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“Study of contact rates between domestic and wild ungulates in Doñana National Park”

TRABAJO FIN DE MÁSTER

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ABSTRACT

Wild boar (*Sus scrofa*) is currently the most widely distributed species in overall Europe. It is also the more relevant wild reservoir of several diseases shared with livestock and/or humans, including tuberculosis (TB) that is cause by mycobacteria of *Mycobaterium tuberculosis* complex (MTC). The transmission of MTC is important in areas with high frequency of effective contacts between potential reservoirs, as it is the case of Doñana National Park (DNP), where domestic and wild ungulates cohabit. Different approaches have been used to determine potential contacts between individuals. In this study, using GPS-GSM tracked wild boar (n=18) and cattle (n=12), we aimed to (i) determine intra and interspecific contacts for domestic and wild ungulates; (ii) describe the seasonal contacts rates between wild boar and cattle, but also the intraspecific for wild boar; and (iii) identify the environmental variables increasing the probability of interspecific contacts occurrence. In this study, contacts were defined using two spatial (52 – 127 m) and three temporal (1 – 72 – 288 h) windows, so finally six spatio-temporal windows were used. In addition, contact presence was modelled in order to determine the environmental predictors explaining the contact pattern in DNP and its seasonality. For this purpose, random points were placed within the overlapping areas between seasonal home ranges of each pair of interacting individuals. Our results pin pointed to spring and autumn as the more relevant seasons for establishing interspecific contact. Whether these contacts involve higher potential for pathogen transmission in our study area should be addressed (for instance, less frequency of contact but occurring at localized environmental sources of pathogens may involve more risk in summer season). This study also suggests that contacts do not occur in areas with dense vegetation, as dense shrublands and woodlands but highlights the relevance of the proximity to water points and vera ecotone in explaining contacts patter in DNP. Even our results are relevant to improve the understanding of the epidemiology of TB in DNP and to support intervention measures for minimize the effective contacts between domestic and wild ungulates, a more in detail exploration of the contacts determined in our study is needed. For instance, by determining the contacting individuals, exploring the daily patterns of the contacts, and characterizing the contacts in terms of selected resources would provide better understanding of the seasonal patterns of both intraspecific and interspecific contacts.

Key words: GPS relocations, home range, inter and intraspecific contact, spatio-temporal window.

1. INTRODUCTION

1.1. Population status of wild boar

Wild ungulate populations have grown notably in Europe in the last decades (Apollonio et al., 2010), and the Iberian Peninsula has been not an exception (Acevedo et al., 2005). Among ungulates, wild boar (*Sus scrofa*) should be highlighted, since it is currently the most widely distributed species both in Europe (Apollonio et al., 2010) and in the Iberian Peninsula (Palomo et al., 2007; Acevedo et al., 2014), where populations have recently expanded both in densities and range due to management changes and changes in land uses associated to rural abandonment (Gortázar et al., 2000; Acevedo et al., 2006; 2011). But this increasing trend, in some circumstances, leads to conflicts involving several sectors, among others, traffic accidents (Lagos et al., 2012), agriculture damages (Herrero et al., 2006), conservation problems (Bueno et al., 2009) and health risks (Gortázar et al., 2007; 2011). Wild boar current distribution includes Europe, north of Africa, Asia and, after its introduction in some countries, hybrids between wild boar and domestic pigs can be found in America and Australia (Figure 1; see Lever, 1994; Ruiz-Fons et al., 2008).

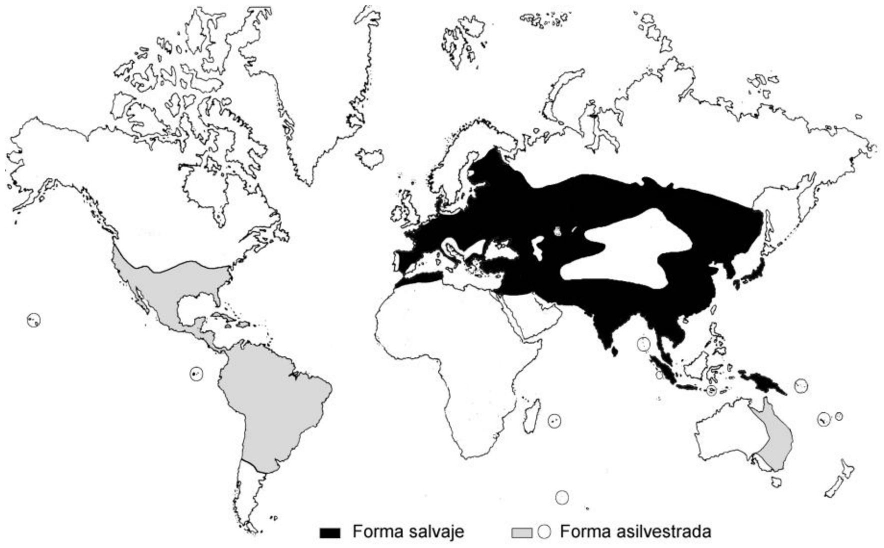

Figure 1. Geographic distribution of wild and feral forms of *Sus scrofa*. Source: Sjarmidi & Gerard (1988). Should be noted that the current distribution of the species is wider in most of the occupied areas (e.g. Portugal; see Vingada et al., 2010) and from 1980s this species also inhabits England (Wilson, 2013).

In absence of natural predators modulating wild boar populations in most of its distribution range, hunting activity becomes the major cause of mortality for wild boar both in natural and managed populations (Keuling et al., 2013). However, hunting seems to be insufficient to control the populations of this prolific species in Europe, and then overabundance situations can emerge. Overabundance is an undesirable situation occurring when the population abundance of a given species: (a) affects human life or well-being, (b) affects the fitness of the overabundant species, (c) reduces the density of species with an economic or esthetical value, or (d) causes dysfunctions in the ecosystem (Caughley, 1981). Several examples can be found in which wild boar produces overabundant scenarios (reviewed in Gortázar et al., 2006). But the diagnostic of overabundance situations is not a simple task as it requires that the admissible levels of “damage” on each indicator are defined. These admissible levels can be not considered as fixed thresholds that wild boar populations should be never exceeded; they can vary according to the specific objectives of each concrete study area. For instance, in a private hunting estate with supplementary feeding and the hunting as the unique economic activity the admissible levels of wild boar abundance are higher than in an area where livestock is a relevant activity and therefore wild boar population should be regulated to minimize the interspecific contacts, and therefore disease transmission, between domestic and wild animals (Gortázar et al., 2007).

1.2. Wild boar as a reservoir of tuberculosis

In the context of animal and public health, wild boar is a potential host of numerous pathogens (Ruiz-Fons et al., 2008). This is important not only for public health (Michel et al., 2010), but also for other issues such as economic losses in livestock industry (WorldBank, 2012), conservation of threatened species (Gortázar et al., 2008) and animal welfare (Sainsbury et al., 1995).

Bovine tuberculosis (bTB) is a zoonosis caused by *Mycobacterium bovis* and related with mycobacteria of *Mycobacterium tuberculosis* complex MTC (Gortázar et al., 2005; Neill et al., 2005). Wild boar is the biggest reservoir of MTC in the Iberian Peninsula (Gortázar et al., 2012) and shares it with cattle, goats and domestic pigs

(Parra et al., 2003; Aranaz et al., 2004; Gortázar et al., 2005). Previous studies have showed the complexity of this epidemiological system, involving several wild and domestic species, high prevalence in wildlife and no complete eradication in livestock, mainly in areas where the wild ungulates are abundant (Vicente et al. 2007; Gortázar et al., 2008). In addition, the complexity of the Mediterranean habitats in the Iberian Peninsula, characterized by severe droughts during the summer also modulates the epidemiology of these diseases (Vicente et al., 2013). The transmission of MTC becomes important in areas with frequent contacts between wild and domestic animals, as the Doñana National Park (DNP), in southern Spain, where traditional cattle husbandry of extensive regime still exist (González & Murphy, 2000). Furthermore, in this area it has been documented an increasing prevalence of MTC in wild ungulates (Parra et al., 2006), the highest ever described in literature for wild ungulates (Gortázar et al., 2008; Gortázar et al., 2011) and it has been shown a close link between wild boar MTC prevalence, wild boar abundance and livestock incidence (Boadella et al., 2012).

1.3. Contacts between wildlife and livestock

Studying the ecology of potential hosts of bTB lets to determine the factors modulating direct and indirect contacts, both within the same species and inter species (Cooper et al., 2010). These studies are needed to understand complex epidemiological systems, such as MTC in the Iberian Peninsula. Contacts between wildlife and livestock respond to several factors, such as biophysical characteristics of the habitat (e.g., precipitation, soil type, topography), ecological features (e.g., fodder, spatial behavior) and human practices (e.g., cattle husbandry, wildlife management) (Miguel et al., 2013). However, wildlife often present elusive behaviors and are not easily detectable, so contacts have been rarely quantified (Patz et al., 2004; Smieszek, 2009).

Different approaches have been used to determine contacts rates between livestock and wild animals in order to clarify the transmission of different pathogens (Table SI.1). Direct observation allowed determining the risk of bTB transmission in Michigan (Hill, 2005). More often, proximity data loggers, radio-tracking of individuals and camera trapping are used for this purpose. For instance, Böhm et al. (2009) studied the contact rate between cattle and badgers (*Meles meles*) in northeast England by proximity data loggers. Radiotracking (and also GPS-GSM technology) was used to study the transmission of bTB between cattle and elk (*Cervus canadensis*) in Canada (Brook & McLachlan, 2009). Kukielka et al. (2013) used camera-trapping to determine the nature and frequency of interactions between domestic animals (cattle and pigs) and wild animals (wild boar and red deer (*Cervus elaphus*)) in the central-south of the Iberian Peninsula. Recent advances in Global Positioning System (GPS) have permitted to determine the intra – interspecific interactions on a smaller spatial scale (Latham et al., 2015). This approach has been used to study the transmission of foot and mouth disease among wild and domestic animals in south Texas (Cooper et al., 2010), or the transmission of foot and mouth disease between cattle and buffaloes in Zimbabwe (Miguel et al., 2013). Finally, GPS-GSM technology was also used to estimate an index of potential contact between wild boar and cattle based on the seasonal patterns of habitat use expressed by these species in DNP (Barasona et al., 2014a).

1.4. Justification and aims of this study

Given the relevance of bTB eradication in livestock in the Iberian Peninsula and the role of wildlife host in the epidemiology of this and other shared diseases, the main aim of this study was to determine and describe the spatial pattern of contacts between domestic and wild ungulates. This study is the first to investigate real contacts between wild boar and cattle at spatial scale and to predict contact probabilities at landscape level.

Thus, our concrete objectives were:

1. Determining intra and interspecific contacts for domestic and wild ungulates.
2. Determining the seasonal contacts rates between wild boar and cattle, but also the intraspecific for wild boar.
3. Identifying the environmental variables increasing the probability of interspecific contacts occurrence.

2. MATERIALS AND METHODS

2.1. Study area

This study was performed in DNP (Lat. 37° 0’ N; Long. 6° 30’ W) (Figure 2). DNP is mainly located in the province of Huelva, but also in Sevilla and Cádiz provinces (Andalusia), in the southwest of the Iberian Peninsula. The total area of DNP is 52,252 ha, and its maximum elevation is 47 m.

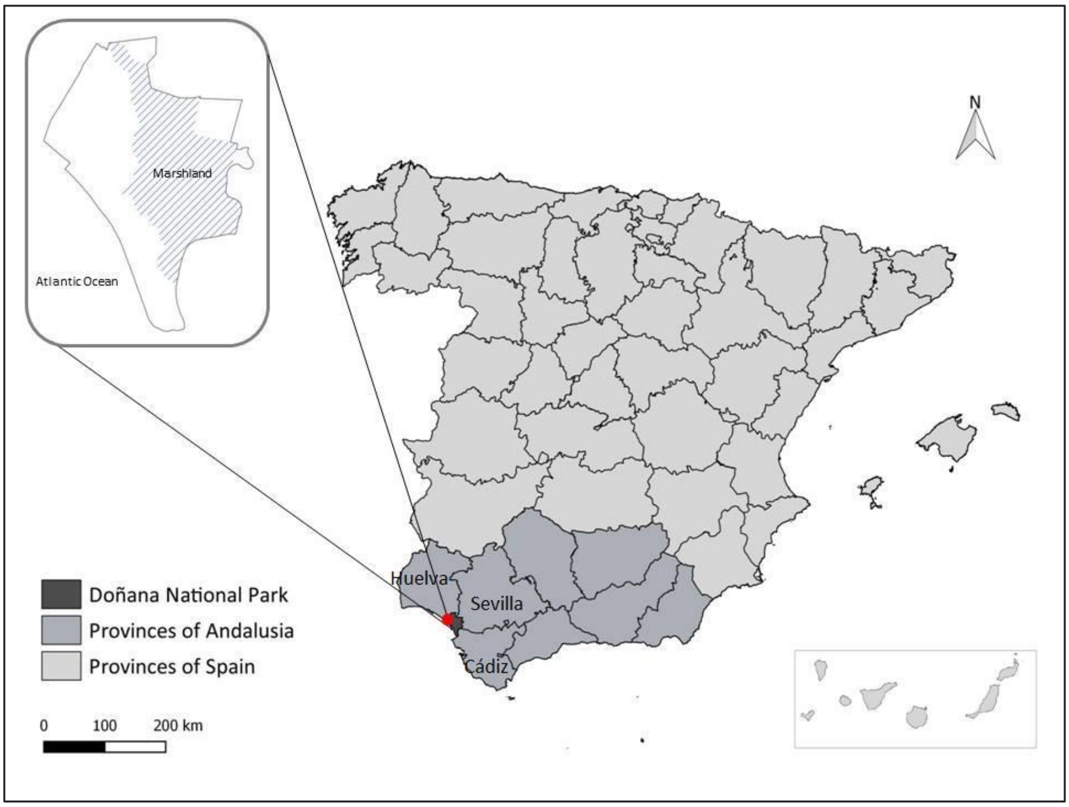

Figure 2. Location of the study area, Doñana National Park.

DNP and its surroundings have a sub-humid Mediterranean climate with Atlantic influence, which makes softer the temperature: the average annual temperature is 17ºC, with large seasonal fluctuations. The annual rainfall is 575 mm (20% in spring, 5% in summer, 35% in autumn and 40% in winter) with high intra and interannual variability, which determines the irregularity of the river inputs. The actual evapotranspiration has an average value of 420 mm per year, equivalent to 73% of the rainfall (Almonte observatory “Bodegones”, Geological and Mining Institute of Spain, Ministry of Economy and Competitiveness, Spain).

DNP is a sandy soils area formed by great diversity of biotopes: the marsh occupies 27 ha of the park, is a seasonal wetland flooded by streams and rainwater which has great importance for its role as a passage place, breeding and wintering European and African birds. The beaches are the adjacent sea areas modified by intense coastal dynamics; mobile dunes and “corrales” have characteristic vegetation of scrub and pines. Scrublands represents an intermediate stage of the mature Mediterranean forest and are the preferred habitat by large ungulates such as red deer, fallow deer (*Dama dama*) and wild boar, and also by large predators such as the Iberian lynx (*Lynx pardinus*). Finally “la vera”, it is the area between 200 – 1.500 m wide which connects scrublands with the marsh, here bulrushes and grasses growth, and aggregates animals such as birds, reptiles, amphibians, small mammals and – mainly – ungulates (Network of National Parks, Ministry of Agriculture, Food and Environment).

The traditional husbandry –“vaca marismeña”– takes place in five areas within the National Park. Each area is separated from the adjacent ones by proof fenced for cattle, which limits the movement of herds to its management area. In DNP there is a moderate – high density of red deer (6,26 ind/100ha), fallow deer (3,89 ind/100ha) and wild boar (5 ind/100 ha) according to abundance estimations calculated in 2013 (J. Vicente, unpublished data).

2.2. Sampling animals

Capture and marking of individuals was conducted between July 2011 and October 2013 following the protocol approved by the Animal Experiment Committee of Castilla-La Mancha University and by the Spanish Ethics Committee; the protocol was designed by scientists (B and C animal experimentation categories) according to EC Directive 86/609/EEC for animal handling and experiments. In total 18 wild boars and 12 cattle were equipped with GPS-GSM radio-collars (Barasona et al., 2014a).

Wild boars were captured in different trapping areas in order to monitor multiple social groups. Briefly, six padded foothold cage traps monitored by camera traps were used, and each one was activated when a wild boar stepped on a mobile bottom platform in the center of the trap, causing the simultaneous closure of the two gates from the trap. Once captured, each wild boar was anesthetized following the protocol from Barasona et al. (2013) (3 mg/kg of tiletamine-zolazepam and 0.05 mg/kg of medetomidine). Once anesthetized, each individual was identified by ear tags and were radio-collared, weighed, and assessed for condition, age and sex. Eleven of the 18 wild boars captured were males (8 adults and 3 subadults [<24 months]), and 7 were females (5 adults and 2 subadults). In addition, cattle were marked in different areas of management in DNP and thus belonged to different social groups. All of them were radio-collared during routine veterinary inspections of each farm. Further details can be found in Barasona et al. (2014a).

Each radio-collar transmitted a GPS location per hour and sent 20 locations packages with GSM (Global System for Mobile Communications) (Microsensory System, Spain) (Cano-Manuel et al., 2007). Each GPS location registered an identification of each animal, date, time, geographical coordinates and location acquisition time (LAT; a measure of the precision of a fix and ranges between 0 – 166 s). According to the last parameter, GPS locations with LAT $\geq$ 154 s were remove because they were considered anomalous relocations. Also, GPS locations obtained during the day of collar deployment were discarded.

2.3. Determining contact rates: the spatio-temporal windows

To define a contact using telemetry data two parameters should be previously defined: the geographical distance and time between two given relocations to be considered as contacting. Six spatio-temporal windows, using two spatial windows and three temporal windows, were defined in this study (Table 1).

- Spatial windows:
  - The minimum spatial distance considered as a contact was 52 m. It was fixed according to the mean positional error of the GPS that was estimated in 26 m.
  - The maximum spatial distance considered as a contact was 127 m. This is the average distance between two consecutive locations, which indicates the distance that can be traveled in one hour. It was estimated using our field data.

- Temporal window:
  - 1 h; collars were programmed to acquire one GPS location per hour, thus this is the minimum temporal resolution of our data.
  - 3 days (72 h); that corresponds to the survival of *M. bovis* during the dry season (Kukielka et al., 2013).
  - 12 days (288 h); that is related to survival of *M. bovis* during the wet season (Kukielka et al., 2013).

Table 1. Spatio-temporal windows used to describe contacts.

Window	Distance (m)	Time (h)
1	52	1
2	52	72
3	52	288
4	127	1
5	127	72
6	127	288

2.4. Data analysis

2.4.1. *Analysis of GPS location: contacts*

The analytical rationale used to determine contacts can be summarized in 5 steps:

1. For each relocation, for both cattle and wild boar, we identified the positions of a different individual within the larger spatio-temporal window (window 6).
2. The resulting contacts were characterized with the following information: ID of each contacting relocations, ID of each contacting individual, distance between contacting relocations, time between relocations, date (season) and the geographical coordinates of the mean point between both relocations.
3. As in this analysis each contact was identified twice (relocation$_i$-relocation$_j$ and relocation$_j$-relocation$_i$), we removed duplicates by considering the ID of each contacting relocation.
4. Type of contact, namely cattle intraspecific, wild boar intraspecific, and wild boar-cattle interspecific, were determined by using IDs of the contacting individuals.
5. Filtering was applied in order to split the data base with contacts into independent bases for each spatio-temporal window. Each data base was exported as Shape file to be represented in GIS.

The script used for these analyses was included as Supplementary Material II Script SII.1.

2.4.2. *Frequency of the contacts*

We estimated the frequencies of contacts to check for differences among seasons (spring, summer, autumn and winter) and contact type (wild boar intraspecific and wild boar-cattle interspecific), in each window. We excluded of these analyses the intraspecific cattle contacts because they are related to cattle management. As the number of monitored animals varied along the study period, frequencies should be relativized by the number of relocations. That is, intraspecific contacts frequencies were calculated by dividing the number of contacts in each season by the total relocations obtained for the species, and interspecific contacts were calculated by dividing the number of contacts in each season by the minimum number of relocations for any specie. We also calculated standard deviation of each estimated frequency using the formula:

$$SD = \sqrt{\frac{n\,contacts\ \cdot\ (1 - n\,contacts)}{n\,relocations}}$$

Finally we tested differences between groups of frequencies using 2 x 2 tables and Chi square tests (www.semergen.es/semergen/calc/apcalc.htm).

2.4.3. Home ranges, home ranges intersections, statistical models and contact probability

These analyses were just focused in the interspecific contacts detected using the minimum temporal windows (i.e., windows 1 and 4) because of this is the configuration with higher relevance in the transmission of MTC. The aim of these analyses was to identify the environmental variables increasing the probability of interspecific contacts occurrence. For this purpose, the contacts previously defined were modelled against random points within the overlap area of the seasonal home ranges of the interacting individuals.

Seasonal home ranges (95% Utilization Distribution; see Sodeikat & Pohlmeyer, 2003) of each animal were estimated using fixed-kernel function from the ADEHABITATHR package in R (Calenge, 2006). Intersection of the home ranges of each pair of interacting animals was determined and then a number of points (10 points for each contact between the interacting animals) were randomly located in this area. For both contacts and random points, we extracted eight environmental variables as main predictors of spatial patterns of host abundance and aggregation (Barasona et al., 2014b): surface occupied by dense shrubland (T1), low-clear shrubland (T2), herbaceous grassland (T3), woodland (T4), bare land (T5), watercourse vegetation and water body (T6), distance to water body (DWAT), and distance to the vera (DVER). Information was in raster format (1ha spatial resolution).

Generalized mixed lineal models, with binomial distribution and logit link function, were performed for each window and season. In all cases contact vs. random points was the response variable, environmental variables the predictors and the ID of each pair of contacting individuals the random factor. Models were parameterized using 80% of data and the remaining 20% was reserved for validation purposes. On this independent information the predictive performance of the models was explored using the area under the ROC curve (AUC) for assessing discrimination capacity, and calibration plots and the associated Hosmer-Lemeshow test, for assessing for model reliability (see Jiménez-Valverde et al., 2013).

Finally, we estimated the environmental domain of the models in order to delimit the area within DNP for which models can be projected. The multivariate environmental similarity surface (MESS; see Elith et al., 2010), which represent how similar each 10 ha grid cells (territorial units) in DNP is in relation to conditions in the set of points used for models parameterization, was estimated.

3. RESULTS

3.1. Sampled animals and relocations

During the study period 30 individuals were GPS-collared, 18 wild boars and 12 cattle heads (Figure 3). From this individuals we got 75,372 GPS locations, and after R analyses, 602,873 contacts were identified for windows 6 (see below). A high potential overlapping between tracked domestic and wild ungulates was observed in the study area (Figure 4).

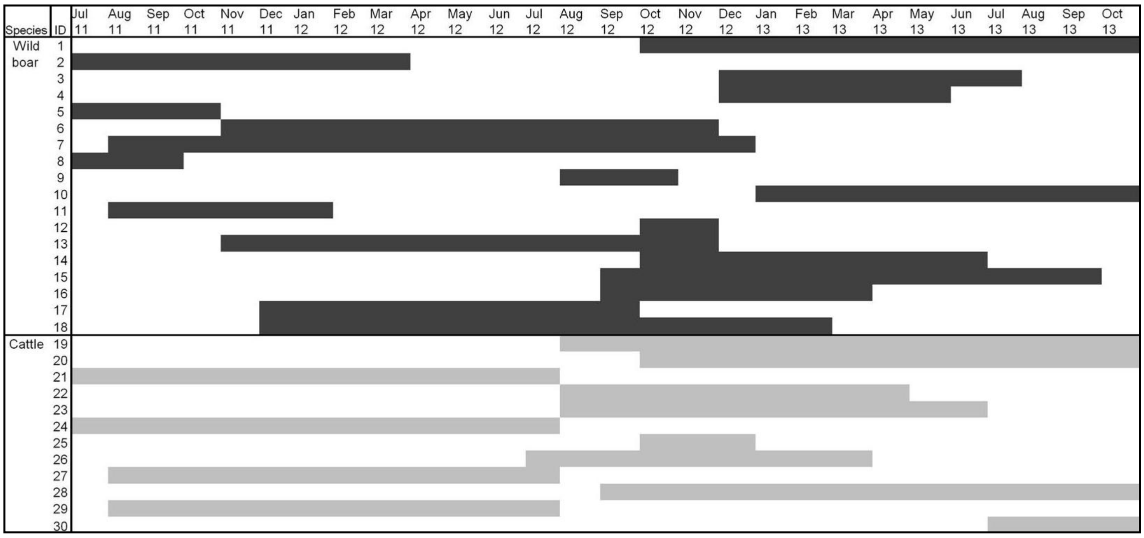

Figure 3. Individuals GPS-collared and duration of the GPS data collection for each wild boar and cattle throughout the study period. Source: Adapted from Barasona et al. (2014a).

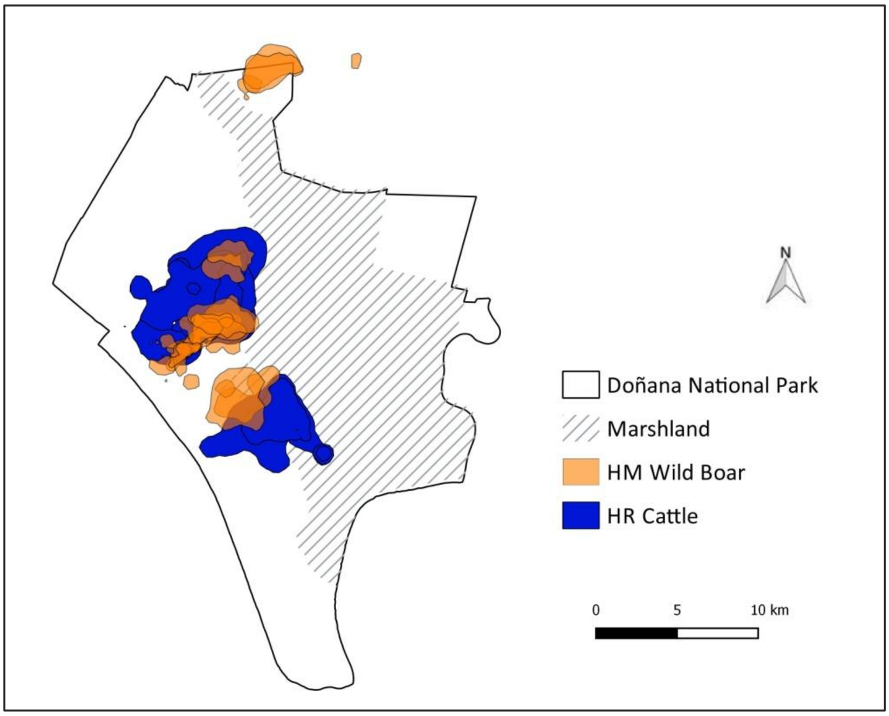

Figure 4. Home ranges (defined as the 95% isopleth of kernel density estimators) of the GPS collared individuals of the study (18 wild boar and 12 domestic cattle).

3.2. Frequency of the contacts

Frequency graphs for both interspecific and intraspecific wild boar contacts for all spatio-temporal windows are shown in Figure 5 (Chi square values can be found in Supplementary Material I: Table SI.2.). Results showed that the relative frequencies of intraspecific contacts were higher in winter, followed by spring and autumn, for all spatio-temporal windows, except for window 1, where the frequency of contacts in winter were smaller than that in spring. Frequencies of interspecific contacts were higher in spring and autumn, and smaller in winter and summer. Finally, contact frequencies were significantly higher for intraspecific than interspecific in winter and spring in all spatio-temporal windows. On the contrary, interspecific frequencies in summer and autumn were significantly higher than intraspecific ones in all windows except in window 1 and 4.

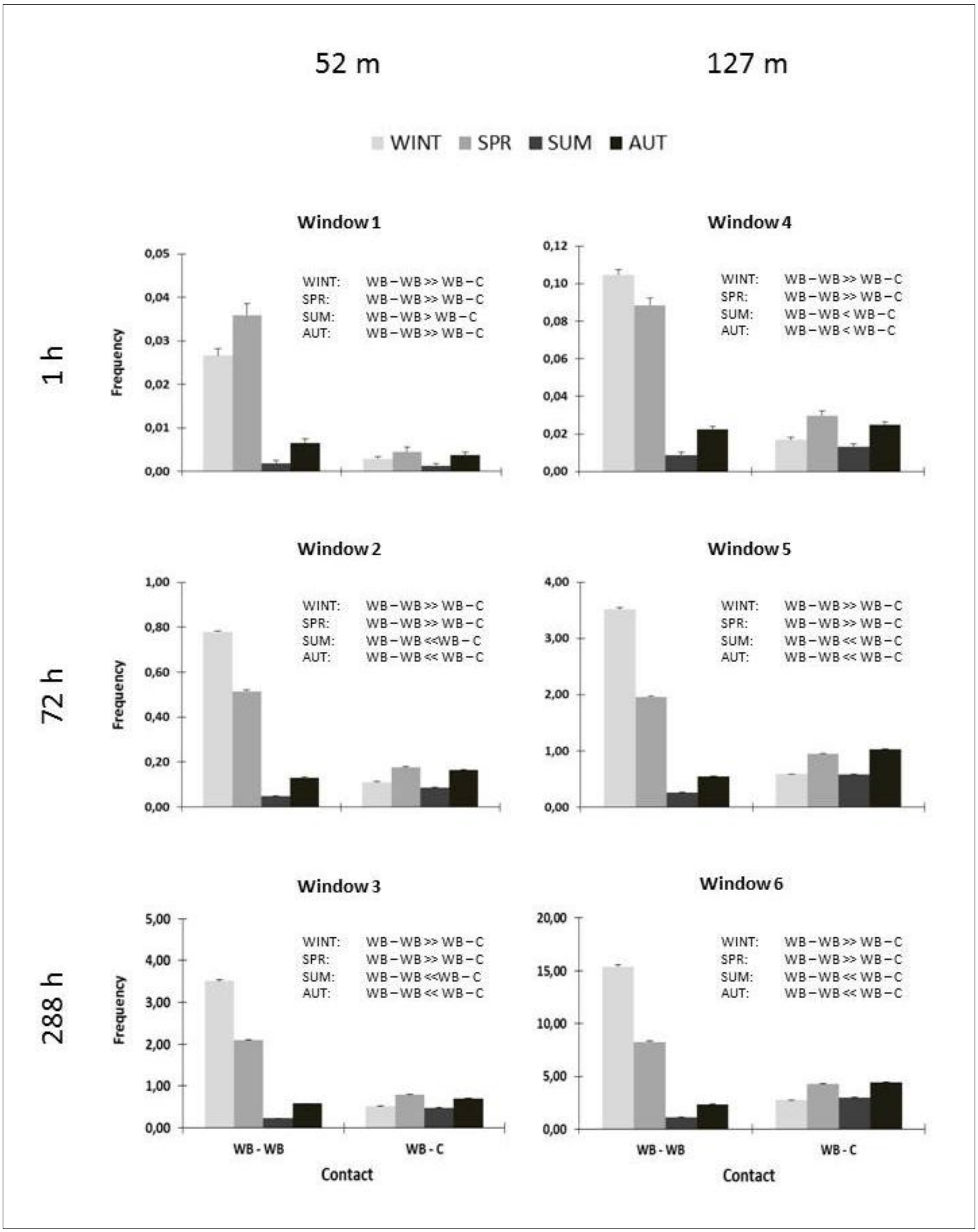

Figure 5. Frequency of the contacts according to contact type (wild boar intraspecific WB-WB, and wild boar and cattle interspecifica WB-C) and season (WINT = winter; SPR = spring; SUM = summer; and AUT = autumn) in each spatio-temporal window. (>> represent significant differences between parameters, > represent not significant differences).

3.3. Spatial patterns of contacts

Interspecific contacts for windows 1 and 4 (Figure 6) presented similar seasonal spatial patterns, with a higher number of contacts in window 4 than in window 1. Visual representation suggests that the number of contacts varied among seasons: spring and summer with a lower number of contacts than winter and autumn, in both windows.

Regarding to the intraspecific contacts between wild boar in windows 1 and 4 (Figure 6), a similar pattern in the distribution range of contacts can be observed. Contacts seem to occur mainly in winter, autumn and spring, and less in summer.

Comparing both type of contacts, there are more intraspecific contacts than interspecific ones, except in summer, where the interspecific were significantly higher than the intraspecific ones. We can also see that both types of contacts appear in the same areas, with the exception of contacts in winter, where intraspecific contacts appear in the north of the park.

Figure 6. Distribution of intraspecific contacts between wild boars (WB – WB) and interspecific contacts between wild boar and cattle (WB – C) in DNP according to season, in Windows 1 and 4. (See also Supplementary material III, Figures SIII.1. and SIII.2.).

The final models carried out to identify the environmental predictors explaining seasonal interspecific contacts can be found in Table 2 (statistical parameters of the models in Supplementary Material I: Table SI.3. and Table SI.4.). No models for winter and spring in window 1 were obtained, likely related to a low number of contacts. Briefly, all seasonal models highlighted the relevance of habitat variables (e.g. T1, T4) and distance to water sources (e.g. DWAT, DVERA) to explain the pattern of interspecific contacts.

Table 2. Seasonal models calibrated to explain the spatial pattern of interspecific contact between wild boar and cattle in Doñana National Park. Results of models validation on independent data are also shown: area under de ROC curve (AUC) and the Chi-square associated to Hosmer-Lemeshow test of the calibration plot. See text for codes of predictors (* = $p < 0.05$).

Window	Season	Model	AUC	χ^2 (*p*)
1	All Seasons	~ -T1 -T4 -DWAT -DVERA	0.67	1.11
	SPR	~ -T1 -DVERA	0.71	17.50 *
	AUT	~ -DVERA	0.49	1.83
4	All Seasons	~ -T1 -T5 -DWAT -DVERA -T4 -T6 -T2	0.69	5.77
	WINT	~ -T4 -T1 -T6 -T2 -T5	0.71	4.16
	SPR	~ -T1 -DVERA -DWAT -T2 -T5 -T4 -T6	0.82	18.44 *
	SUM	~ -T1 -T5 +T4 -DWAT -T6	0.72	9.25
	AUT	~ -DWAT -T4 -T1 -DVERA -T5 -T6 -T2	0.64	7.82

MESS excluded the westernmost area of DNP. Figure 7 shows the prediction of the statistical models in DNP. Cartographic representations of the models showed the relevance of DVERA, and that the pattern obtained for winter (window 4) marked areas of high probability of interspecific contacts that had not been identified by the other models.

In the cartographic representation of the predicted probability for interspecific contact occurrence (Figure 7) we observed a clear pattern of high probability around vera: This pattern is no so marked in the model for all the seasons, neither for winter and summer. It is also remarkable the high probability of contact predicted for areas far away from vera in summer.

Figure 7. Predicted probability of interspecific (wild boar-cattle) contact occurrence according to the seasonal models showed in Table 2.

4. DISCUSSION

4.1. On the methodological approach

Global positioning system is nowadays the most reliable and employed technology used to study fine-scale interaction between species (Latham et al., 2015). Some studies have developed mathematical functions to predict contacts between species (Kilpatrick et al., 2009) but these approaches are not useful to determine real contact rates and potential transmission of diseases. Other techniques allow to detect contacts, as data logger and camera traps (Böhm et al, 2009; Kukielka et al, 2013), however, these ones have limitations in collection and storage of useful data for inter and intraspecific real contacts studies, like date, time or identification of individuals, allowing us to identify risky areas for contacts or individuals prone to interspecific contacts.

4.2. Relative frequency of the contacts

Higher relative frequencies of intraspecific contacts were observed in winter, spring and autumn, for all spatio-temporal windows. Only one interesting exception was observed window 1 (the smallest one), where the frequency of intraspecific contacts was lower in winter than in spring. The intraspecific contacts can be considered as contacts among different wild boar groups since only one animal by group was marked in this study. Bearing this fact in mind, the results suggested that different groups are using the same territories in winter but not direct contacts between animals are established, likely due to the absence of limitation of key resources during this season. The distribution of resource limitation in spring, likely linked to the presence of scarce unflooded areas, can determine the high frequency of contacts for the window 1 (the more similar configuration in our study to direct contacts between individuals). Likely this could be explained by an expansion of wild boar territories to marshland reducing the contact between familiar groups during this season. To our best knowledge, this is the first study determining intraspecific contacts in wild boar and therefore we have not information to contrast our results. They suggested that spring could be a relevant season for establishing intraspecific direct contacts in DNP and that the dry season does not seem to determine high contact rates.

Interestingly, the frequency of intraspecific contacts is quite higher than the interspecific ones for winter and spring, but this relation is inverse in summer and autumn for most of the windows. Fernández-Llario et al., (1996) described that social groups of wild boars depends on the biological cycle of the species that appears to be aggregated in the mating season (winter and spring) and then females tend to separate from other individuals when giving close to birth in summer (Martínez-Rica, 1980). This may explain our observation of increases of the frequency of intraspecific contacts in winter and spring and then a decrease in summer and autumn. Possibly, these separated groups of wild boars tend to contact with cattle in summer and autumn near to limiting resources which increase interspecific contacts.

The relative frequency of interspecific contacts was higher in spring and autumn, than in winter and summer, and the summer was the season that, consistently for all spatio-temporal windows, achieved the lowest frequency. This result, a priori, does not match with previous studies (e.g., Kukielka et al., 2013; Miguel et al. 2013), in which higher interspecific contact rates were observed during the dry seasons (summer and autumn) near to commonly used restricted resources. However, in DNP resources are limited at the end of summer and autumn, and likely this environmental asynchrony is able to explain the low number of contacts determined in summer.

Similarly to the results obtained for the intraspecific contacts, spring seems to be a critical season for establishing higher interspecific contacts in our study area. As previously stated, the marshland dynamics could explain these results. Summarizing, our results pin pointed that spring and autumn are the more relevant seasons for establishing interspecific contacts, and therefore with higher potential of pathogen transmission in our study area. This result also highlights the relevance of the environmental gradients explaining interspecific contact rates. However, a more in detail exploration of the contacts determined in our study, for instance, by determining the contacting individuals, exploring the daily patterns of the contacts, and characterizing the contacts in terms of selected resources, would be carried out for a better understanding of the seasonal patterns of both intraspecific and interspecific contacts.

4.3. Where do the contacts occur?

Spatially explicit statistical modelling clearly shows the relevance of some habitat uses and the proximity to water for establishing direct contacts. According to previous studies, our results suggested that contacts do not occur in areas with dense vegetation as dense shrublands and woodlands and also highlighted the relevance of the proximity to water points and vera in explaining contacts patter in DNP (Barasona et al., 2014a). Therefore, contacts generally occurred in the habitats forcing high aggregation of hosts (Barasona et al., 2014b).

The predicted pattern of probability for interspecific contact occurrence was quite consistent among seasons and spatio-temporal windows of analyses. However, a higher potentiality for interspecific contacts was predicted for summer, mainly in southern areas. This result appears because the environmental potential for contacts is scarce in this area, and therefore animals should aggregate in some favorable areas (Barasona et al., 2014b). Looking for predicted patterns, some differences in the expected contact rates between seasons are observed. So, for instance, in southern areas the higher frequency of interspecific contacts is expected for summer, which reinforces the idea of higher contact rates during dry season (Kukielka et al., 2013). Therefore, interspecific contacts patterns and their seasonality are not consistent in all areas of DNP, and they are likely modulated by the effects of dynamic of marshlands and the presence and abundance of risk points in the area.

5. CONCLUSIONS

The main conclusions obtained in this study are:

I. Frequency of intraspecific contacts between wild boars are higher in spring and winter, probably due to aggregation of wild boar groups during the mating season in unflooded areas.
II. Frequencies of interspecific contacts are higher in autumn, which can be explained by the aggregation of wild boars and cattle around limiting resources which start to be scarce at the end of summer. Spring seem to be critical too in the establishment of interspecific contact because of the marshland dynamics.
III. The proximity to water points and to vera ecotone are crucial to determine the contact probability in Doñana National Park.
IV. Pattern of contact probabilities are consistent in values and also in distribution among seasons, except on summer, where we found higher probabilities of contact located in southern areas because of the aggregation of individuals in scarce favorable areas.

After this study we can conclude that potential transmission of pathogens occur in dry seasons (autumn and summer) as shown by previous studies, but also in spring due to marshland dynamics. Distance to vera and to water points are key factors to predict contact probability joined to other environmental resources.

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SUPLEMENTARY MATERIAL I: Tables

Table SI.1. Techniques used in controlling the transmission of different diseases between wild and domestic animals.

Technique	Wildlife - Livestock	Disease	Study
Latent selection difference functions (LSDs)	Wild boar - Cattle	Bovine tuberculosis	Barasona et al., 2014a
Radio collar, GPS collar, interviews from local farmers	Elk – Cattle	Bovine tuberculosis	Brook et al., 2009
GPS collar	Feral swine – Domestic swine	Brucellosis	Wyckoff et al., 2009
Mathematic functions	Bison – Cattle	Brucellosis	Kilpatrick et al., 2009
Proximity data loggers	Badgers – Cattle	Bovine tuberculosis	Böhm et al., 2009
GPS collar	Feral swine – Cattle	Foot-and-mouth disease	Cooper et al., 2010
Camera trapping	Wild boar, red deer – Cattle, domestic pigs	Bovine tuberculosis	Kukielka et al., 2013
GPS collar	African buffalo – Cattle	Foot-and-mouth disease	Miguel et al., 2013

Table SI.2. Chi square values (χ^2) from season frequencies according to the three different contacts in the spatio-temporal windows. (Values in bold represent those no significant differences between parameters). (WB = Wild Boar; C = Cow; WINT = Winter; SPR = Spring; SUM = Summer; AUT = Autumn).

		Season			
Window	**Contact**	WINT	SPR	SUM	AUT
1	WB – WB /WB – C	212.56	119.04	**0.53**	6.86
2	WB – WB /WB – C	4199.11	634.25	50.39	32.83
3	WB – WB /WB – C	11273.81	1290.22	335.01	72.4
4	WB – WB /WB – C	686.82	138.67	**4.63**	**0.88**
5	WB – WB /WB – C	10197.82	752.96	438.75	772.81
6	WB – WB /WB – C	16520.07	945.56	1577.13	1460.77

Table SI.3. Statistical parameters of the models carried out to determine the probability of interspecific contact occurrences in DNP, using contacts determined by window 1.

		Estimate	**Std. Error**	**z value**	**Pr (>|z|)**	
All Seasons	**(Intercept)**	-2.798	0.335	-8.354	< 2E-16	***
	T1	-1.565	0.509	-3.072	2.130E-03	**
	T2			-		
	T4	-3.122	1.919	-1.627	1.038E-01	
	T5			-		
	T6			-		
	DWAT	-0.628	0.243	-2.578	9.940E-03	**
	DVERA	-0.709	0.346	-2.048	4.053E-02	*
WINT			Model null			
SPR	**(Intercept)**	-3.741E+00	1.029E+00	-3.635	2.790E-04	***
	T1	-1.469E+03	1.465E+07	0	9.999E-01	
	T2			-		
	T4			-		
	T5			-		
	T6			-		
	DWAT			-		
	DVERA	-1.721E+00	1.118E+00	-1.54	1.236E-01	
SUM			Model null			
AUT	**(Intercept)**	-4.298	1.017	-4.226	2.380E-05	***
	T1			-		
	T2			-		
	T4			-		
	T5			-		
	T6			-		
	DWAT			-		
	DVERA	-2.268	1.086	-2.087	3.690E-02	*

P-values are shown as: ( ) = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Table SI.4. Statistical parameters of the models carried out to determine the probability of interspecific contact occurrences in DNP, using contacts determined by window 4.

		Estimate	Std. Error	z value	Pr (>|z|)	
All Seasons	**(Intercept)**	-2.462	0.127	-19.340	< 2E-16	***
	T1	-2.270	0.213	-10.668	< 2E-16	***
	T2	-0.862	0.162	-5.305	1.130E-07	***
	T4	-1.968	0.335	-5.877	4.170E-09	***
	T5	-3.418	0.555	-6.160	7.280E-10	***
	T6	-0.860	0.159	-5.413	6.210E-08	***
	DWAT	-0.956	0.099	-9.631	< 2E-16	***
	DVERA	-0.864	0.118	-7.340	2.130E-13	***
WINT	**(Intercept)**	-1.314	0.152	-8.651	< 2E-16	***
	T1	-1.762	0.336	-5.243	1.580E-07	***
	T2	-1.237	0.305	-4.061	4.890E-05	***
	T4	-3.307	1.006	-3.288	1.010E-03	**
	T5	-2.526	0.901	-2.802	5.070E-03	**
	T6	-1.390	0.303	-4.595	4.330E-06	***
	DWAT			-		
	DVERA			-		
SPR	**(Intercept)**	-3.387	0.516	-6.569	5.050E-11	***
	T1	-4.649	0.808	-5.754	8.690E-09	***
	T2	-1.860	0.380	-4.890	1.010E-06	***
	T4	-1.828	0.637	-2.872	4.080E-03	**
	T5	-2.678	0.764	-3.506	4.550E-04	***
	T6	-1.055	0.364	-2.900	3.736E-03	**
	DWAT	-1.717	0.329	-5.219	1.800E-07	***
	DVERA	-2.092	0.548	-3.817	1.350E-04	***
SUM	**(Intercept)**	-2.040E+00	2.161E-01	-9.438	< 2e-16	***
	T1	-9.438E+00	5.261E+00	-1.794	0.073	·
	T2					
	T4	1.917E+00	7.001E-01	2.739	0.006	**
	T5	-3.290E+03	1.852E+07	0.000	1.000	
	T6	-9.785E-01	4.588E-01	-2.133	0.033	*
	DWAT	-5.640E-01	2.396E-01	-2.354	0.019	*
	DVERA			-		
AUT	**(Intercept)**	-2.586	0.261	-9.905	< 2E-16	***

T1	-1.729	0.302	-5.730	1.000E-08	***
T2	-0.832	0.278	-2.992	2.771E-03	**
T4	-5.377	1.465	-3.670	2.430E-04	***
T5	-4.407	1.258	-3.504	4.590E-04	***
T6	-1.163	0.287	-4.044	5.240E-05	***
DWAT	-1.262	0.160	-7.898	2.830E-15	***
DVERA	-0.930	0.268	-3.475	5.110E-04	***

P-values are shown as: ( ) = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

SUPLEMENTARY MATERIAL II: R Script

Script SII.1. Spatio-temporal windows: contacts.

```
##################################################
#                                                #
# ANALYZING DATA FOR SPATIO-TEMPORAL CONTACTS  #
#     20-02-2015 R Triguero, JA Barasona, P Acevedo       #
#                                                #
##################################################

# The aim of this analysis is to identify contacting relocations of different radio-tracked animals. Two
# relocations are considered as contact when:
# 1) they are of different animals
# 2) they are closer than a previously defined spatial window
# 3) they are closer in time than a previously defined temporal window
# The script starts with relocations of the animals and generates a table containing the identified
contacts

DIST<-c();  TIME<-c();  DATE<-c();IND_ref<-c();  IND_par<-c();  LOC_ref<-c();  LOC_par<-c();  Xmean<-c();
Ymean<-c() # empty vectors are created to save the parameters associates to each contact

for (i in 1:length(loc_IDs)) # The loop, for each relocation
  ID.i<-loc_IDs[i]
  data.i<-data[data$ID_loc==ID.i,]
  x<-data.i$X
  y<-data.i$Y
  fecha_ref<-data.i$Date
  hora_ref<-data.i$H
  Indiv<-data.i$ID
  ID_ref<-data.i$ID_loc

  data.i2<-data[data$ID!=Indiv,]
  data.i2$horas<-abs(as.numeric(fecha_ref-data.i2$Date))*24+abs(hora_ref-data.i2$H)
  data.i2<-data.i2[data.i2$horas<=288,] #maximum temporal window
  data.i2$dist<-sqrt((x-data.i2$X.X)**2+(y-data.i2$X.Y)**2) # Euclidean distance
  data.i2<-data.i2[data.i2$dist<=127.7,] # Maximum spatial window
```

```
if(dim(data.i2)[1]>0){
  for (j in 1:dim(data.i2)[1]){
  xj<-data.i2$X.X[j]
  yj<-data.i2$X.Y[j]
  fecha_par<-data.i2$Date[j]
  hora_par<-data.i2$H[j]
  Indiv_par<-data.i2$ID[j]
  ID_par<-data.i2$ID_loc[j]

  horas<-abs(as.numeric(fecha_ref-fecha_par))*24+abs(hora_ref-hora_par) # Distance in hours to LOC_ref
  dist<-sqrt((x-xj)**2+(y-yj)**2) # Euclidean distance to LOC_ref

  xmean<-((abs(x-xj))/2)+min(x,xj) # Average coordinate between LOC_ref and LOC_par
  ymean<-((abs(y-yj))/2)+min(y,yj)

  LOC_ref<-c(LOC_ref, ID_ref)
  LOC_par<-c(LOC_par, ID_par)
  Xmean<-c(Xmean,xmean)
  Ymean<-c(Ymean,ymean)
  DIST<-c(DIST, dist)
  TIME<-c(TIME,horas)
  DATE<-c(DATE,fecha_ref)
  IND_ref<-c(IND_ref, Indiv)
  IND_par<-c(IND_par, Indiv_par)
 }}}

data.i3<-data.frame(IND_ref, LOC_ref, IND_par, LOC_par, Xmean, Ymean, DIST, TIME, DATE)

data.i3$ID_unique<-paste(pmin(data.i3$LOC_ref,data.i3$LOC_par)
pmax(data.i3$LOC_ref,data.i3$LOC_par), sep="-") # We remove duplicated contacts
data.i4 <- data.i3[!duplicated(data.i3$ID_unique),]
```

SUPLEMENTARY MATERIAL III: Figures

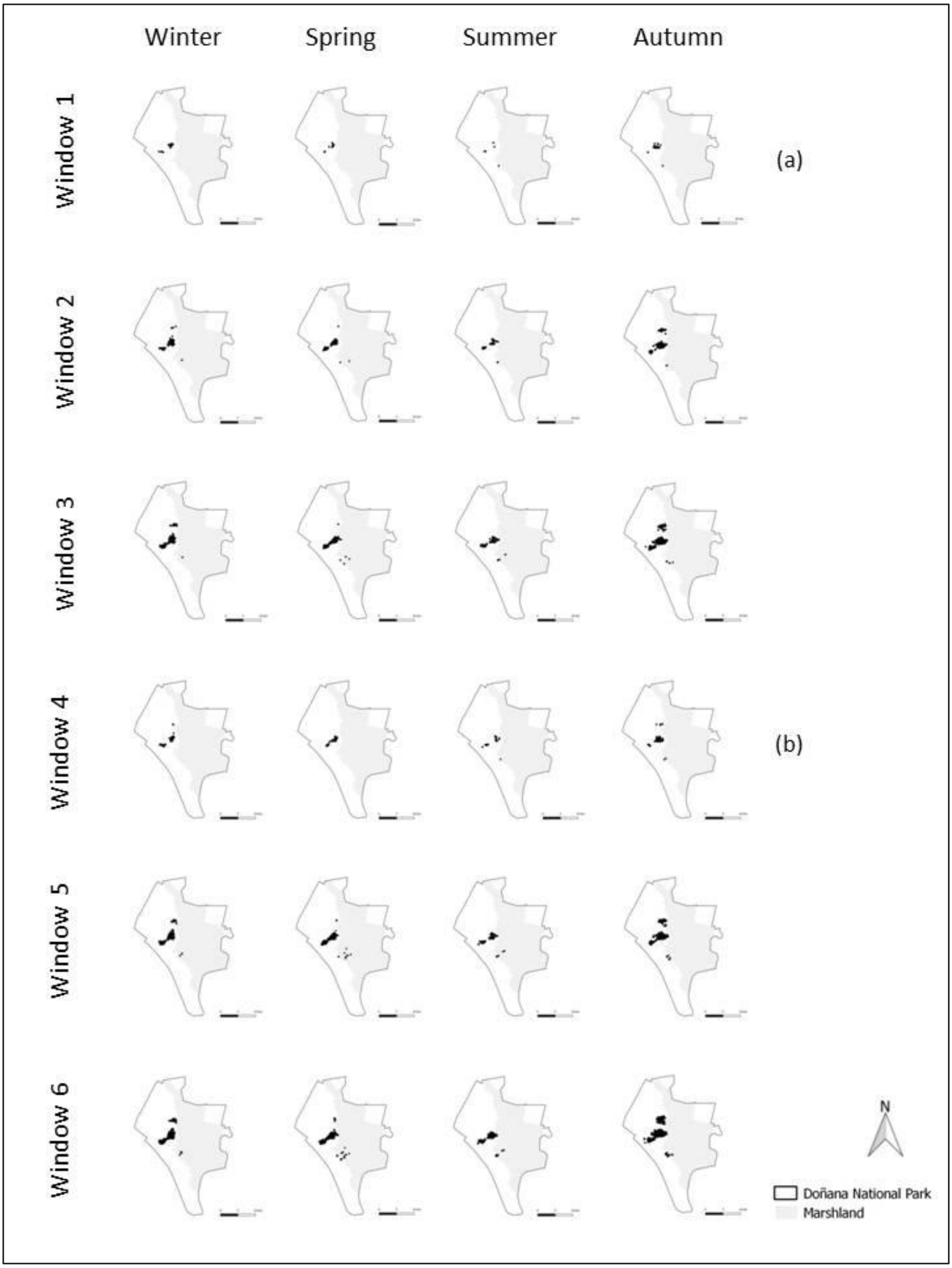

Figure SIII.1. Distribution of interspecific contacts (WB – C) in DNP according to season, in Windows 1 to 6.

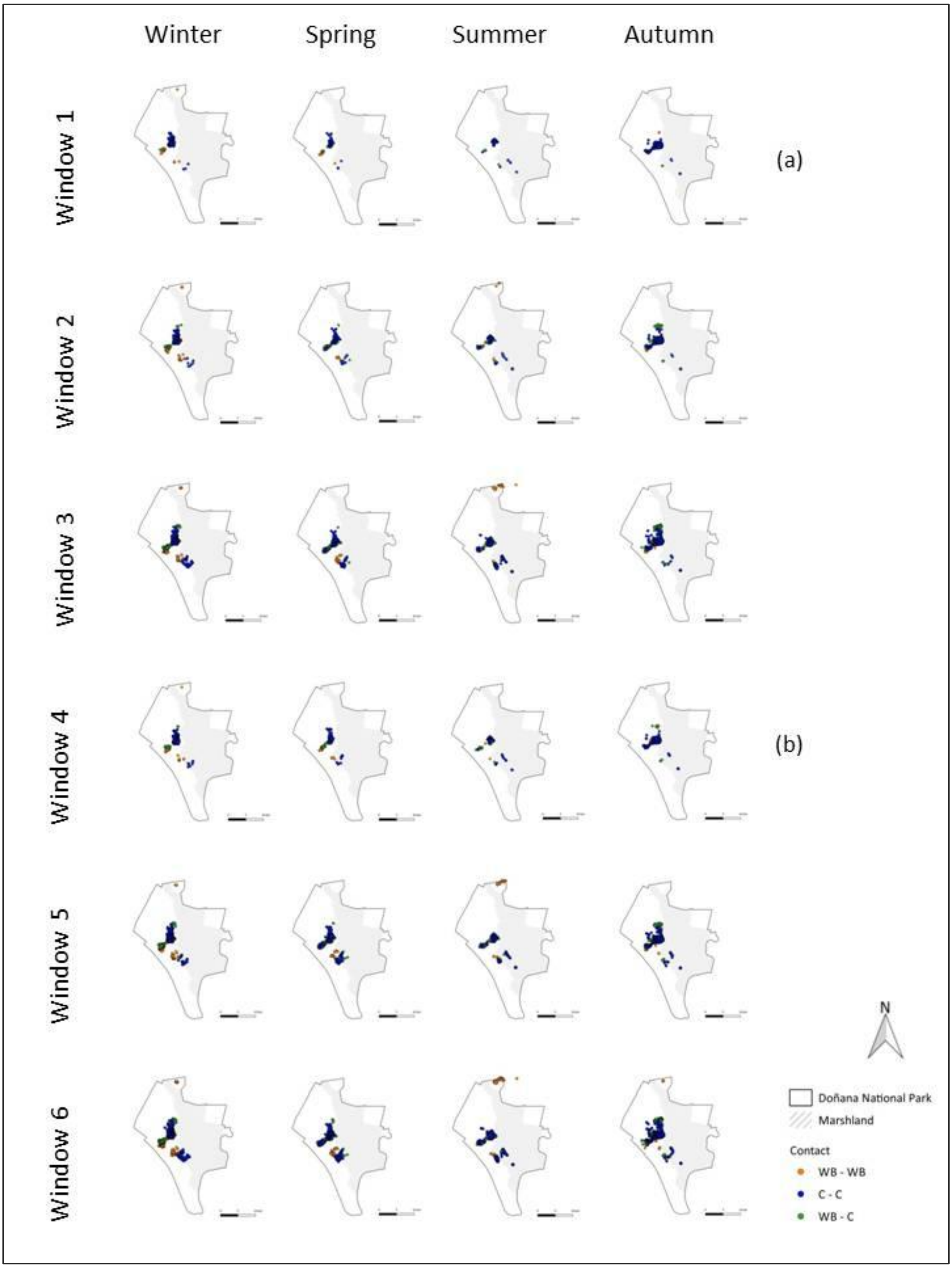

Figure SIII.2. Distribution of intra and interspecific contacts (WB – C, C – C, WB – C) in DNP according to season, in Windows 1 to 6.

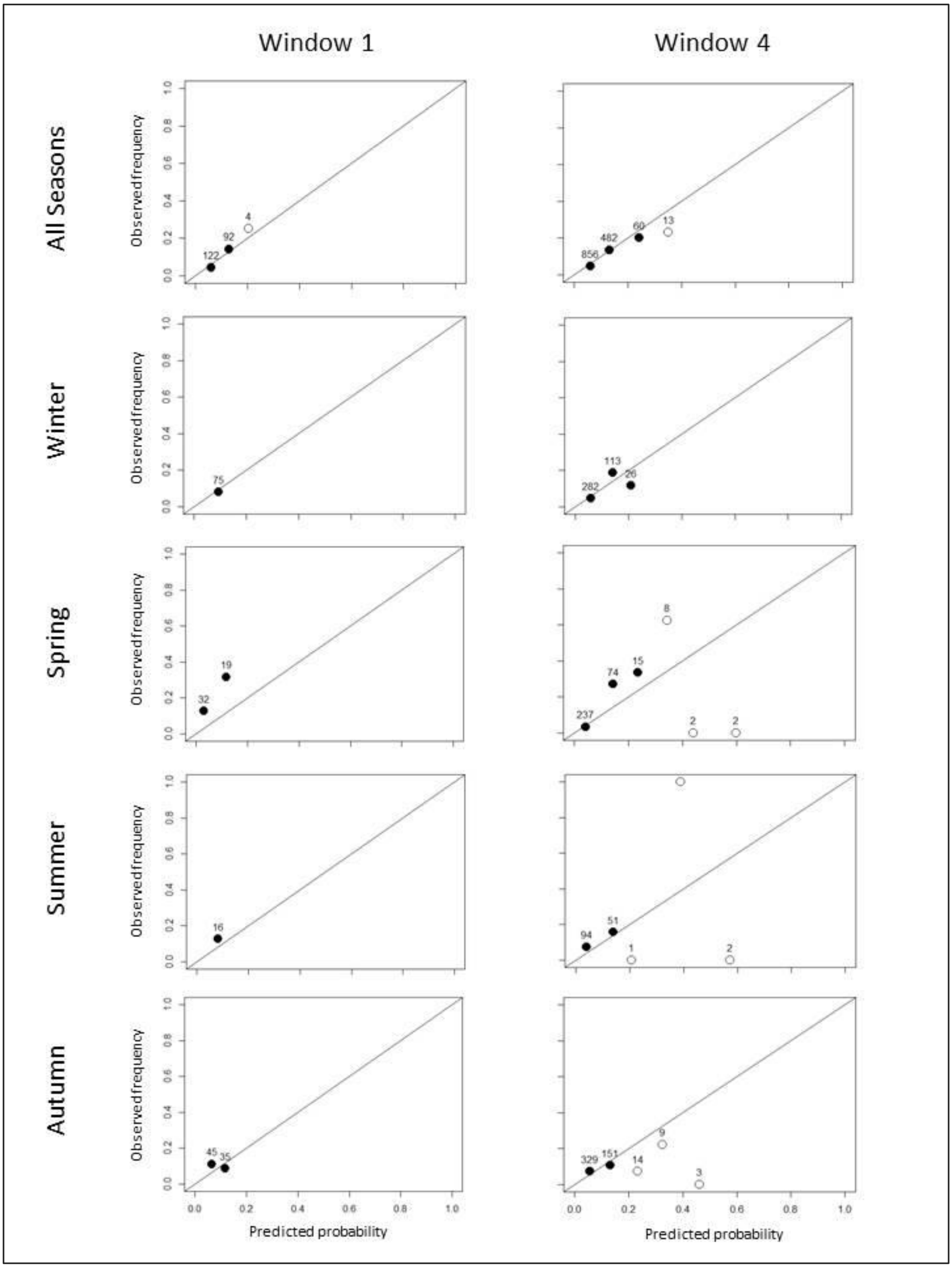

Figure SIII.3. Calibration plots of the studied model for Window 1 and 4 according to each season and all the season together.