Because dogs develop similar bonds to their owners as those created between infants and mothers during early ontogeny (Miklósi and Topál 2013), the SSP has been adopted to examine domestic dog bond strength towards owners (Topál et al. 1998) in behavioural assessments in companion dogs (e.g., Rehn et al. 2014), rescue dogs (e.g., Scandurra et al. 2016), working dogs (e.g., Lenkei et al. 2021), and in physiological assessments measuring cortisol reactivity (e.g.,

Schöberl et al. 2016). Complementary, to assess the owners' perception, the Monash Dog Owner Relationship Scale questionnaire (MDORS, Dwyer et al. 2006) is the most extensively used (review in Payne et al. 2015). This tool follows the theory of social exchange, which defines a relationship as successful when costs and benefits are balanced, or when benefits overcome the costs of the relationship (Emerson 1976). Following Netting et al. (1987) this theory can also be applied to companion animals. As with the SSP, physiological assessments showed correlations between the questionnaire and the dog's oxytocin and cortisol levels (e.g., Handlin et al. 2012).

Our study aim was to test whether dog-human bonds influence the spatial movements of free-ranging dogs. For our study, we prefer using the term caregiver over owner according to the World Organization of Animal Health, which defines dog ownership as accepting responsibility for the physical and behavioural needs of the dog as well as ensuring not roaming out of control (OIE 2019). We predicted that dogs with a stronger bond to the caregiver would stay closer to home, similarly to dogs with caregivers who report successful relationships (as defined by Emerson 1976). Besides the bonds, we also considered dog characteristics and husbandry-related factors from earlier studies and predicted that female (e.g., Vaniscotte et al. 2011; Sparkes et al. 2014; Dürr et al. 2017; but see Van Kesteren et al. 2013), older (Pérez et al. 2018), adequately fed (Ruiz-Izaguirre et al. 2015), and sterile dogs (e.g., Sparkes et al. 2014; Dürr et al. 2017; Molloy et al. 2017; but see Garde et al. 2016) roam less. We tested this through: (i) remote monitoring of dog movements; (ii) questionnaires on the dog's background; (iii) assessment of the dog-caregiver bond from the dog's perception; and (iv) from the caregiver's perception. This socio-ecological framework was tested on 41 free-ranging, mixed-breed village dogs with close access to pristine sub-Antarctic ecosystems in southern Chile. This is a pioneer study that allows researchers to predict which aspects of the dog-caregiver bond influence a dog's willingness to venture into natural settings, thus providing a novel platform for dog management strategies for biological conservation.

2. Methods

2.1 Ethical note

We fitted 41 dogs with light-weight GPS data-loggers (I-gotU GT-600, Mobile Action, Taiwan, 37 g). The device was sealed in weatherproof bags, placed inside hand-made leather cases, and attached to their own or a commercial dog collar with safety tapes. We did not weigh the dogs to avoid stress, but the approximate percent body weight of the device in its bag was 0.19 - 0.44% for large-sized and medium-sized animals, respectively. Dogs were tracked for three weeks $(20.5 \pm 5.3 \text{ days}, \text{ range} = 6 - 35 \text{ days})$ from December to March either during summer one (2016 - 2017) or summer two (2018 - 2019). All devices were removed from all dogs. No dog was forced to enter the room to perform the SSP. Only one dog refused to enter and was excluded from the analysis. All caregivers signed a consent form with information on the project aims, absence of risks, access to the results, and guaranteed anonymity. At the end of the study, participation was compensated with an economic incentive (CLP \$10 000/US \$12.50). The Scientific Ethical Committee of the University of Magallanes certified the ethical approval of the study (N°003/CEC/2018).

2.2 Study area

Our study was conducted on Navarino Island, southern Chile (Fig. 1), with Puerto Williams as the only major settlement (74.5 ha, 2100 inhabitants). Each summer, the pristine character of Navarino attracts an increasing number of tourists interested in trekking. On Navarino Island, 30.6% of owned dogs roam free (Schüttler et al. 2018) and the majority of free-ranging dogs in this small town are dogs with a clearly referable caregiver, following a photographic four-season-census (Schüttler et al. unpublished data) and a classification of dogs photographed in camera-traps outside the town from which 74% of 26 individuals were identified as owned (Contardo et al. 2020). We also know free-ranging dogs on Navarino Island preferred peatbog over forest and shrubland and that there is evidence of a feral population of dogs (Contardo et al. 2020). As the island is free of native, terrestrial predators (Anderson et al. 2006), dogs can have significant impacts on the native fauna, particularly on birds such as geese or ducks (Schüttler et al. 2009) and southernmost guanacos (*Lama guanicoe*, González 2010). Moreover, dogs are involved in conflicts with local farmers as they often attack livestock (Schüttler et al. 2018).

[Please insert Fig. 1 here, colour online only]

2.3 Subjects

We approached only adult dog caregivers (\geq 18 years) in Puerto Williams whose dogs ranged free, were adult (\geq 1 year), and lived together with their caregivers for \geq 6 months (Rehn et al. 2014). The majority of subject dogs (81%) originated from Navarino Island, which lacks an animal shelter. Most dogs (76%) were also obtained as puppies or adolescents (available information for 29 dogs); hence, they were able to develop their bond with their caregivers from an early age onwards. All dogs had either access to the caregiver's house and/or to the caregiver's yard. To avoid data dependency, we only selected one dog per caregiver, the one with presumable forays away from home. We contacted 44 dog caregivers, which represented approximately half of the extrapolated free-ranging dog population in Puerto Williams (estimated n = 84, Schüttler et al. 2018); three contacted caregivers refused to participate. A health check (general aspect, lymph nodes, skin, mucous membranes, body condition, heart rate) assured that the selected dogs were in adequate condition to participate in the study. The body condition was based on a 5-point score, with 5 meaning obese (e.g., McGreevy et al. 2005). Once finished, digital video material and GPS positions of the dogs were handed to each caregiver.

2.4 Dog background

Based on previous research in the study area (Schüttler et al. 2018), we created a questionnaire with 24 closed and open questions (Supplementary material S1) about dog characteristics, husbandry, dog-caregiver interaction, dog-wildlife interaction, and basic personal owner information (gender, age, residence time on Navarino Island, education level, first time dog caregiver).

2.5 Dog movements

All GPS devices recorded locations in 10-min intervals only when movement was detected. The device error was evaluated by performing a series of mobile and static tests, following Cargnelutti et al. (2007) and Camp et al. (2016). According to those tests, we first excluded locations with abnormal elevation parameters (i.e., 9.1%, n = 3754/41519). Second, we asked caregivers to report excursions with their dog outside town. The locations of those accompanied dogs were then removed (i.e., 3.6%, n = 1371/37765), yielding a total of 36394 reliable locations.

168 2.6 Dow-caregiver bonds

During January and April 2018, we tested dog attachment behaviour towards the caregiver by performing the SSP (Topál et al. 1998). We carried out and filmed six 3-min experimental episodes (Fig. 2), adding a second room to evaluate exploration behaviours (e.g., Palmer and Custance 2008; Rehn et al. 2014, sketch in Supplementary material S2). A woman without previous contact with the dogs performed as the stranger in all tests. Throughout the procedure caregivers were instructed through headphones. This included to not interact with their dogs even if the dog approached the caregiver. After each session, we disinfected the test area and the stranger used a fresh overall.

[Please insert Fig. 2 here]

The videos were analysed using instantaneous (5 s intervals) and continuous sampling, facilitated by the software BORIS (Friard and Gamba 2016). We classified behaviours into 20 categories following the ethograms in Palmer and Custance (2008) and Rehn et al. (2013) (Supplementary material S3, revised by a veterinarian) and summarized them as the proportion of time/episode and time/min during reunion (Rehn et al. 2014), apart from greeting, which was classified according to its intensity (Palmer and Custance 2008). In room 2 we only recorded the total time the dog spent in it, not behaviours. Only five individuals played (3.9% social play and 2.1% independent play of overall possible sample points); therefore, play behaviour was excluded from analyses.

We evaluated caregivers' bonds with their dogs by asking 27 closed questions from the MDORS questionnaire (Dwyer et al. 2006), grouped into three subscales: (i) dog-caregiver interaction, (ii) emotional closeness, and (iii) perceived cost; higher scores of the 5-point Likert scales represented a stronger bond (Supplementary material S4). We used the Mexican Spanish translation of González-Ramírez et al. (2017) and adapted it to Chilean Spanish. Internal consistency of each subscale was calculated using Cronbach's alpha.

2.7 Statistical analyses

We used generalized linear modelling (Nelder and Wedderburn 1972) to investigate which variables (n = 16, Table 1) from the dog's background and the dog-caregiver bonds best predicted the spatial movements

of dogs. To describe the movement of each dog, we used three different response variables: home range size, mean distance to the caregiver's home, and whether the dog entered natural areas (Table 1). Thus, those dogs with high values in these categories exhibited more intensive forays in nature, possibly interacting with wildlife. We applied Gaussian error structure (linear model) for home range and distance and binomial error structure with logit link for whether the dog entered natural areas.

Home range size (HOME) was calculated by autocorrelated kernel density estimation for the monitoring period of each dog after fitting continuous-time stochastic process models using the ctmm package (Calabrese et al. 2016) in program R (R Core Team 2019). In ctmm, we also confirmed that individuals were range residents by visually inspecting whether the semi-variance in the variograms reached an asymptote. We used the 95% home range area for all dogs but three (n = 38), as these dogs had multiple overnight excursions outside of town. For those dogs, we used the low estimate (i.e., low value of the 95% confidence intervals of the 95% home range area) to adjust for over-estimation of home range size. We excluded physical barriers from the analysis. For this, we selected the farthest dog location in the Beagle Channel (i.e., 236.8 m from the coastline) and added the GPS error (6.2 m, mobile test), deleting areas beyond 243 m from the coast. The mean distance (DISTANCE) to the caregiver's home was the mean linear distance from all dog's locations to its home over the dog's sampling period. Finally, we denoted a 1 when a dog entered natural areas in > 5% of all recorded locations (NATURE), but a 0 otherwise (stayed in urban areas or left them in \leq 5% of all recorded locations). Thus, we ensured a more equal distribution of the data. Locations, home ranges, and distances to caregivers' homes were projected in WGS 1984 UTM zone 19S and mapped in ArcMap 10.4 (ESRI, Redlands, USA).

We selected explanatory variables from the dog's background, SSP, and MDORS results (Table 1). From the questionnaire on the dog's background, we selected the dog's age (AGE), sex (SEX), food provisioned (FOOD), and whether it was sterilized (STERILE) due to their importance in dog-wildlife interactions. We also included access to the caregiver's house (ACCESS) and the reported number of days the dog had been missing (MISSING). In SSP, we evaluated significant differences between episodes with the caregiver present versus the stranger present and the dog alone versus the stranger present, using Wilcoxon signed rank tests. The most relevant behaviours among those with significant differences were identified via principal component analysis (PCA) for each of the six episodes and greeting minutes, among which we created five change behaviour variables and one greeting intensity variable (similar to Rehn et al. 2014).

Finally, we used the score of each subscale of the MDORS questionnaire as explanatory variables

(INTERACTION, EMOTION, COST).

We evaluated collinearity for numerical variables by Spearman's correlations excluding those variables with $r_s > |0.6|$. For categorical predictors we used Chi-square and Fisher's exact tests with significance levels of $P \le 0.05$. Two-way relationships were found for ACCESS and STERILE ($X^2_1 = 4.95$, P = 0.03; Fisher's exact test, P = 0.02, STERILE retained), for TAIL and GREETING ($r_s = 0.64$, N = 39, P < 0.01, GREETING retained) and INTERACTION and EMOTION ($r_s = 0.65$, N = 40, P < 0.01, EMOTION retained). For each model set, we did not consider cases that contained NAs in the explanatory variables. We log-transformed DISTANCE and HOME due to their large span, but report back-transformed values for estimated coefficients and standard errors (Cade 2015). Explanatory variables were measured on different scales and therefore were z-transformed.

Table 1

Overview of response and explanatory variables used in modelling the movement of free-ranging dogs in southern Chile.

Assessment	Variable	Description
GPS MONITORING	DISTANCE (R) HOME (R) NATURE (R)	Mean linear distance to caregiver's home (km) during summer Home range area (ha) for each dog in one summer season $0 = \text{dogs with} \le 5\%$ locations in natural areas 1 = dogs with > 5% locations in natural areas
BACKGROUND	ACCESS (E) AGE (E) FOOD (E) MISSING (E) SEX (E) STERILE (E)	Access inside to caregiver's house: never, 1 – 2 times a week, 3 – 5 times a week, daily Continuous integers (years) Feeding mainly by: commercial dog food and/or meat, leftovers, mix of above Continuous integers (i.e., 24 h, days missing during last year) Male/Female Yes/No
SSP	C/S ZONE (E) DOOR (E) GREETING (E) PASSIVE (E)	Change in dog's position in caregiver's vs. stranger's presence (i.e., caregiver's zone or stranger's zone, range = $-0.25 - 0.80$) Change in dog's position in proximity to the door in caregiver's versus stranger's presence (range = $-0.8 - 0.4$) Change in intensity of greeting in caregiver's vs. stranger's greeting (low to high: $0 - 3$ on 0.5-point scale) Change in passive behaviour (i.e., dog is sitting, lying, or standing without any obvious attention to physical or social environment) in caregiver's vs. stranger's presence (range = $-0.6 - 0.7$)

	ROOM 2 (E)	Change in access to room 2 in stranger's presence vs. dog alone (range = $-0.8 - 0.2$)					
	TAIL (E)	Change in tail wagging during caregiver's vs. stranger's greeting (range = $-0.5 - 0.8$)					
	COST (E)	Low to high level of perceived cost of caring for a dog (range = $30-45$)					
MDOR	EMOTION (E)	Low to high level of emotional closeness perceived by caregiver (range = $28 - 49$)					
	INTERACTION (E)	Low to high level of dog-caregiver interaction (range = $15 - 33$)					

Positive ranges in the SSP represent values of the dog's behaviour in company of the caregiver, while negative values are in company of the stranger, except for ROOM 2. Here negative values indicate the dog is alone and positive values with the stranger. Explanatory variables are ordered alphabetically. Variable type R = Response, E = Explanatory.

Since we had 13 potential explanatory variables with only 41 observations, to avoid overfitting (Mundry 2014), we first built three separate model sets: (i) dog background questionnaire (BACKGROUND), (ii) dog's perspective of the bond (SSP), and (iii) caregiver's perspective (MDORS). We compared all potential combinations of explanatory parameters using Akaike's information criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002). We then built a final model set (iv) OVERALL using the variables from the best model (Δ AIC_c = 0) of the previous model sets. We analysed each of the three response variables separately.

For all models, variance inflation factors were < 5 and no obvious deviations were found by visual inspection of normality and homoscedasticity in the residuals' plots for the linear models (Supplementary material S5). For each model set, the significance of the full model was evaluated through comparison with the null model by Likelihood Ratio Tests (LRT). All full models were different from the null model, unless otherwise stated. The relative importance of parameters within each model was calculated by adding the weights (ω AIC_c) for each explanatory variable. All statistical analyses were carried out in program R (R Core Team 2019), using the packages MuMIn (Barton 2019) and AICcmodavg (Mazerolle 2019).

3. Results

Caregivers had a mean age of 41.5 years (range = 18 - 89), 54.5% were female, with a residence time of 20.4 years (0.5 - 48) and different levels of education: primary (9.7%), secondary (48.8%), and tertiary (41.5%); only two participants were first time dog caregivers.

3.1 Dog background

The participating dogs had a mean age of 5 (\pm 2.8) years, were slightly skewed towards males (63.4%), and received a moderate to high level of husbandry with 56.1% given commercial dog food, 70.7% sterilized, and 63.4% having access to the caregiver's house. Only one dog was underweight (i.e., mean body condition score < 2.5). Over half (56.1%) were 24-h free-ranging, whereas 46.3% had gone missing for \geq 1 day, during a mean period of 4.9 (\pm 3.1) days (Table 2). The caregivers' responses also indicated that wildlife interaction existed: prey categories brought home were native birds (41.7% of 12 records) and invasive muskrat (*Ondatra zibethicus*, 33.3%); harassed animals included livestock (51.5% of 66 records) and native birds (18.2%).

Table 2

Summary of information on the background of 41 free-ranging dogs in southern Chile.

Dog information

Demographic data	
Sex ratio (male: female)	1.7: 1
Mean dog age (years) (SD, range)	5 (2.8, 1 – 11)
Number of large/medium-sized dogs	31/10
Reproductive control	
Sterilized (%)	70.7
Number of offspring in previous year	6 (1 dog)
Health	
Vaccinated against rabies (%)	26.8
Treated for parasites (%)	34.1
Food provisioning	
Commercial food and/or meat (%)	56.1
Leftovers (%)	7.3
Mix of above (%)	36.6
Dogs fed in more than one household (%)	52.2
Mean body condition score (SD, range)	3.3/5 (0.7, 2 – 5)
Dog movement	
Unconfined dogs during day or night (%)	43.9
Unconfined during 24 h (%)	56.1
Dogs missing for ≥ 1 day (%)	46.3
Mean number of lost days (SD, range)	4.9 (3.1, 1 – 14)
Dog-caregiver interaction	
Mean daily dog-caregiver interaction (h) (SD, range)	4.5 (4.0, 0.1 – 16)

Access to caregiver's house (%)	63.4
Dog-animal interaction	
Dogs having brought home prey (%)	24.4
Dogs harassing animals (%)	80.5

3.2 Dog movement

We collected 36394 locations from 41 unaccompanied, free-ranging dogs with a mean of 887.7 \pm 281.7 (median = 868.0, range = 298 – 1517) locations per dog. The mean home range size of all dogs was 310.4 \pm 1016.7 ha (19.2, 1.7 – 4227), with a mean linear distance to the caregiver's home of 0.3 \pm 1.3 km (0.04, 0 – 28.4). Dogs entered natural areas every 4.4 \pm 5.4 days (2.1, 0 – 22); 8.5% of locations were in natural areas and 16 dogs (39%) had > 5% of their locations outside the urban area. The majority of dogs (n = 38) stayed within 0.1 \pm 0.3 km of the caregiver's home and had only 7% of their locations in natural areas (range = 0 – 58.5%); three dogs exhibited multiple overnight excursions with 22.1% of their locations in natural areas (13.2 – 38.6%).

3.3 Dog-caregiver bonds

In summary, dogs preferred the caregivers over the stranger's presence in the SSP (Fig. 3), i.e., dogs showed significantly more proximity-seeking behaviours, secure-base effects behaviours, and greeting behaviours (ethogram in Supplementary material S3) in the presence of their caretakers versus the presence of the stranger (P < 0.001 for all Wilcoxon signed rank tests of behavioural comparisons between episodes with caretakers versus stranger, Supplementary material S6). All dogs accessed room 2, almost exclusively in the absence of their caregivers and more often when being alone than with the stranger. After performing Wilcoxon tests (Supplementary material S6) and PCA we selected five change behaviour variables (Fig. 3).

[Please insert Fig. 3 here]

Cronbach's α was 0.37 for the interaction subscale of MDORS, 0.75 for emotional closeness, and 0.74 for perceived costs. Lacking internal consistency, we excluded interaction from modelling. The mean scores of each question, subscale, and total score for the 40 questionnaires are detailed in Supplementary material S4.

3.4 Predictors of dog movements

When considering the dogs' background, dogs exhibited larger home ranges when they had been missing for more days ($\omega AIC_c = 0.95$) and when older ($\omega AIC_c = 0.53$; model set BACKGROUND). With regard to the dog-caregiver attachment, dogs that explored room 2 longer when they were alone ($\omega AIC_c =$ 0.94) and with a higher greeting intensity towards their caregiver ($\omega AIC_c = 0.59$) had larger home ranges (model set SSP). When considering the caregiver's perception of the relationship, the full model was not significantly different from the null model (LRT, $F_{MDORS} = 0.71$, P = 0.47; model set MDORS). Combining the best predictors of the three model sets in an overall model set, the best model included dogs that had been missing for several days ($\omega AIC_c = 0.86$) and explored room 2 longer ($\omega AIC_c = 0.90$).

Older dogs (ω AIC_c = 0.79) and dogs missing for more days (ω AIC_c = 0.89) exhibited larger mean distances to the caregiver's home (model set BACKGROUND). Again, dogs that explored room 2 longer when alone (ω AIC_c = 0.77) and those that greeted their caregivers more intensively (ω AIC_c = 0.66) went farther from home, but also dogs exhibiting more passive behaviours (ω AIC_c = 0.53; model set SSP). However, in this model set the full model was only marginally significantly different from the null model (LRT, F_{SSP} = 2.4, P = 0.06). Again, the full model in model set MDORS was not significantly different from the null model (LRT, F_{MDORS} = 0.70, P = 0.50). As for home range, the best model of the overall model set revealed missing dogs (ω AIC_c = 0.69) and longer exploration of room 2 (ω AIC_c = 0.72) as important predictors, but also dogs exhibiting more passive behaviours (ω AIC_c = 0.55).

Consistent with the former models, dogs missing for more days tended to frequent natural areas more than dogs missing less days ($\omega AIC_c = 0.83$), but also males ($\omega AIC_c = 0.71$) did so. Dogs with a longer exploration of room 2 ($\omega AIC_c = 0.97$, model set SSP) were also located more frequently in natural than urban areas. Note that the full model was only significantly different from the null model at the alpha level of 0.1 (LRT, Deviance_{BACKGROUND} = 1.96, P = 0.08). Again, the full model in model set MDORS was not significantly different from the null model (LRT, Deviance_{MDORS} = -1.71, P = 0.42). In the overall model set, missing dogs ($\omega AIC_c = 0.68$), male dogs ($\omega AIC_c = 0.75$), and dogs exploring room 2 longer ($\omega AIC_c = 0.94$) were the most important predictor variables. See Table 3 for an overview on all parameter estimates, weights, and p-values of all model sets; Fig. 4 for predictors from the best model for each model set.

3

3**3**0 Table 3

331 5 Estimates of all predictors of free-ranging dog movement in southern Chile.

	0												
Model	7 N 0	HOME					DISTANCE				NATURE		
	Bredictors	Е	SE	Р	$\sum (\omega AIC_c)$	Е	SE	Р	$\sum (\omega AIC_c)$	Е	SE	Р	$\sum (\omega AIC_c)$
	10 1AGE	15.31	11.08	0.18	0.53	13.57	6.03	0.04	0.79	0.07	1.14	0.62	0.28
	1 ₽ OOD LEFTOVERS	-37.10	203.55	0.68	0.20	-37.64	85.70	0.45	0.21	1.11	1.56	0.48	0.14
ROI	¹ MIXED FOOD	124.70	82.66	0.19	0.30	30.90	39.91	0.42	0.21	0.81	0.83	0.33	0.14
КG	1 MISSING	23.70	7.87	0.01	0.95	11.52	4.31	0.01	0.89	0.27	0.13	0.04	0.83
BAC	1SEX M	36.60	81.76	0.61	0.26	33.49	39.52	0.39	0.39	1.86	0.97	0.06	0.71
д	¹ ₁₈ TERILE YES	7.21	95.14	0.92	0.21	-23.36	45.16	0.48	0.33	0.26	0.93	0.77	0.24
	1 ¢/s zone	-58.45	194.0	0.42	0.28	-33.84	85.82	0.51	0.28	0.53	1.73	0.76	0.26
_	2DOOR	22.44	140.34	0.82	0.23	22.99	65.52	0.68	0.25	0.66	1.42	0.64	0.23
SSP	²¹ GREETING	77.00	38.68	0.09	0.59	42.93	20.67	0.07	0.66	0.52	0.61	0.40	0.30
	2 PASSIVE	60.03	138.07	0.59	0.27	110.56	64.61	0.14	0.53	-0.94	1.41	0.51	0.25
	2 ₽ 00M 2	-94.42	206.82	0.01	0.94	-75.61	90.45	0.04	0.77	-5.52	2.31	0.02	0.97
ORS	² cost	3.01	6.43	0.64	0.24	2.68	3.61	0.46	0.27	0.01	0.02	0.55	0.27
<u>Ā</u>	2€MOTION	-6.08	5.25	0.23	0.39	-3.03	2.96	0.30	0.33	-0.02	0.02	0.23	0.29
	² AGE	8.87	9.02	0.33	0.30	7.53	5.24	0.16	0.43	-	-	-	-
Ļ	3 GREETING	30.67	30.58	0.32	0.34	21.16	17.02	0.23	0.45	-	-	-	-
M	3 MISSING	16.45	6.84	0.03	0.86	7.80	3.95	0.06	0.69	0.23	0.13	0.08	0.68
VER	³ PASSIVE	-	-	-	-	126.37	59.22	0.09	0.55	-	-	-	-
Ó	3 ₽ OOM 2	-91.71	161.00	0.01	0.90	-74.04	81.71	0.03	0.72	-5.70	2.56	0.03	0.94
	3 S EX	-	-	-	-	-	-	-	-	2.20	1.15	0.06	0.75

332 Predictors were derived from the dog's background (Model set BACKGROUND, n = 39), the dog attachment 333 behaviour towards the caregiver (Model set SSP, n = 39) and the caregiver's perception on his/her relationship 394 with his/her dog (Model set MDORS, n = 40). A final model set (OVERALL) used predictors of the best **3**65 models from the previous three model sets. We tested for three response variables each: 95% Autocorrelated **\$**36 Kernel Density Estimation (AKDE) home range (HOME)*, mean distance to caregiver's home (DISTANCE), and entered natural areas (NATURE). E = Estimate, SE = Standard error, P = P-value, $\sum (\omega AIC_c)$ = summed AIC_c weight; variable descriptions are in Table 1. The full model selection containing models with $\Delta AIC_c < 2$ is provided in Supplementary material S7. Predictors' weights of the best model are highlighted in bold. * For three dogs with multiple overnight excursions we used the lower value of the 95% CI of the 95% AKDE home range.

[Please insert Fig. 4 here]

4. Discussion

Free-ranging dogs are an increasing threat to wildlife globally. In Latin America, owners often allow

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their dogs to roam (Gompper 2014; Sepúlveda et al. 2015; Dos Santos et al. 2018). Therefore, it is essential to

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better understand why some dogs roam farther than others. For the first time, this interdisciplinary study
brings together which aspects of the dog-caregiver bond predict how dogs move on forays away from home.
Indeed, in this study 98% (n = 40/41 dogs) accessed nature unaccompanied, whereas 44% entered nature in
company of their caregivers. This indicates that free-ranging dogs foray in nature and possibly interact with
wildlife, as also indicated by our questionnaire data on harassment and prey brought home. The median home
range size was 19 ha and dogs stayed within 300 m of the caregiver's home, similar to other studies in Chile
(Sepúlveda et al. 2015; Pérez et al. 2018) and elsewhere (Vaniscotte et al. 2011; Ruiz-Izaguirre et al. 2015).
However, three dogs behaved completely different. They exhibited extensive excursions into natural habitats
(on average 22% of their locations, some on trekking trails) with distances away from home of up to 28 km
and home ranges over 4227 ha (or 6170 ha 95% Minimum Convex Polygon (MCP); 8766 ha 100% MCP),
surpassing the records reported by previous studies (Meek 1999: 140 – 2450 ha 100% MCP; Pérez et al. 2018:
60 – 2100 ha 95% MCP). This indicates that some dogs may be more problematic for wildlife and highlights
that even dogs detected at very large distances from any urban settlement may be owned.

When investigating the dog's perception of the dog-caregiver bond (SSP), we found that dogs with higher levels of exploration behaviours had larger home ranges, moved farther away from home, and accessed natural habitats more than dogs with lower exploration behaviours; i.e., they exhibited more intensive forays. All dogs explored room 2 and according to the PCA, dogs explored room 2 more during isolation episodes and in the presence of the stranger, not when the caregiver was present. In studies incorporating a second room (Palmer and Custance 2008; Rehn et al. 2014), dogs explored room 2 in company with their owners and only few individuals even entered the room. Compared to confined dogs, we suggest that caregivers of free-ranging dogs do not play an important role as secure bases. This might be due to less positive interactions between caretakers and their dogs in comparison to confined dogs. The development of positive-human animal relationships requires repeated occasions of positive interactions such as playing, stroking, or talking (review on dogs, Pop et al. 2014), although further research is needed concerning the type, length, and frequency of the interaction (review on animals, Rault et al. 2020). The fact that dogs with higher levels of exploration behaviours might be exhibited in a more original, non-domestic context, i.e., search for resources or marking territory (Cafazzo et al. 2012; Dos Santos et al. 2018). Although the SSP is a widely used

assessment to study attachment in dogs, future research on free-ranging dogs also might consider alternative approaches, such as manipulative tasks in the presence or absence of caregivers (Horn et al. 2013) or shifting the experimental setting to the caregiver's homes (Wedl et al. 2010). Rehn et al. (2016) also suggest taking into account individual dog attachment styles and caregiver strategies.

Unfortunately, we could not analyse the sister behaviour of exploration, play, as it occurred infrequently (upon invitation only five dogs marginally played with the stranger). The fact that our participating dogs did not play much could be a result of free-ranging status. When comparing object manipulation between three groups of dogs with different life experiences, free-ranging, pet, and captive dogs, Lazzaroni et al. (2019) found that free-ranging dogs where less persistent, possibly due to less socially guided interaction with objects. In a similar vein, free-ranging dogs responded less to human attentional states in a gazing experiment than pet or captive dogs (Brubaker et al. 2019). In consequence, how dogs behave towards humans apparently depends on their life experiences with wider implications for their behaviour outside the home.

Dogs with larger home ranges and roaming distances to their homes also greeted their caregivers more intensively than the stranger (see also Mariti et al. 2013; Schöberl et al. 2016). Following Bowlby (1969), the evolutive explanation of a greeting is the re-establishment of bonds after reunion with the attachment figure; in social mammals, greeting ceremonies are performed to reconciliate among pack members (Smith et al. 2011). In this sense, dogs spending more time away from their homes might need to express their bond with their caregiver more than dogs staying at or near home most of their time.

Lastly, dogs that went farther from their homes, often sat, laid, or stood around (passive behaviours) in the presence of their caregivers. In the literature, passive behaviours are controversially interpreted; Prato-Previde et al. (2003) for example suggested that they are related to secure base behaviours, whereas Mongillo et al. (2013) believe that they rather actively suppress behavioural signs or emotional distress (Topál et al. 1998). Therefore, we abstain from interpreting passive behaviours in our study and see further research need here. To better understand which behaviours are dominant in free-ranging dogs versus confined dogs, future research could compare both dog categories in the same experimental setting.

Considering the dog-caregiver relationship from the caregiver's perception (MDORS), all subscales were poor predictors of dog movements. There might be a trend in dogs with caregivers reporting lower scores of emotional closeness to move farther from home, but this needs further investigation. Additionally, the

404 MDORS has been developed (Dwyer et al. 2006) for and mostly used in industrialized countries (Mariti et al. 1 405 3 405 407 407 8 408 2013; Rehn et al. 2014; Schöberl et al. 2016). Therefore, questions might not match Latin American and/or free-ranging dog culture. For example, if dogs are mainly kept in the streets, they likely will not be taken to visit people and kissing free-ranging dogs might be seen as unhygienic. It is therefore important to develop instruments adjusted to dog cultures and even more – to improve our understanding on how deep cultures 10 **409** 12 influence dog-owner relationships and husbandry. This will answer the question whether measures for **4**}0 14 responsible pet ownership (e.g., indoor-keeping) are a universal tool. 151 17 48 19 21 21 21 24 23 21 24 25 24 25 26 6 28 27 6 28 27 7 In contrast to the dog-caregiver bond, the influence of dog characteristics and husbandry on free movements have been addressed by various studies during the last decade. Here, we found that dogs missing for several days, older, and male dogs exhibited more intensive forays. Asking caregivers about how often their dogs disappear thus seems to be a reliable predictor to identify dogs with more access to wilderness. The fact that caregivers did not try to hide this information from the interviewer (e.g., to appear as a responsible pet owner, social desirability bias, Maccoby and Maccoby 1954) is also an indicator that information in other sensitive questions (e.g., prey brought home, diet) is probably not influenced by this type of bias. Following 30 **41**8 32 most caregivers, their dogs got missing because they followed other persons or tourists. Indeed, two dogs were 339 34 tracked on trekking trails and dogs were also frequently sighted on trails (Schüttler et al. 2018). In this sense, 35 420 36 37 421 tourism can have a negative influence on conservation if norms restricting the access of dogs on trails are not implemented (Bessa et al. 2019). Those norms should consider that dogs are highly social animals (Marshall-39 402 41 423 4443 4445 4675 4677 5027 545

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Older and male dogs also forayed more intensively. Older dogs tend to show more aggressive behaviours (Chopik and Weaver 2019) standing for territory defence, food resource acquisition, and reproductive opportunities (Lockwood 2017) – all aspects require roaming from home (but see Pérez et al. 2018). Also, male dogs in this study had larger home ranges (e.g., Sparkes et al. 2014; Dürr et al. 2017; Molloy et al. 2017). According to Scandurra et al. (2018:1) behavioural differences in dogs' sex are "mainly rooted in their biological and evolutionary heritage, remaining unchanged despite artificial selection". Therefore, biological characteristics of dogs should be included in educational campaigns on responsible dog ownership.

Pescini and Kaminski 2014) that form bonds with other dogs and humans (Cimarelli et al. 2019); even

unowned animals preferred being groomed by a stranger over food (Bhattacharjee et al. 2017).

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5. Conclusion

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In conclusion, we demonstrate that dog-caregiver bonds significantly influence the roaming behaviour of free-ranging dogs. This opens a new field for mitigating the impacts of dogs on wildlife through culturally adjusted management and education strategies. Dog-positive attitudes and their integration into the family depends on the society and even determines the ability to recognize emotions in dogs (Amici et al. 2019). In general terms, we think that responsible pet ownership policies should be adapted to the socio-cultural context and should not simply be copied from industrialized countries. For Latin America for example, Ceballos et al. (2014) identify a need for increased education on the owner's commitment beyond physical pet care. Actually, the concept of the responsible dog owner itself seemingly is of limited use as a message: The owning behaviour of dog owners in the UK considerably varied in important aspects, although they considered themselves as responsible (Westgarth et al. 2019). This finding is supported by the fact that in our study the dog's perspective on the relationship differed from the caregiver's (all Spearman's correlations between attachment variables and MDORS scales were P > 0.05, but see Rehn et al. 2014). In this study, we identify the need for a better understanding of the role of the caregiver as an attachment figure in free-ranging dogs. In specific terms, we recommend using exploration behaviours and the number of days caregivers report their dogs missing to distinguish between dogs that stay close to their homes and dogs with intensive forays. That way, efforts to raise awareness on the dog-wildlife conflict can be focused on caregivers of possible problematic dogs. In form of a simple test and questionnaire, this could be easily addressed through responsible ownership programs. Finally, fostering the knowledge of the importance of bonds between dogs and their owners, such as the lifelong high attachment in dogs (Mongillo et al. 2013), matching of dog-owner endocrine systems (Oliva et al. 2016), and the bond's influence in behaviours relevant for wildlife (this study), will likely help to reduce roaming. The evolution of the dog through domestication can be an ally in conservation: dogs have shown that they prefer to be close to humans. Improving the links between the two species can be beneficial, not only for human and dogs, but also for wildlife.

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References

Ainsworth MDS, Bell SM. 1970. Attachment, exploration and separation: illustrated by the behavior of one-year-olds in a strange situation. Child Dev. 41:49-67. https://doi.org/10.2307/1127388

Ainsworth MS. 1989. Attachments beyond infancy. Am Psychol. 44:709-716.

https://doi.org/10.1037//0003-066x.44.4.709

Amici F, Waterman J, Kellermann CM, Karimullah K, Bräuere J. 2019. The ability to recognize dog emotions depends on the cultural milieu in which we grow up. Sci Rep. 9:16414.

https://doi.org/10.1038/s41598-019-52938-4

- Anderson CB, Rozzi R, Torres-Mura JC, McGehee SM, Sherriffs MF, Schüttler E, Rosemond AD. 2006. Exotic vertebrate fauna in the remote and pristine sub-Antarctic Cape Horn Archipelago, Chile. Biodivers Conserv. 15:3295-3313. https://doi.org/10.1007/s10531-005-0605-y
- Arahori M, Kuroshima H, Hori Y, Takagi S, Chijiiwa H, Fujita K. 2017. Owners' view of their pets' emotions, intellect, and mutual relationship: cats and dogs compared. Behav Processes. 141:316-321. https://doi.org/10.1016/j.beproc.2017.02.007
- Barton K. 2019. MuMIn: Multi-Model inference. R package version 1.43.6. https://CRAN.Rproject.org/package=MuMIn (accessed 23 September 2019).
- Bessa E, Blumstein DT, Samia DSM, Geffroy B. 2019. Pets at ecotourism destinations: cute mascot or trojan horse? Curr Issues Tour. 22:1523-1525. https://doi.org/10.1080/13683500.2018.1449192
- Bhattacharjee D, Sau S, Das J, Bhadra A. 2017. Free-ranging dogs prefer petting over food in repeated interactions with unfamiliar humans. J Exp Biol. 220:4654-4660. https://doi.org/10.1242/jeb.166371

- 487 Bowlby J. 1969. Attachment and loss, Volume I: Attachment. New York: Basic Books.
- 488 3 489 490 490 8 491 10 492 12 Brubaker L, Bhattacharjee D, Ghaste P, Babu D, Shit P, Bhadra A, Udell MAR. 2019. The effects of human attentional state on canine gazing behaviour: a comparison of free-ranging, shelter, and pet dogs. Anim Cogn. 22:1129-1139. https://doi.org/10.1007/s10071-019-01305-x
 - Burnham K, Anderson, D. 2002. Model selection and multimodel inference: a practical informationtheoretic approach. New York: Springer.
 - Ceballos NA, Karunaratna D, Setién AA. 2014. Control of canine rabies in developing countries: key features and animal welfare implications. Rev Sci Tech. 33:311-321. https://doi.org/10.20506/rst.33.1.2278

Cade B. 2015. Model averaging and muddled multimodal inferences. Ecology 96:2370-2382. https://doi.org/10.1890/14-1639.1

- Cafazzo S, Natoli E, Valsecchi P. 2012. Scent- marking behaviour in a pack of free- ranging domestic dogs. Ethology 118:1-12. https://doi.org/10.1111/j.1439-0310.2012.02088.x
- Calabrese JM, Fleming CH, Gurarie E. 2016. Ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. Methods Ecol Evol. 7:1124-1132. https://doi.org/10.1111/2041-210X.12559
- Camp, MJ, Rachlow JL, Cisneros R, Roon D, Camp RJ. 2016. Evaluation of global positioning system telemetry collar performance in the tropical Andes of southern Ecuador. Nat Conservacao. 14:128-131. https://doi.org/10.1016/j.ncon.2016.07.002

Cargnelutti B, Coulon A, Hewison AJM, Goulard M, Angibault JM, Morellet N. 2007. Testing global positioning system performance for wildlife monitoring using mobile collars and known reference points. J Wildl Manage. 71:1380-1387. https://doi.org/10.2193/2006-257

- Chopik WJ, Weaver JR. 2019. Old dog, new tricks: Age differences in dog personality traits, associations with human personality traits and links to important outcomes. J Res Pers. 79:94-108. https://doi.org/10.1016/j.jrp.2019.01.005
- Cimarelli G, Marshall-Pescini S, Range F, Virányi Z. 2019. Pet dogs' relationships vary rather individually than according to partner's species. Sci Rep. 9:1-9. https://doi.org/10.1038/s41598-019-40164-x

57 583

59

1

- Contardo JE, Grimm-Seyfarth A, Cattan PE, Schüttler E. 2020. Environmental factors regulate occupancy
 of free-ranging dogs on a sub-Antarctic island, Chile. Biol Invasions 23:677-691.
 https://doi.org/10.1007/s10530-020-02394-3
 - Doherty TS, Dickman CR, Glen AS, Newsome TM, Nimmo DG, Ritchie EG, Vanak AT, Wirsing AJ. 2017. The global impacts of domestic dogs on threatened vertebrates. Biol Conserv. 210:56-59. https://doi.org/10.1016/j.biocon.2017.04.007
 - Dos Santos CLA, Le Pendu Y, Giné GAF, Dickman CR, Newsome TM, Cassano CR. 2018. Human behaviors determine the direct and indirect impacts of free-ranging dogs on wildlife. J Mammal. 99:1261-1269. https://doi.org/10.1093/jmammal/gyy077
 - Dürr S, Dhand NK, Bombara C, Molloy S, Ward MP. 2017. What influences the home range size of freeroaming domestic dogs? Epidemiol Infect. 145:1339-1350. https://doi.org/10.1017/S095026881700022X
 - Dwyer F, Bennett PC, Coleman GJ. 2006. Development of the Monash Dog Owner Relationship Scale (MDORS). Anthrozoös 19:243-256. https://doi.org/10.2752/089279306785415592

Emerson RM. 1976. Social exchange theory. Annu Rev Sociol. 2:335-362.

https://doi.org/10.1146/annurev.so.02.080176.002003

- Friard O, Gamba M. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol Evol. 7:1325-1330. https://doi.org/10.1111/2041-210X.12584
- Garde E, Pérez GE, Vandersttichel R, Dalla Villa PF, Serpel JA. 2016. Effects of surgical and chemical sterilization on the behaviour of free-roaming male dogs in Puerto Natales, Chile. Prev Vet Med. 123:106-120. https://doi.org/10.106/j.prevetmed.2015.11.011

Gompper E. 2014. The dog-human-wildlife interface: assessing the scope of the problem. In: Gompper E., editor. Free-ranging dogs and wildlife conservation. Oxford: Oxford University Press, p. 9-54.

González BA. 2010. ¿Qué problemas de conservación tienen las poblaciones de guanaco en Chile? Rev Extensión Ambient For. 9:28-38.

- 540 González-Ramírez M, Vanegas-Farfano M, Landero-Hernández R. 2017. Versión mexicana de la escala 1 541 3 542 573 544 10 512 544 10 512 544 10 512 1246 1748 1949 212 252 2572 30Monash de relación del dueño con su perro (MDORS-M). Altern Psicol. 37:107-123. http://dx.doi.org/10.1016/j.jveb.2017.03.007
 - Gray PB, Young SM. 2011. Human-pet dynamics in cross-cultural perspective. Anthrozoös 24:17-30. https://doi.org/10.2752/175303711X12923300467285
 - Handlin L, Nilsson A, Ejdebäck M, Hydbring-Sandberg E, Uvnas-Moberg K. 2012. Associations between the psychological characteristics of the human-dog relationship and oxytocin and cortisol levels. Anthrozoös 25:215-228. https://doi.org/10.2752/175303712X13316289505468

Horn L, Huber L, Range F. 2013. The importance of the secure base effect for domestic dogs – Evidence from a manipulative problem-solving task. PLoS One 8(5): e65296. https://doi.org/10.1371/journal.pone.0065296

- Hughes J, Macdonald DW. 2013. A review of the interactions between free-roaming domestic dogs and wildlife. Biol Conserv. 157:341-351. https://doi.org/10.1016/j.biocon.2012.07.005
- Jackman J, Rowan A. 2007. Free-roaming dogs in developing countries: the benefits of capture, neuter, and return programs. In: Salem DJ, Rowan AN, editors. The state of the animals. Washington, D.C.: Humane Society Press, p. 55-78
- Kungl MT, Gabler S, Bovenschen I, Lang K, Zimmermann J, Spangler G. 2019. Attachment, dependency, and attachment-related behaviors in foster children: A closer look at the nature of the foster childcaregiver relationship. Dev Child Welf. 1:107-123. https://doi.org/10.1177/2516103219845374
- Lazzaroni M, Range F, Bernasconi L, Darc L, Holtsch M, Massimei R, Rao A, Marshall-Pescini S. 2019. The role of life experience in affecting persistence: A comparative study between free-ranging dogs, pet dogs and captive pack dogs. PLoS One 14(4): e0214806. https://doi.org/10.1371/journal.pone.0214806
- Lea SEG, Osthaus B. 2018. In what sense are dogs special? Canine cognition in comparative context. Learn Behav. 46:335-363. https://doi.org/10.3758/s13420-018-0349-7
 - Lenkei R, Carreiro C, Gácsi M, Pongrácz P. 2021. The relationship between functional breed selection and attachment pattern in family dogs (Canis familiaris). Appl Anim Behav Science 235:105231 https://doi.org/10.1016/j.applanim.2021.105231

63 64 65

62

57 566

59 60 61

Lockwood R. 2017. Ethology, ecology and epidemiology of canine aggression. In: Serpell J., editor. The domestic dog, its evolution, behavior and interactions with people. Cambridge: Cambridge University Press, p. 161-181

- Lord K, Schneider R, Coppinger R. 2016. Evolution of working dogs. In: Serpell J., editor. The domestic dog, its evolution, behavior and interactions with people. Cambridge: Cambridge University Press, p. 42-66
- Maccoby E, Maccoby N. 1954. The interview: a tool of social science. In: Lindzey G., editor. Handbook of social psychology. Cambridge: Addison-Wesley, p. 449-487
- MacDonald D, Carr GM. 2017. Variation in dog society: between resource dispersion and social flux. In: Serpell J., editor. The domestic dog, its evolution, behavior and interactions with people. Cambridge: Cambridge University Press, p. 320-338
- Mariti C, Ricci E, Zilocchi M, Gazzano A. 2013. Owners as a secure base for their dogs. Behaviour 150:1275-1294. https://doi.org/10.1163/1568539X-00003095
- Marshall-Pescini S, Kaminski J. 2014. The social dog: history and evolution. In: Marshall-Pescini S, Kaminski J., editors. The social dog: behaviour and cognition. Amsterdam and Boston: Academic Press, p. 3-33
 - Mazerolle M. 2019. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.2-2. https://cran.r-project.org/package=AICcmodavg (accessed 23 September 2019)
- McGreevy PC, Thomson PC, Pride C, Fawcett A, Grassi T, Jones B. 2005. Prevalence of obesity in dogs examined by Australian veterinary practices and the risk factors involved. Vet Rec. 156:695-702. https://doi.org/10.1136/vr.156.22.695
 - Meek P. 1999. The movement, roaming behavior and home range of free-roaming domestic dogs, *Canis lupus familiaris*, in coastal New South Wales. Wildl Res. 26:847-855. https://doi.org/10.1071/WR97101
 - Miklósi Á, Topál J. 2013. What does it take to become "best friends"? Evolutionary changes in canine social competence. Trends Cogn Sci. 17:287-294. https://doi.org/10.1016/j.tics.2013.04.005

- 593 Molloy S, Burleigh A, Dürr S, Ward MP. 2017. Roaming behaviour of dogs in four remote Aboriginal 1 594 3 555 596 597 10 598 12 communities in the Northern Territory, Australia: preliminary investigations. Aust Vet J. 95:55-63. https://doi.org/10.1111/avj.12562 Mongillo P, Pitteri E, Carnier P, Gabai G, Adamelli S, Marinelli L. 2013. Does the attachment system towards owners change in aged dogs? Physiol Behav. 120:64-69. https://doi.org/10.1016/j.physbe.2013.07.011 **59**9 14 Mundry R. 2014. Statistical issues and assumptions of phylogenetic generalized least squares. In: 1500 17 691 19 **20**2 Garamszegi L., editor. Modern phylogenetic comparative methods and their application in Evolutionary Biology. Berlin and Heidelberg: Springer, p. 131-154 Nelder J, Wedderburn RWM. 1972. Generalized linear models. J R Stat Soc Ser. A 135:370-384. 21 **60**3 23 24 25 26 25 26 29 5 28 28 **2**9 5 https://doi.org/10.2307/2344614 Netting FE, Wilson CC, New JC. 1987. The human-animal bond: Implications for practice. Soc Work. 32:60-64. https://doi.org/10.1093/sw/32.1.60 OIE 2019. World Organization for Animal Health. Terrestrial Animal Health Code. Chapter 7.7. Stray dog 30 **607** 32 population control, p. 1-12 208 34 35 909 37 510 Oliva JL, Rault JL, Appleton B, Lill A. 2016. Oxytocin blocks pet dog (Canis familiaris) object choice task performance being predicted by owner-perceived intelligence and owner attachment. Pet Behav Sci. 1:31-46. https://doi.org/10.21071/pbs.v0i1.3991 39 **60**1 41 **6**72 43 44 45 3 46 **6**77 48 **69**5 50 Palmer R, Custance D. 2008. A counterbalanced version of Ainsworth's Strange Situation Procedure reveals secure-base effects in dog-human relationships. Appl Anim Behav Sci. 109:306-319. https://doi.org/10.1016/j.applanim.2007.04.002 Payne E, Bennett PC, McGreevy PD. 2015. Current perspectives on attachment and bonding in the doghuman dyad. Psychol Res Behav Manag. 8:71-79. https://doi.org/10.2147/PRBM.S74972 50 51 52 53 7 54 7 Pérez GE, Conte A, Garde EJ, Messori S, Vanderstichel R, Serpell J. 2018. Movement and home range of owned free-roaming male dogs in Puerto Natales, Chile. Appl Anim Behav Sci. 205:74-82. 55 648 https://doi.org/10.1016/j.applanim.2018.05.022 57 58 59 60 61
- 63 64

- 619 Pop, DA, Rusu AS, Pop-Vancea V, Papuc I, Contantinescu R, Miresan V. 2014. Physiological effects of 1 human-animal positive interaction in dogs – Review of the literature. Bull Univ Agric Sci. 71:102-110. http://dx.doi.org/10.15835/buasvmcn-asb:10398
 - Prato-Previde E, Custance DM, Spiezio C, Sabatini F. 2003. Is the dog-human relationship an attachment bond? An observational study using Ainsworth's strange situation. Behaviour 140:225-254. https://doi.org/10.1163/156853903321671514
 - R Core Team 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ (accessed 2 June 2019)
 - Rault J-L, Waiblinger S, Boivin X, Hemsworth P. 2020. The power of a positive human-animal relationship for animal welfare. Front Vet Sci 7:857. https://doi.org/10.3389/fvets.2020.590867
 - Rehn T, McGowan RTS, Keeling LJ. 2013. Evaluating the Strange Situation Procedure (SSP) to assess the bond between dogs and humans. PLoS One 8(2): e56938. https://doi.org/10.1371/journal.pone.0056938
 - Rehn T, Lindholm U, Keeling L, Forkman B. 2014. I like my dog, does my dog like me? Appl Anim Behav Sci. 150:65-73. https://doi.org/10.1016/j.applanim.2013.10.008
 - Rehn T, Keeling LJ. 2016. Measuring dog-owner relationships: Crossing boundaries between animal behaviour and human psychology. Appl. Anim Behav Science 183:1-9. https://doi.org/10.1016/j.applanim.2016.07.003
 - Ruiz-Izaguirre E, van Woersem A, Eilers K(C)HAM, van Wieren SE, Bosch G, van der Zijpp AJ, de Boer IJM. 2015. Roaming characteristics and feeding practices of village dogs scavenging sea-turtle nests. Anim Conserv. 18:146-156. https://doi.org/10.1111/acv.12143
 - Scandurra A, Alterisio A, D'Aniello B. 2016. Behavioural effects of training on water rescue dogs in the Strange Situation Test. Appl Anim Behav Science 174:121-127. http://dx.doi.org/10.1016/j.applanim.2015.10.007
 - Scandurra A, Alterisio A, Di Cosmo A, D'Aniello B. 2018. Behavioral and perceptual differences between sexes in dogs: An overview. Animals 8(9):151. https://doi.org/10.3390/ani8090151
 - Schöberl I, Beetz A, Solomon J, Wedl M, Gee N, Kotrschal K. 2016. Social factors influencing cortisol modulation in dogs during a strange situation procedure. J Vet Behav Clin Appl Res. 11:77-85.
 - https://doi.org/10.1016/j.jveb.2015.09.007

57 **64**5

59 646

61

62

647 Schüttler E, Klenke R, McGehee S, Rozzi R, Jax K. 2009. Vulnerability of ground-nesting waterbirds to 1 $6\frac{4}{3}$ $6\frac{4}{9}$ $6\frac{4}{9}$ 10 $6\frac{4}{9}$ 10 $6\frac{4}{9}$ 10 10 10 12 $6\frac{4}{9}$ 10 $2\frac{6}{9}$ $2\frac{6}{9}$ 28 269 28 26 29 28 26 29 28 29 28 29 28 29 29 28 29 predation by invasive American mink in the Cape Horn Biosphere Reserve, Chile. Biol Conserv. 142:1450-1460. https://doi.org/10.1016/j.biocon.2009.02.013 Schüttler E, Saavedra-Aracena L, Jiménez JE. 2018. Domestic carnivore interactions with wildlife in the Cape Horn Biosphere Reserve, Chile: husbandry and perceptions of impact from a community perspective. Peer J 6:e4124. https://doi.org/10.7717/peerj.4124 Sepúlveda M, Pelican K, Cross P, Eguren A, Singer R. 2015. Fine-scale movements of rural free-ranging dogs in conservation areas in the temperate rainforest of the coastal range of southern Chile. Mamm Biol. 80:290-297. https://doi.org/10.1016/j.mambio.2015.03.001 Smith JE, Powning KS, Dawes SE, Estrada JR, Hopper AL, Piotrowski SL, Holekamp KE. 2011. Greetings promote cooperation and reinforce social bonds among spotted hyaenas. Anim Behav. 81:401-415. https://doi.org/10.1016/j.anbehav.2010.11.007 Sparkes J, Körtner G, Ballard G, Fleming PJS, Brown WY. 2014. Effects of sex and reproductive state on interactions between free-roaming domestic dogs. PLoS One 9(12): e116053. 30 **56**1 32 **262** 34 35 35 36 37 **56**4 https://doi.org/10.1371/journal.pone.0116053 Topál J, Miklósi Á, Csányi V, Dóka A. 1998. Attachment behavior in dogs (*Canis familiaris*): A new application of Ainsworth's (1969) Strange Situation Test. J Comp Psychol. 112: 219-229. https://doi.org/10.1037/0735-7036.112.3.219 39 Twardek WM, Peiman KS, Gallagher AJ, Cooke SJ. 2017. Fido, Fluffy and wildlife conservation: The environmental consequences of domesticated animals. Environ Rev. 25:381-395. https://doi.org/10.1139/er-2016-0111 Van Kesteren F, Mastin A, Mytynova B, Ziadinov I, Boufana B, Torgerson PR, Rogan MT, Craig PS. 2013. Dog ownership, dog behaviour and transmission of *Echinococcus* spp. in the Alay Valley, southern Kyrgyzstan. Parasitology 140:1674-1684. https://doi.org/10.1017/S0031182013001182 Vanak AT, Gompper ME. 2009. Dogs Canis familiaris as carnivores: Their role and function in intraguild competition. Mamm Rev. 39:256-283. https://doi.org/10.1111/j.1365-2907.2009.00148.x 57 **6**73 Vaniscotte A, Raoul F, Poulle ML, Romig T, Dinkel A, Takahashi K, Guislain MH, Moss J, Tiaoying L, 59 694 Wang Q, Qiu J, Craig PS, Giraudoux P. 2011. Role of dog behaviour and environmental fecal 61 26 62 63

contamination in transmission of *Echinococcus multilocularis* in Tibetan communities. Parasitology 1
138:1316-1329. https://doi.org/10.1017/S0031182011000874
Wang GD, Zhai W, Yang HC, Wang L, Zhong L, Liu YH, Fan RX, Yin TT, Zhu CL, Poyarkov AD, Irwin, DM, Hytönen MK, Lohi H, Wu CI, Savolainen P, Zhang YP. 2016. Out of southern East Asia: The natural history of domestic dogs across the world. Cell Res. 26:21-33.
https://doi.org/10.1038/cr.2015.147
Wedl M, Schöberl I, Bauer B, Day J, Kotrschal K. 2010. Relational factors affecting dog social attraction to human partners. Interact Stud. 11:482-503. https://doi.org/10.1075/is.11.3.09wedWestgarth C, Christley RM, Marvin G, Perkins E. 2019. The responsible dog owner: The construction of responsibility. Anthrozoös 32:631-646 https://doi.org/10.1080/08927936.2019.1645506
Young JK, Olson KA, Reading RP, Amgalanbaatar S, Berger J. 2011. Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. Bioscience 61: 125-132.

https://doi.org/10.1525/bio.2011.61.2.7

Figure captions

Fig. 1. Study area where we assessed if dog-caregiver bonds influenced spatial movements of free-ranging dogs. A: Dog movement data of 41 dogs (n = 36394 locations in 10-min intervals) during summer (2016 – 2019); B: Navarino Island; C: southern Chile, South America.

Fig. 2. Description of the SSP adapted (time lapsus) from Rehn et al. (2014). In the background of each image is the main door and on the left side the door to room 2. C = caregiver, D = dog, E = episodes, S = stranger. C and S always enter and leave through the main door. E1 (D+C, min 1 – 3): C sits quietly in chair and ignores dog. D is free to explore room 1; E2 (C+D+S, min 4 – 6): S enters room 1 and sits quietly for 1 min. During min 5, she starts talking with C. When min 6 starts, S sits on floor and initiates play with dog using toy (one toy at a time). S returns to chair if D does not want to play. C quietly leaves test area 20 s before end of episode; E3 (D+S, min 7 – 9): S continues/initiates play with dog and returns to chair after 45 s if dog does not want to play. S opens door to room 2 and leaves test area 20 s before end of episode; E4 (D, min 10 – 12): Dog remains alone and can explore rooms 1 and 2; E5 (C+D, min 13 – 15): C enters room 1, waits for 7 s and

greets D for 10 s (without specific instructions of how to greet). Then, C sits on chair and ignores D; E6 (D+S, also C at beginning, min 16 - 18) S enters room 1, waits for 7 s and greets D for 10 s (S first greets D verbally and starts physical contact only if D shows signs of acceptance). Then, S sits on chair and ignores D. C leaves the test area when S stopped greeting D.

Fig. 3. Magnitude of change in behaviours (mean proportion of time and intensity for GREETING, respectively, \pm standard deviation) for dogs (n = 39) during the SSP in southern Chile. Differences considered comparisons between: (i) greeting behaviours: GREETING = greeting intensity (min 13 vs. 16); TAIL = tail wagging during greeting (min 13 vs. 16); (ii) proximity-seeking behaviours: C/S ZONE = dog's position during greeting (i.e., proximity to caregiver or stranger, min 13 vs. 16); DOOR = dog's position in proximity to the door (episode 1+5 vs. 3+6); and (iii) secure-base effects behaviours: PASSIVE = passive behaviour (episode 5 vs. 6); ROOM 2 = access to room 2 (episode 6 vs. 4). The X-axis indicates the presence of the stranger (negative) vs. caregiver (positive) and of the dog alone (negative) vs. stranger (positive) for ROOM 2, respectively.

Fig. 4. Predictors from the best model for each model set: BACKGROUND, SSP, and MDORS for freeranging dog movement in southern Chile, alphabetically ordered. For each response variable different colours are used: logHOME (red), logDISTANCE (blue), and NATURE (green). Solid lines show trends of fitted models. For variable description see Table 1. For PASSIVE, negative values indicate the presence of the stranger, while positive the presence of the caregiver. For ROOM 2, negative values indicate the dog alone, while positive indicate the presence of the stranger.

Table 1

Overview of response and explanatory variables used in modelling the movement of free-ranging

dogs in southern Chile.

Assessment	Variable	Description
NG	DISTANCE (R)	Mean linear distance to caregiver's home (km) during summer
2S ORI	HOME (R)	Home range area (ha) for each dog in one summer season
15 LIN	NATURE (R)	$0 = \text{dogs with} \le 5\%$ locations in natural areas
OM		1 = dogs with > 5% locations in natural areas
	ACCESS (E)	Access inside to caregiver's house: never, $1 - 2$ times a week, $3 - 5$ times a week,
	AGE (E)	daily Continuous integers (years)
ROI	FOOD (E)	Feeding mainly by: commercial dog food and/or meat, leftovers, mix of above
CKG	MISSING (E)	Continuous integers (i.e., 24 h, days missing during last year)
3AC	SEX (E)	Male/Female
-	STERILE (E)	Yes/No
	C/S ZONE (E)	Change in dog's position in caregiver's vs. stranger's presence (i.e., caregiver's zone or stranger's zone, range = $-0.25 - 0.80$)
	DOOR (E)	Change in dog's position in proximity to the door in caregiver's versus stranger's
	GREETING (E)	presence (range = $-0.8 - 0.4$) Change in intensity of greeting in caregiver's vs. stranger's greeting (low to high:
		0-3 on 0.5-point scale)
SSP	PASSIVE (E)	Change in passive behaviour (i.e., dog is sitting, lying, or standing without any obvious attention to physical or social environment) in caregiver's vs. stranger's presence (range = $-0.6 - 0.7$)
	ROOM 2 (E)	Change in access to room 2 in stranger's presence vs. dog alone (range = $-0.8 - 0.2$)
	TAIL (E)	Change in tail wagging during caregiver's vs. stranger's greeting (range = $-0.5 - 0.8$)
S	COST (E)	Low to high level of perceived cost of caring for a dog (range = $30-45$)
OR	EMOTION (E)	Low to high level of emotional closeness perceived by caregiver (range $= 28 - 49$)
MD	INTERACTION (E)	Low to high level of dog-caregiver interaction (range = $15 - 33$)

Positive ranges in the SSP represent values of the dog's behaviour in company of the caregiver, while negative values are in company of the stranger, except for ROOM 2. Here negative values indicate the dog is alone and positive values with the stranger. Explanatory variables are ordered alphabetically. Variable type R = Response, E = Explanatory.

Table 2

Summary of information on the background of 41 free-ranging dogs in southern Chile.

Dog	infor	mation
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Demog	raphic data							
	Sex ratio (male: female)	1.7:1						
	Mean dog age (years) (SD, range) Number of large/medium-sized dogs	5 (2.8, 1 – 11) 31/10						
Reproductive control								
	Sterilized (%)	70.7						
	Number of offspring in previous year	6 (1 dog)						
Health								
	Vaccinated against rabies (%)	26.8						
	Treated for parasites (%)	34.1						
Food pr	rovisioning							
	Commercial food and/or meat (%)	56.1						
	Leftovers (%)	7.3						
	Mix of above (%)	36.6						
	Dogs fed in more than one household (%)	52.2						
Dog mo	Mean body condition score (SD, range)	3.3/5 (0.7, 2 – 5)						
e	Unconfined dogs during day or night (%)	43.9						
	Unconfined during 24 h (%)	56.1						
	Dogs missing for ≥ 1 day (%) Mean number of lost days (SD, range)	46.3 4.9 (3.1, 1 – 14)						
Dog-ca	regiver interaction							
	Mean daily dog-caregiver interaction (h) (SD, range)	4.5 (4.0, 0.1 – 16)						
	Access to caregiver's house (%)	63.4						
Dog-an	imal interaction							
	Dogs having brought home prey (%)	24.4						
	Dogs harassing animals (%)	80.5						

Table 3

Estimates of all predictors of free-ranging dog movement in southern Chile.

odel		HOME					TT.	NATURE					
M SS	Predictors	Е	SE	Р	$\sum (\omega AIC_c)$	Е	SE	Р	$\sum (\omega AIC_c)$	Е	SE	Р	$\sum (\omega AIC_c)$
QN	AGE	15.31	11.08	0.18	0.53	13.57	6.03	0.04	0.79	0.07	1.14	0.62	0.28
	FOOD LEFTOVERS	-37.10	203.55	0.68	0.20	-37.64	85.70	0.45	0.21	1.11	1.56	0.48	0.14
ROI	MIXED FOOD	124.70	82.66	0.19	0.30 30.90	30.90	39.91	0.42		0.81	0.83	0.33	
KG	MISSING	23.70	7.87	0.01	0.95	11.52	4.31	0.01	0.89	0.27	0.13	0.04	0.83
BAC	SEX M	36.60	81.76	0.61	0.26	33.49	39.52	0.39	0.39	1.86	0.97	0.06	0.71
д	STERILE YES	7.21	95.14	0.92	0.21	-23.36	45.16	0.48	0.33	0.26	0.93	0.77	0.24
	C/S ZONE	-58.45	194.0	0.42	0.28	-33.84	85.82	0.51	0.28	0.53	1.73	0.76	0.26
•	DOOR	22.44	140.34	0.82	0.23	22.99	65.52	0.68	0.25	0.66	1.42	0.64	0.23
SSF	GREETING	77.00	38.68	0.09	0.59	42.93	20.67	0.07	0.66	0.52	0.61	0.40	0.30
	PASSIVE	60.03	138.07	0.59	0.27	110.56	64.61	0.14	0.53	-0.94	1.41	0.51	0.25
	ROOM 2	-94.42	206.82	0.01	0.94	-75.61	90.45	0.04	0.77	-5.52	2.31	0.02	0.97
ORS	COST	3.01	6.43	0.64	0.24	2.68	3.61	0.46	0.27	0.01	0.02	0.55	0.27
Ш	EMOTION	-6.08	5.25	0.23	0.39	-3.03	2.96	0.30	0.33	-0.02	0.02	0.23	0.29
	AGE	8.87	9.02	0.33	0.30	7.53	5.24	0.16	0.43	-	-	-	-
Ļ	GREETING	30.67	30.58	0.32	0.34	21.16	17.02	0.23	0.45	-	-	-	-
SAL	MISSING	16.45	6.84	0.03	0.86	7.80	3.95	0.06	0.69	0.23	0.13	0.08	0.68
VEF	PASSIVE	-	-	-	-	126.37	59.22	0.09	0.55	-	-	-	-
0	ROOM 2	-91.71	161.00	0.01	0.90	-74.04	81.71	0.03	0.72	-5.70	2.56	0.03	0.94
	SEX	-	-	-	-	-	-	-	-	2.20	1.15	0.06	0.75

Predictors were derived from the dog's background (Model set BACKGROUND, n = 39), the dog attachment behaviour towards the caregiver (Model set SSP, n = 39) and the caregiver's perception on his/her relationship with his/her dog (Model set MDORS, n = 40). A final model set (OVERALL) used predictors of the best models from the previous three model sets. We tested for three response variables each: 95% Autocorrelated Kernel Density Estimation (AKDE) home range (HOME)*, mean distance to caregiver's home (DISTANCE), and entered natural areas (NATURE). E = Estimate, SE = Standard error, P = P-value, $\sum(\omega AIC_c)$ = summed AIC_c weight; variable descriptions are in Table 1. The full model selection containing models with $\Delta AIC_c < 2$ is provided in Supplementary material S7. Predictors' weights of the best model are highlighted in bold. * For three dogs with multiple overnight excursions we used the lower value of the 95% CI of the 95% AKDE home range.









Supplementary Material

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