The wildlife-livestock interface on extensive free-ranging pig farms in central Spain during the “montanera” period

Interspecific interactions during montanera period (running head)

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SUMMARY

The effective management of shared pathogens between wild ungulates and livestock requires the understanding of the processes of interaction between them. In this work we studied the interspecific frequency of interaction (ifreq) and its spatio-temporal pattern between wild and domestic ungulates that coexist in free-ranging farms. For this purpose, 6 red deer, 6 wild boar, 8 Iberian pigs and 3 cattle were monitored using GPS devices during the “montanera” period (the period in which Iberian pigs are maintained in extensive conditions to feed on acorn). The ifreq was quantified for two spatio-temporal windows: 30 m – 10 minutes, for inferring potential direct interactions (short window), and 30 m – 12 days for indirect interactions (large window). Secondly, the variation in the ifreq was modelled with regards to 2 temporal (time of the day and week of the year) and 4 environmental factors (distance to water, distance to vegetation cover, tree density of the genus *Quercus* and distance to supplementary feeding points). The interactions at the short window were scarce (N = 13), however, they were very frequent at the large one (N = 37,429), with the red deer as the species with the greatest involvement in the interactions. Models showed that the time of the day and distance to water were the variables that best predicted the ifreq and they were conditioned by differences in the activity pattern of the targeted species. Food resource availability also predicted the ifreq, especially at the short window and between wild species. The results presented here highlight the role that wild ungulates may play in the transmission of pathogens to extensive livestock in general and pigs in particular, and show the epidemiological risk of certain areas, periods of time and management practices (for wildlife and livestock) as well as providing useful information in the prevention of the transmission of shared pathogens.

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45 **KEYWORDS**

46 Frequency of interaction; Iberian pig; quantitative methodology; risk factor analysis; shared
47 infections; wild ungulates

48

49 **INTRODUCTION**

50 Infections shared between wildlife and livestock are a major concern in society, due to the
51 economic repercussions and because many of them are zoonotic (Wiethoelter et al. 2015).
52 The definition of the wildlife-livestock interface (W/L interface) implies direct and indirect
53 interactions between wildlife and livestock, and responds to the specific case of study, since
54 it can be linear (e.g. fences), habitat dependent by focal (e.g. water points) or even more
55 diffuse shared resources (e.g. pastures) (see Bengis et al. 2002). Infectious pathogens at this
56 interface may be transmitted bidirectionally between groups of animals, mainly through
57 indirect interactions at shared resources, or through vectors (Bengis et al. 2002; Gortázar et
58 al. 2007). The correct management of the W/L interface, therefore, requires science-based
59 information (Vicente et al. 2019) and that has become a challenge for managers, veterinarians
60 and ecologists (e.g. Cozza et al. 1996; Gortázar et al. 2015), especially in the case of
61 transboundary emerging diseases, such as currently African swine fever (ASF, e.g. Sánchez-
62 Vizcaíno et al. 2013).

63 In Spain, the pig production system accounts for 37% of the total livestock produced,
64 providing the largest production of pork at European level, together with Germany (Martínez-

Avilés et al. 2018). In the south-west of Spain, the production of Iberian pig as an autochthonous breed, highly appreciated for the organoleptic quality of its meat, is carried out in free-ranging production systems. Recent studies have highlighted the epidemiological risk of this type of production for domestic pigs due to interaction with wildlife, as potential disease reservoirs (Cano-Terriza et al. 2018; López-López et al. 2018). The production cycle of Iberian pig mostly ends with fattening through feeding the acorn mast in extensive conditions between autumn and winter, a period called “montanera” (Rodríguez-Estévez et al. 2009; de Miguel et al. 2015). This practice is mainly located in the so-called “dehesas”, agroforestry systems characterized by the presence of trees in low density of the genus *Quercus*, low shrubland and pasture (Cañellas et al. 2007). The dehesas are complex systems which maintain the extensive mixed production of domestic animals such as pigs, cattle, sheep and goats, but they are also used for big game, mainly, red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) (Olea and San Miguel 2006). These farms are usually parcelled with livestock fencing to differentiate and manage herds among domestic animals. However, this fencing is permeable to wildlife (Carrasco-García et al. 2016) and therefore wild animals share space and resources with domestic ones, entailing a high epidemiological risk (e.g. Carrasco-García et al. 2016; Cowie et al. 2016; LaHue et al. 2016; Barasona et al. 2017).

An epidemiological interaction is the event during which different individuals potentially come directly/indirectly into contact. The frequency of interactions, defined as the number of interactions per time and available animal to interact (Böhm et al. 2009), is a key parameter to determine the process of pathogen transmission (White and Harris 1995; McCallum et al. 2017). Therefore, obtaining accurate values of this parameter, as well as the determination of the areas with the highest risk for these interactions to occur, is essential for the

implementation of effective disease control measures (Osnas et al. 2009; Williams et al. 2014). Previous works have described the pattern of interaction between domestic animals (i.e. cattle and backyard pigs) and wildlife, showing the importance of: i) indirect interactions as regards direct ones, ii) the limiting resources such as water and food points as risky areas, and iii) the autumn as a critical season for the occurrence of interactions in Mediterranean environments (e.g. Kukielka et al. 2013; Carrasco-García et al. 2016; Cowie et al. 2016; Jori et al. 2017; Cadenas-Fernández et al. 2019). These studies used camera trapping, proximity loggers, GPS at low fixation frequency and epidemiological questionnaires to characterize the interactions at this W/L interface. Specifically, a recent study addressing the characterization of interactions between wild boar and cattle through GPS technology showed that these two species interact approximately 3 times per day in Mediterranean environments and highlighted the crepuscular hours and the key resources (such as water points) as relevant factors driving interactions (Triguero-Ocaña et al. 2019). However, to our knowledge there are no previous works characterizing the frequency of interaction between wild ungulates and livestock and its spatio-temporal variation in free-ranging farms used for Iberian pig production. Therefore, in the present work we aimed to study the interactions between domestic (cattle and Iberian pigs) and wild (red deer and wild boar) ungulates coexisting in free-ranging production systems, characterizing for the first time the potential relevance of different domestic and wild species in the transmission of pathogens during a critical period of time in these systems, such as the montanera period. To this end we used GPS technology at a high spatio-temporal resolution. Specifically, we aimed i) to quantify the frequency of interaction among species as a potential source of cross-transmission of pathogens and ii) to explore temporal and spatial patterns in the interaction frequency. In the

present study, we detect and estimate the frequency of interaction as a proxy of the real interactions taking place in our study area. These interactions do not necessarily imply a real transmission of pathogens, but a potential for the transmission of pathogens during the process of interaction.

MATERIALS AND METHODS

Study area

The study was conducted in five free-ranging adjoining farms within the province of Cáceres, in the southern border of Sierra de San Pedro, Extremadura region, central Spain (39°10'40"N 6°37'43"O). The total surface of these farms is 3530 ha. The typical vegetal cover is the dehesa, a savannah-like open tree layer ecosystem dominated by the presence of Mediterranean evergreen oaks: holm oak (*Quercus ilex*) and cork oak (*Q. suber*) (Joffre et al. 1999). The area has a Mediterranean climate with a continental influence: the average annual temperature is 17.1°C, and the average annual rainfall is 447 mm with high intra-annual variability (from 4 – 69 mm per month) (29 years of monitoring) (AEMET, Badajoz meteorological observatory). All these farms are characterised by the free-ranging maintenance of Iberian pigs within large fenced (only livestock proof) pens during the montanera period (October/November – January/February). Commercial hunting of red deer and wild boar also takes place. The average annual hunting bag (as a proxy for the abundance of wild ungulates) of the study area, was 10 red deer/km² and 1 wild boar/km² for the 2016-2019 hunting seasons (data provided by the landowners and game managers).

Animal capture and monitoring

During the montanera of 2017/2018, 6 red deer, 6 wild boar, 8 Iberian pigs and 3 cattle were captured and marked with GPS devices. Since wild animals can move freely inside and outside the farms, both red deer and wild boar were captured inside the farms where the targeted livestock was maintained in order to maximise the probability that wild individuals had these farms within their home ranges. Wild animals were captured in different trapping areas in order to obtain individuals from different social groups. Red deer were captured using corral traps, which consist of seven 5 m wide panels and a drop door that closes once the deer releases the holding rope of the door (Vassant and Brandt 1995). Red deer were anesthetized with a combination of xylazine-ketamine following the protocol described by Marco and Lavin (1999). Five of the 6 captured red deer were males (2 yearlings [< 1 year old] and 3 sub-adults [between 1 and 2 years old]) and 1 adult female (>2 years old). The wild boar were captured with portable padded foothold cage traps that were triggered when a wild boar stepped on a mobile-bottomed platform in the centre of the trap. The wild boar were anesthetized with a combination of tiletamine-zolazepam and medetomidine (for further details about wild boar capturing procedure see Barasona et al. 2013a). From the 6 targeted wild boar, 3 were males (2 yearlings and 1 sub-adult) and 3 females (2 sub-adults and 1 adult). Both the domestic pigs and the cattle were collared during routine veterinary inspections. All targeted pigs were sub-adults (following the cycle of pig production in free-ranging conditions), 5 males and 3 females, and were marked in different pig batches (except two batches which had 2 marked pigs in each one) in order to monitor the movement of the different groups among different plots. Finally, 3 adult female cattle were marked in the same farm (only one of the 5 selected farms in our study had cattle production).

Three types of devices were employed to monitor animals' activity: (i) red deer and cattle were collared with GPS-GSM devices manufactured by Digitanimal S.L. (Madrid, Spain), which had a positioning error of 12 m; (ii) wild boar were collared with GPS-GSM devices manufactured by Microsensory S.L. (Córdoba, Spain), which had a positioning error of 12 m; (iii) finally, the domestic pigs were marked with GPS ear-tags (Microsensory S.L.), which had a positioning error of 13 m, according to field trials carried out at the beginning of the captures following the protocol presented by Barasona et al. (2014a). The fixation interval was set to 10 minutes in all devices. For each relocation, devices recorded the geographical coordinates, date, time and the ID of the individual. For wildlife species, we removed the location data of the first day, since after the handling procedure animals could have anomalous behaviours (see Morellet et al. 2009; Barasona et al. 2013a). Finally, the average fix-rate success for devices was 70%. See the number of GPS locations per species in Supplementary Material: Table S1.

Interaction rate modelling

Determination and frequency of interactions

In our specific case of study, an interaction is defined as the location of a specific individual at a certain distance and within a temporal window from the location of another individual. So, the first step before determining the existence of interactions is to define the spatio-temporal window that is going to be considered, that means, the Euclidean distance and the time between relocations of different animals. In our case, two windows were defined. The period of time for the first spatio-temporal window was 10 minutes, given the technical specifications of the devices and the consideration of potential transmission of pathogens

through direct interactions (e.g. Aujeszky's virus; Donaldson et al. 1983), and the spatial threshold was 30 m due to the mean positioning error of the devices ($13 \text{ m} \pm 0.2 \text{ SE}$) (hereafter short window). The second spatio-temporal window was established according to the potential transmission of pathogens through indirect pathways. In this case, the temporal window was set as 12 days due to the average environmental survival time of bacteria of the *Mycobacterium tuberculosis* complex that cause animal tuberculosis (TB; an endemic disease in wild ungulates in south-central Spain; see Vicente et al. 2013) under the climatic conditions found during the montanera period (high humidity and low temperature) (see Kukielka et al. 2013), and the spatial window remained the same (30 m; hereafter large window). Since the spatial window remained equal for the two windows considered, we will talk about "spatio-temporal" or "temporal" window interchangeably hereafter.

The interaction frequency between species pair (ifreq) was estimated following the methodology proposed by Böhm et al. (2009). Briefly, using R software 3.5.3 (R Core Team 2018), for each relocation of a given ID (i) we identified the relocations of other individuals (j) that were inside the predefined spatio-temporal window, and consequently resulted in an interaction (#int). After that, we calculated the number of individuals of different species with a valid relocation within the temporal window considered and the home range (minimum convex polygon 95%, Calenge 2006) of the reference individual (i) (#avail). The home range of (i) was obtained using all the locations within a temporal window of 12 days (according to the larger temporal window used to define interactions). Finally, the ifreq of an individual (i) at date (x) and time (y) was calculated as: $ifreq_{i,x,y} = \frac{int_{i,x,y}}{avail_{i,x,y}}$ (see also Triguero-Ocaña et al. 2019). This value, therefore, represents the number of interactions that

generates a given relocation in 10 minutes/12 days (depending of the window), per the number of available individuals to interact. The ifreq was calculated using the two temporal windows for all possible pairings: red deer – wild boar, red deer – cattle, red deer – pig, wild boar – cattle, wild boar – pig and cattle – pig.

Spatio-temporal factors predicting the frequency of interaction

In order to study the spatio-temporal variation in the frequency of interactions, we modelled the ifreq in each temporal window using a generalised linear mixed model with a negative binomial distribution (after confirming over-dispersion when modelling with a Poisson distribution) and a logarithmic link function, with the “lme4” R package (Bates et al. 2015). IDs of the interacting individuals were considered as random effect factors in order to account for spatio-temporal dependence in data, mostly related with the range of the interacting individuals. Two temporal and four environmental predictors were considered to explain variation in ifreq. The first temporal predictor was the hour of the interaction (Hour), reclassified in four categories according to common activity patterns observed in the targeted species (H1: 0:00 – 5:59, night hours ; H2: 6:00 – 11:59, sunrise; H3: 12:00 – 17:59, central hours of the day; H4: 18:00 – 23:59, sunset) (for more information about activity patterns see Supplementary Material: Figure S1). The other temporal predictor was the week of the year (Week), as a measure of the time elapsed within the study period, since environmental conditions and farm management, and therefore the risk of interaction, are expected to vary along the montanera period. The environmental predictors were selected according to the most probable risk factors in this environment (e.g. Kukielka et al. 2013): (a) distance to water in meters (DW); (b) distance to supplementary feeding points for wildlife in meters, which was only considered for the interactions between red deer and wild boar (although the

supplementation of food to wildlife for hunting purposes is not allowed, it is a common practice in several extensive farms during the hunting season) (DFP); (c) density of oak trees (n° of trees per 2500 m²) as providers of acorn (DT), which was derived through LiDAR technology (LiDAR – PNOA, Instituto Geográfico Nacional) and the “ForestTools” package (Plowright 2018); and (d) distance in meters to dense vegetation as a refuge for wildlife (DV) (Spanish Land Use Information System, SIOSE 2014). The environmental predictors were normalised in order to use the same scale for all of them. See the range, mean value and standard deviation of each environmental predictor per type of interspecific interaction in Supplementary Material: Table S2.

In the model parameterized for the short window, data for all type of interspecific interactions (red deer – wild boar, red deer – cattle, red deer – pig, wild boar – cattle, wild boar – pig and cattle – pig) were pooled and the type of interaction was included as a fixed effect factor. We opted to combine all data in this model due to the small number of interactions when independent models were tried for each interaction type. For the large-window model, each type of interaction was separately modelled (six models), since the spatio-temporal patterns are expected to vary according to host species distribution and their activity and habitat use patterns. Different hypotheses on the factors explaining variation in ifreq were tested (our candidate models). The first candidate model was that variation in ifreq is mainly explained by the temporal predictors, responding to the different activity patterns of the species (explained by the predictor Hour) and environmental and management changes along the study period (explained by the predictor Week). In the subsequent candidate models, we have forced the predictor Hour since we hypothesised that the use of the environmental resources by the different species will vary over the day (see also Triguero-Ocaña et al. 2019).

Therefore, the second candidate model included Hour plus water resources (DW), the third candidate model included Hour and refuge for wildlife (DV), and the fourth candidate model included Hour and food resources (DT, including DFP in the case of red deer – wild boar interactions). The fifth candidate model included Hour and resources related ones (food and water), since the last predictors can act combined as wildlife attractants to domestic plots. Finally, we checked the capability of all the predictors together explaining the ifreq in the last candidate model (see the candidate models in Table 1). We compared the candidate models and the most parsimonious one was selected using the Akaike’s Information Criterion (AICc; Akaike 1974) (see model selection in Supplementary Material: Table S3 and S4). Finally, the validation of the selected models was carried out following the protocol presented by Zuur and Ieno (2016). We calculated the conditional R^2 (R^2_c) values of these models using the function `r.squaredGLMM` of the R package “MuMIn” (Bartoń 2018), and the effect size and the confidence interval of the models were plotted using “jtools” R package (Long 2020). Spatial dependence in the models’ residuals was assessed by relating them with the geographical latitude and longitude, using the same random effect factors and model specifications than in the previous models (see Supplementary Material: Table S5 and S6).

RESULTS

Descriptive results

The number of interspecific interactions for both temporal windows are shown in Table 2. In the short window the interactions were performed by 3 red deer, 1 wild boar, 1 pig and the 3

cattle. However, in the large window, all the monitored individuals participated in the interactions, except for 2 wild boar (both sub-adult females) and 1 pig (sub-adult male).

Overall, wild ungulates ranged through all the management areas where cattle and pigs were kept (see Supplementary Material: Figure S2). Interactions among wild and domestic animals occurred more frequently in the cattle plot and its surrounding areas (see Figure 1). On the other hand, the interactions between red deer and wild boar occurred both in and outside the domestic management areas, being more frequent inside the areas used by livestock ($p < 0.001$).

Spatio-temporal pattern of the frequency of interactions

For the short window the frequency of interactions between wild boar – cattle was statistically higher than the frequency between wild boar – red deer (see Table 3 and Figure 2). The best model parameterized for the short window included DFP and DT (see Supplementary Material: Table S3), and was highly explanatory ($R^2_c = 0.91$). The interaction frequency was higher near to supplementary feeding points for wildlife and in those plots with a higher density of oak trees. The model also showed that interspecific interactions tended to occur at the central and crepuscular hours of the day (see Figure 3 and Table 3). We could not test for differences between pairs of species in the spatio-temporal pattern modeled for the short window, since we did not have enough information per type of interaction.

There were also statistical differences among all type of interactions in the large window, with the pig – cattle interactions the least frequent, and the red deer – wild boar, the most frequent (see Figure 2, Table 4 and Supplementary Material: Table S7). High explanatory

power was also obtained for this model ($R^2_c = 0.71$). The independent models for each type of interaction are shown in Table 5 and Figure 4. All models were highly explanatory according to their R^2_c values ($R^2_c_{[RD-WB]} = 0.80$; $R^2_c_{[RD-C]} = 0.40$; $R^2_c_{[RD-P]} = 0.66$; $R^2_c_{[WB-C]} = 0.90$; $R^2_c_{[WB-P]} = 0.74$; $R^2_c_{[C-P]} = 0.59$). The frequency of interactions was generally higher near to water points, except when cattle was involved in the interaction. Food resources also predicted the ifreq, especially for the interactions between wild ungulates. The interactions between wildlife and livestock tended to occur in areas with a lower tree density and close to dense vegetation. Also, the results showed that the temporality of interactions depended on the species involved, being higher during the central hours of the day for the interactions in which livestock was involved and also higher during the crepuscular hours for the interactions between wild ungulates (see Figure 4 and Table 5).

DISCUSSION

We evidenced that the W/L interface occurring at free-ranging pig farms in Spanish dehesas is a risk for shared infections, since interactions, and the subsequent potential for pathogen transmission, take place in these scenarios. In our study focused on a critical period of the year, the montanera, red deer interacted with all the targeted domestic species in both temporal windows, highlighting its potential significance to the disease spread process. However, we cannot rule out the possibility that the wild animals tagged in this study were more likely to interact with livestock, which could be reflected in their tolerance to the baited traps (although this is not expected since wild boar and red deer are used to be baited in the study area for hunting purposes). Both wild boar and red deer collared interacted with cattle

and pigs regardless of the livestock location away from dense vegetation. Livestock (and/or livestock associated management), therefore, could exert an attractive effect on wildlife and/or show similar preferences when using aggregation points.

In relation to the recorded interactions, the probability of transmission is host and pathogen context-dependent, and therefore, it is not possible to extract direct interpretations about real transmission of pathogens from our results. However, the risk for pathogen transmission during the interactions can be inferred taking into account, for example, the infection rates of TB in wild and domestic animals in the study area: in cattle, the seroprevalence was 2.83% during the study period despite the efforts carried out by the TB eradication program of the Spanish government (MAPA 2020); for the Iberian pigs, the mean seroprevalence in the breeding centres (i.e. before the montanera) was 0.72% and after the montanera 1.64% (unpublished data). In this sense, wild ungulates could be playing a major role in the transmission of TB to livestock, since the seroprevalence of TB during the study period was 22.4% in wild boar and 6.25% in red deer. More studies are needed along this line in order to estimate the real risk of the interactions according to the different types of interaction (direct or indirect) and the health status of the targeted species.

In the present work, the use of GPS devices with a high fixation frequency allowed us to characterise interactions with the potential for the transmission of different types of pathogens, or pathogens transmitted by different pathways (see Cooper et al. 2010; Pepin et al. 2016). Although direct interactions between wildlife and livestock are quite scarce in extensive systems (e.g. Kukiela et al. 2013; Woodroffe et al. 2016), the use of GPS devices in this study permitted the obtention of information about potential direct and indirect interactions. Finally, it is necessary to consider that the interaction rate recorded using this

methodology is an estimate of the actual interaction rate taking place in the studied system. This is a limitation of the methodologies based on the marking of individuals, which will also be conditioned by the sample size and fixation rate considered in the study, and by the particular characteristics of the marked individuals.

Interaction frequencies

The most frequent interactions varied with the temporal window employed. In the short window, the frequency of interactions predicted by the model was higher for the dyad wild boar – cattle. This interaction may be relevant for the transmission via aerosols of pathogens such as the causal agents of animal TB (Morris et al. 1994).

We did not detect any interaction between wild boar – pig at the short window. In contrast to our study, a recent work using camera trapping at aggregation points has described a high frequency of direct interactions between non-registered free-ranging pigs and wild boar in Mediterranean environments of the island of Sardinia (Cadenas-Fernández et al. 2019). In our specific production system, both males and females Iberian pigs are castrated before their release to the field, so the differences between our study and previous works are probably due to that the direct interactions between wild boar and pigs are scarce owing to the lack of attraction during the rut period and because using GPS technology we could only record those interactions between targeted individuals. Also, the differences in the activity patterns of both species and the potential competitive exclusion (i.e. mediated by acorn deployment) between ecologically related groups of animals (Carrasco-García et al. 2016) could explain the absence of close interactions between wild boar and pigs. Curiously, during field work we detected that orphan wild boar piglets found refuge within the groups of domestic pigs, a

fact that could be linked to the possible hunting of mothers during hunting events (E. Laguna and S. Jiménez-Ruiz, personal communication). This observation has great relevance at an epidemiological level, since this type of animal behaves as domestic animals do, sharing space and resources with domestic pigs. For instance, in the current situation of ASF expanding from Georgia to all Eurasia, there is a need to educate farmers and prevent these kinds of events to reduce the risk of the ASF virus spreading to the domestic reservoir (Jurado et al. 2018). Further studies are needed in order to quantify the relevance of these orphan animals and their relationship with hunting activity.

For the large window, the most frequent type of interaction predicted by the model was wild boar – red deer, likely due to the high aggregation of these species at big game supplementary feeding points (see Figure 1). These results could mean an average of 1.32 indirect interactions per day between wild ungulates in the study area (see the analytical procedure and all the direct and indirect daily average number of interactions per pairings in Supplementary Material: Table S8). Red deer – pig and red deer – cattle were the next most frequent type of interactions in the large window context, which could mean 9.76 and 4.90 indirect interactions per day respectively. Although not directly comparable, the number of predicted indirect interactions for the dyad wild boar – cattle was notably lower in this work regarding the number of interactions predicted in a previous study (see Supplementary Material: Table S8 and Triguero-Ocaña et al. 2019). This is probably due to the lower density of wild boar in this study area regarding the Doñana National Park. Despite this fact, these results show the potential risk that wild species may pose in the transmission of shared pathogenic agents through indirect pathways (e.g. Richomme et al. 2006; Guta et al. 2014). Specifically, the high frequencies of interactions between red deer and the rest of studied

species suggest that red deer could be playing a major role in the maintenance and transmission of shared pathogens, even higher than that of wild boar (Carrasco-García et al. 2016; Cowie et al. 2016). This role could be explained by the behaviour or habitat preferences (more similar to livestock in terms of aggregation points than in the case of wild boar) of red deer (e.g. Gortázar et al. 2011).

Spatio-temporal variation in interaction patterns

Regarding the factors predicting the frequency of interaction, both the period of the day and the week of the year, were statistically significant factors in the models for most types of interactions. The time of day is relevant given the different activity patterns of the targeted species (see Supplementary Material: Figure S1; see also Kukielka et al. 2013; Carrasco-García et al. 2016). Wild ungulates tend to be more active during crepuscular and night hours and rest during the central hours of the day (Carranza et al. 1991; Russo et al. 1997; Keuling et al. 2008), so we predicted a higher frequency of interactions during the night or during the crepuscular hours (as previously seen in Triguero-Ocaña et al. 2019). Contrary to expected, the frequency of interactions tended to be higher during the midday. This could be explained by the activity pattern of the wild ungulates in our study area, which was higher during the central hours of the day regarding previous activity reports (e.g. Kukielka et al. 2013; Triguero-Ocaña et al. 2019). This could respond to higher exploitation of acorn by wild ungulates during the whole day previous to a more adverse season (Jędrzejewska and Jędrzejewski 1998).

On the other hand, the week of the year was also an important factor when predicting the frequency of interactions between wild and domestic animals: interactions in which red deer

was involved increased throughout the study period, while those between wild boar – livestock, and cattle – domestic pig decreased. This pattern is consistent with the occasional use by wild boar in extensive farms with an elusive behaviour of open areas in diurnal time (Carrasco-García et al. 2016), that would make wild boar use cattle plots only at the beginning of the montanera, when acorn is more abundant. On the other hand, red deer locate their home range on the farms, especially in autumn, due to similar temporal patterns and use of resources (e.g. Cowie et al. 2016), which explains the increase in the frequency of interactions between red deer and cattle during this period.

Regarding the most important environmental variables explaining the pattern of interactions, the distance to water points and food resources, especially in the case of wild species, were highlighted in all types of interactions. This result is consistent with previous studies that observed that aggregation, and therefore, the interactions among wild and domestic ungulates mostly occurred around water and feeding points in Mediterranean latitudes (Kukielka et al. 2013; Barasona et al. 2014b; Laguna et al. 2018; Triguero-Ocaña et al. 2019). We observed this same pattern regarding water points except when cattle was involved, in which distance to water sources was positively associated with the frequency of interactions (more interactions when further away), which probably is due to a low density of water sources inside the fence plot where cattle is kept. This is especially relevant since water points may also act as a source of pathogens previously deposited through oral fluids or faeces by infected animals visiting the point (e.g. Barasona et al. 2017). The density of oak trees appeared as a positive significant factor only for the dyads red deer – wild boar and red deer – cattle. Oak tree density is higher near to dense vegetation areas, so probably our results regarding the distance to this source of food is related to the location of the plots where

livestock is kept and not to the lack of relevance of this factor, since oak trees have been described in previous studies as attractants for wildlife (Carrasco-García et al. 2016). In addition, due to the relevance of supplementary feeding points for wildlife, we wish to raise awareness of the potential health hazards that this practice performed by farmers and/or game managers may entail for wildlife and livestock, since the potential transmission of pathogens between wild species at these points could mean the subsequent transmission of those pathogens to domestic species. This health hazard could be prevented applying segregation measures at risk points, such as the cattle operated bump gates (Barasona et al. 2013b) or the development of species-specific feeders and wildlife proof water throughs (e.g. Long et al. 2010), which would reduce the risk of interactions among wildlife and livestock, mainly when these measures are linked to a reduction of wild ungulate population size (Boadella et al. 2012). Wildlife – cattle interaction tends to occur far from areas of dense vegetation as a result of cattle ranging far from woodlands (all woodland habitat was outside the fenced plots). The same pattern was observed in a previous study between cattle and wild boar in the south of Spain (Triguero-Ocaña et al. 2019), in this case due to the reduced amount of activity of both species in these areas. Interestingly, the interactions between red deer – wild boar occurred more frequently inside the livestock management plots than outside (i.e. in the woodlands), which suggests the potential attraction of farm resources over the presence of wild species, and highlights the need to develop specific measures to segregate wildlife from livestock.

Our study evidenced that, in free-ranging environments where wildlife and domestic animals exploit the same resources, understanding the spatial use of both groups at a high spatio-temporal resolution is essential in order to quantify the potential role of each host in the

maintenance and transmission of shared infections. This is the first work, to our knowledge, assessing the relationships among wild and domestic ungulates, including the commercial extensive production of domestic pigs, in a multi-host epidemiological environment at such a high spatio-temporal resolution. The results presented in this study provide new information for designing effective management measures to control pathogen transmission, that is both timely and highly relevant, given the current situation in Europe with ASF (Vicente et al. 2019) and also open up new research aimed to model the spread and persistence of pathogens at this interface.

ACKNOWLEDGEMENTS

The authors would like to thank all those who participated in the collection of data for this study. We are very grateful to landowners and gamekeepers for all their support during field trials. The present work has benefitted from the financial aid of the Spanish Ministry of Economy and Competitiveness (MINECO) research grants Ref. AGL2013-49159-C2-2-R and AGL2016-76358-R; and from the research grant by the Regional Ministry of Economy and Infrastructure of the Board of Extremadura Ref. TB-PORCEX. RTO received support from UCLM through a pre-doctoral scholarship and from the Community of Madrid through a post-doctoral contract (PEJD-2019-POST/BIO-16805). SJR holds a predoctoral contract from UCLM. EL is supported by a JCCM predoctoral contract. JAB is supported by the EU project Ref. H2020 VACDIVA 862874. PA received support from UCLM through an extension of Ramón y Cajal contract Ref. RYC-2012-11970.

CONFLICT OF INTEREST

All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest, or non-financial interest in the subject matter or materials discussed in this manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

All the capture and marking procedures were conducted according to the specifications of the protocol approved by the Animal Experiment Committee of Castilla-La Mancha University and by the Spanish Ethics Committee (PR-2016-10-16). This protocol was designed by specifically trained and certified scientists (B and C animal experimentation categories) according to EC Directive 86/609/EEC for animal handling and experiments.

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666
667 **TABLES**

668 Table 1. Candidate models used to explore the most plausible hypothesis explaining
669 variations in the interaction frequency at two spatio-temporal windows (30 m – 10 minutes
670 [short window] and 30 m and 12 days [large window]). For the large - window model, the
671 same candidates were used for all the species dyads, except in the case of the model for red

672 deer (RD) – wild boar (WB), where we tested DFP and DT together as food resources. DW:
673 distance to water; DFP: distance to wildlife feeding points; DT: density of oak trees; DV:
674 distance to dense vegetation; Hour: hour of the interactions; Week: week of the year.

Candidate models (short window)	Candidate models (large window)	RD – WB
1 ifreq ~ Type interaction + Hour + Week	1 ifreq ~ Hour + Week	
2 ifreq ~ Type interaction + Hour + DW	2 ifreq ~ Hour + DW	
3 ifreq ~ Type interaction + Hour + DV	3 ifreq ~ Hour + DV	
4 ifreq ~ Type interaction + Hour + DFP + DT	4 ifreq ~ Hour + DT	+ DFP
5 ifreq ~ Type interaction + Hour + DW + DFP + DT	5 ifreq ~ Hour + DW + DT	+ DFP
6 ifreq ~ Type interaction + Hour + Week + DW + DV + DFP + DT	6 ifreq ~ Hour + Week + DW + DV + DT	+ DFP

675

676

677 Table 2. Number of interspecific interactions and daily average frequency of interactions
678 (ifreq) recorded during the montanera period (October/November – January/February) for
679 the two spatio-temporal windows considered: 30 m – 10 minutes (short window) and 30 m –
680 12 days (large window).

Type of interaction	Window	Number of interactions	Daily average ifreq
Red deer – wild boar	Short	5	1.5E-04
	Large	7436	4E-04
Red deer – cattle	Short	4	5.2E-05
	Large	23,231	4.7E-04
Red deer – pig	Short	2	4.4E-05

	Large	6140	4.1E-04
Wild boar – cattle	Short	2	2E-04
	Large	41	1.5E-04
Wild boar – pig	Short	0	0
	Large	339	3E-04
Cattle - pig	Short	0	0
	Large	242	9E-05

681

682

683 Table 3. Results of the best-fitting generalised mixed linear model (negative binomial
684 distribution and log link function) to explain spatio-temporal variation in the frequency of
685 interactions for the short spatio-temporal window (10 minutes – 30 m; see text for details).
686 RD: red deer; WB: wild boar; C: cattle; P: pig; DFP: distance to wildlife feeding points; DT:
687 density of oak trees; Hour: hour of the interactions reclassified in four categories [Hour1:
688 0:00 – 5:59, Hour2: 6:00 – 11:59, Hour3: 12:00 – 17:59, Hour4: 18:00 – 23:59]. P-values:
689 $p > 0.1$ “ns”; $p < 0.1$ “.”; $p < 0.05$ “*”; $p < 0.01$ “***”. Coefficients are relative to WB – C and
690 Hour1, for “Type of Interaction” and “Hour” predictors, respectively (see material and
691 methods “Spatio-temporal pattern”).

Predictors	Estimate	Std. Error	Z value	P-value
(intercept)	-5.49	3.14	-1.75	.
Type Interaction _{RD – WB}	-19.03	7.24	-2.63	**
Type Interaction _{RD – C}	-11.76	6.39	-1.84	.
Type Interaction _{RD – P}	-8.12	6.36	-1.28	ns
Hour2	11.50	6.43	1.79	.
Hour3	13.50	6.06	2.23	*

Hour4	12.08	5.95	2.03	*
DFP	-6.65	2.77	-2.40	*
DT	0.30	1.63	0.18	ns

Table 4. Results of the global generalised mixed linear model (negative binomial distribution and log link function) explaining the differences among types of interaction at large spatio-temporal window (12 days – 30 m; see text for details). RD: red deer; WB: wild boar; C: cattle; P: pig. P-values: $p < 0.001$ “***”. Coefficients are relative to WB – C, (see material and methods “Spatio-temporal pattern”).

Predictors	Estimate	Std. Error	Z value	P-value
(intercept)	-3.44	0.16	-21.04	***
Type Interaction_{RD – WB}	2.15	0.06	36.44	***
Type Interaction_{RD – C}	1.50	0.05	31.86	***
Type Interaction_{RD – P}	0.75	0.09	8.07	***
Type Interaction_{WB – P}	-0.75	0.06	-12.63	***
Type Interaction_{C – P}	1.60	0.06	24.81	***

Table 5. Results of the best-fitting generalised mixed linear models (negative binomial distribution and log link function) to explain spatio-temporal variation in the frequency of interactions at large spatio-temporal window (12 days – 30 m; see text for details) in the different type of interactions. RD: red deer; WB: wild boar; C: cattle; P: pig; DW: distance to water; DFP: distance to wildlife feeding points; DT: density of oak trees; DV: distance to dense vegetation; Week: week of the year; Hour: hour of the interactions reclassified in four

707 categories [Hour1: 0:00 – 5:59, Hour2: 6:00 – 11:59, Hour3: 12:00 – 17:59, Hour4: 18:00 –
708 23:59]. P-values: $p > 0.1$ “ns”; $p < 0.1$ “.”; $p < 0.05$ “*”; $p < 0.01$ “***”; $p < 0.001$ “****”.
709 Coefficients are relative to Hour1 for “Hour” predictor (see material and methods “Spatio-
710 temporal pattern”).

711

Type of interaction	Predictors	Estimate	Std. Error	Z value	P-value
RD - WB	(intercept)	-3.58	0.90	-4.00	***
	Hour2	-0.27	0.08	-3.30	***
	Hour3	-0.16	0.09	-1.84	.
	Hour4	0.07	0.07	0.94	ns
	DW	-0.62	0.03	-18.90	***
	DFP	-1.36	0.04	-32.71	***
	DT	0.08	0.03	2.82	**
RD – C	(intercept)	-3.75	0.44	-8.54	***
	Hour2	-0.26	0.04	-5.78	***
	Hour3	0.33	0.04	7.56	***
	Hour4	0.25	0.04	5.80	***
	Week	0.03	0.00	8.01	***
	DW	0.44	0.02	21.81	***
	DT	0.14	0.02	7.40	***
	DV	0.95	0.04	23.58	***
RD – P	(intercept)	-2.92	0.97	-3.02	**
	Hour2	0.82	0.09	8.71	***
	Hour3	0.70	0.09	7.75	***
	Hour4	0.82	0.09	8.56	***
	Week	0.01	0.01	0.41	ns
	DW	-0.41	0.04	-9.64	***
	DT	-0.67	0.04	-18.26	***
	DV	0.13	0.04	2.83	**
WB – C	(intercept)	9.34	6.14	1.52	ns
	Hour2	-0.81	1.51	-0.54	ns
	Hour3	0.74	1.27	0.59	ns

	Hour4	-2.66	0.98	-2.71	**
	Week	-0.37	0.13	-2.91	**
	DW	3.30	0.89	3.70	***
	DT	-0.56	0.85	-0.66	ns
	DV	11.14	3.14	3.54	***
WB – P	(intercept)	-2.94	1.33	-2.21	*
	Hour2	0.78	0.33	2.34	*
	Hour3	0.52	0.34	1.52	ns
	Hour4	-1.86	0.42	-4.46	***
	DT	-0.58	0.16	-3.61	***
C – P	(intercept)	26.92	0.01	3313.3 5	***
	Hour2	0.41	0.01	50.61	***
	Hour3	0.32	0.01	39.66	***
	Hour4	-1.61	0.01	-198.45	***
	Week	-0.67	0.01	-109.00	***
	DW	1.67	0.01	205.42	***
	DT	-0.59	0.01	-72.33	***
	DV	2.68	0.01	329.96	***

FIGURES

Figure 1. Location of the study area and distribution of the interspecific interactions recorded for the two spatio-temporal windows (30 m – 10 minutes [short window] and 30 m - 12 days [large window]). The land cover and the risk points for animal aggregation (water and feeding points) are also shown.

Figure 2. Estimated values of the interaction frequency (ifreq) from the statistical models, comparing different types of interaction in the two spatio-temporal windows considered: 30 m – 10 minutes (short window) and 30 m - 12 days (large window). For representation purposes, log(ifreq) is plotted and labels above the bars represent the real ifreq value. Capital

letters represent the differences between the species dyads in the short – window model; lower case letters show differences between species dyads in the large – window model. RD: red deer; WB: wild boar; C: cattle; P: pig.

Figure 3. Coefficients for the predictors included in the statistical model performed to explain the variation in the frequency of interaction for the short spatio-temporal window (30 m - 10 minutes; see text for details). The thin (outer) bars represent 0.9 confidence intervals. RD: red deer; WB: wild boar; C: cattle; P: pig; DFP: distance to wildlife feeding points; DT: density of oak trees; Hour: hour of the interactions reclassified in four categories [Hour1: 0:00 – 5:59, Hour2: 6:00 – 11:59, Hour3: 12:00 – 17:59, Hour4: 18:00 – 23:59]. Coefficients are relative to WB – C and Hour1, for “Type of Interaction” and “Hour” predictors, respectively (see material and methods “Spatio-temporal pattern”).

Figure 4. Coefficients for the predictors included in the statistical models performed to explain the variation in the frequency of interaction for the large spatio-temporal windows (30 - 12 days; see text for details) according to the different type of interaction. The thin (outer) bars represent 0.9 confidence intervals. Types of interaction: red deer – wild boar [RD – WB], red deer – cattle [RD – C], red deer – pig [RD – P], wild boar – cattle [WB – C], wild boar – pig [WB – P] and cattle – pig [C – P]. DW: distance to water; DFP: distance to wildlife feeding points (only considered for the interaction RD – WB); DT: density of oak trees; DV: distance to dense vegetation; Week: week of the year; Hour: hour of the interactions reclassified in four categories [Hour1: 0:00 – 5:59, Hour2: 6:00 – 11:59, Hour3: 12:00 – 17:59, Hour4: 18:00 – 23:59].

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