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Protected areas as refuges for pest species? The case of wild boar

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ABSTRACT

Protected areas are often blamed for offering refuge to pest species populations, giving rise to the so-called “reserve effect”. Nevertheless, this major conservation side effect has seldom been investigated or verified on a local scale. Along the borders of two protected areas of different size, we modelled wild boar individual likelihood of being either inside or outside the protected areas throughout the year, considering their activity rhythms and resource availability. No evidence of reserve effect was found in the small protected area, yet the percentage of wild boar moving across the border was smaller in the large one. Moreover, although wild boar use of the large protected area resulted to increase in autumn, we showed that this was not the consequence of hunting avoidance. Our results clearly highlighted the importance to verify reserve effect on a local scale with studies based on detailed information on animal spatial behaviour and environmental variables.

1. Introduction

In the last few decades protected areas showed a rapid growth in number and extension worldwide (UNEP-WCMC & IUCN, 2016). Their geographical expansion was associated with the increase of their functions. Indeed, nowadays protected areas are expected to serve their original purpose of conservation of landscapes, wildlife, and ecosystems in combination with further social and economic objectives (Watson et al., 2014). Nonetheless, although protected area effectiveness for in situ conservation is known and undoubted (Caro, 1999; Chu et al., 2018), their establishment can cause the rise of social conflicts with local human populations (Tisdell and Zhu, 1998; Brockington and Schmidt-Soltau, 2004). Protected areas are often blamed for offering refuge also to pest species, thus preventing the implementation of management activities and reducing the effectiveness of pest population control plans (Coffey and Johnston, 1997). This may result in a high population density of such species inside the reserves, either constantly or in limited time spans characterized by high levels of human disturbance in their surroundings.

For several species, the main source of human disturbance is hunting, which often causes displacements of individuals from unprotected to protected areas during the hunting season (Tolon et al., 2009; Grignolio et al., 2011). The so-called “reserve effect” can be a major concern for both protected area conservation purposes and human activities implemented nearby. On the one hand, the unnatural concentration of individuals inside protected areas can have a huge impact on their biodiversity (Côté et al., 2004; Bongi et al., 2017). On the other hand, individuals seeking refuge into reserves to avoid hunting are often blamed for causing damages to the nearby unprotected lands (Amici et al., 2012). Despite its crucial importance for protected area management, researchers seldom attempted to verify the occurrence of reserve effect on a local scale. The few

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authors who approached such study found evidence of no-reserve effect (white-tailed deer, *Odocoileus virginianus*, Root et al., 1988), reserve effect limited to a part of the population (wild boar, *Sus scrofa*, Tolon et al., 2009), or reserve effect varying according to sex and age classes (roe deer, *Capreolus capreolus*, Grignolio et al., 2011). Despite the limited number of studies and the variability of their results, reserve effect is generally considered a common issue for protected areas by both local human populations and a large part of wildlife technicians. In this light, further investigations are necessary to evaluate the real spread, impact, and patterns of this conservation side-effect.

Previous studies never considered the role potentially played by protected area extension in shaping reserve effect patterns. Several authors contributed to the SLOSS (Single Large Or Several Small) longstanding debate, by attempting to evaluate the relationship between size and conservation effectiveness of protected areas (Lomolino, 1994; Ovaskainen, 2002; McCarthy et al., 2005). It has been shown that protected area effectiveness strictly depends on the comparison between its size and the average home range size of the target species (Bertocci et al., 2017; Di Franco et al., 2018). Thus, one may expect that the larger the protected area, the higher the portion of the population which can take advantage of its protection. As for reserve effect, this would imply that only protected areas which are large enough can offer an even temporary refuge to pest populations. On the other hand, large protected areas may be able to permanently host more individuals inside their boundaries, thus reducing negative impacts of pest species on the surrounding unprotected areas.

Other aspects should be taken into consideration when examining reserve effect, including the overall resource availability, their temporal variations, and their selection by animal species as well as the level of protection from hunting activities the area can offer. The importance of resource availability is underlined by its high potential to shape animal movements (e.g. Morelle and Lejeune, 2015) and to affect reserve effect patterns (Adam et al., 2016). Indeed, animals require a minimum availability of food resources even in case of temporary occupation of protected areas. When resource availability of protected areas is low, animals may be forced to choose between safety and food abundance. Conversely, protected areas offering abundant pulsed resources may be expected to temporarily attract animals with patterns very similar to those of individuals avoiding hunting.

A further fundamental issue to take into account regards the activity rhythms of the focal population. In a number of studies, researchers failed to distinguish the use of refuge areas during daily active and inactive phases. This information, combined with high-resolution movement data, may allow to identify daily patterns of reserve effect and their relationship with animal activities. This can be particularly useful when disturbance in unprotected lands is limited to a certain part of the day (for example, hunting tends to be performed only during daytime, Thurfjell et al., 2013; Tolon et al., 2009). In these cases, to fully understand reserve effect, it is necessary to know whether animals are moving or resting when disturbed and how they change their use of protected areas accordingly.

In the present study, we investigated the use of reserves as a potential strategy to avoid human disturbance, also taking into account ecological variables and food resource availability, by using high resolution spatial data obtained by means of GPS tracking. To do this, we studied the behaviour of wild boar, one of the most important mammal pest species in Europe. Given its major impact on both biodiversity (Massei & Genov 2004; Barrios-Garcia and Ballari, 2012; Bongi et al., 2017) and human activities (Frackowiak et al., 2013), along with the high hunting pressure it commonly experiences (Massei et al., 2015; Merli et al., 2017; Keuling et al., 2016), wild boar has the highest potential to be affected by reserve effect, with several negative consequences for its management. Nevertheless, despite the relatively high attention paid to hunting influence on wild boar spatial behaviour (Keuling et al., 2008; Scillitani et al., 2010; Saïd et al., 2012; Sodeikat and Pohlmeyer, 2002; Thurfjell et al., 2013), only Tolon et al. (2009) investigated reserve effect in wild boar, by focusing on VHF telemetry-based home range distribution in respect to the boundaries of a single protected area. This study showed that reserve effect consisted in a concentration of home ranges inside the protected area during the hunting season. Such effect only regarded the individuals with pre-hunting home ranges “in contact” with the protected area.

In this framework, we selected a study area hosting two protected areas of different size in order to analyse the role their extension plays in shaping reserve effect patterns. For each location of wild boar, we modelled the likelihood of being either inside or outside the protected area and developed the following predictions:

1) Although both protected areas provided total shelter from hunting, the large protected area was expected to have a higher potential to cope with other needs of wild boar (e.g., food resources, safe resting sites). Thus, wild boar were predicted to show a strong reserve effect in the large protected area and a weak or null reserve effect in the small protected area.
2) Given the strictly nocturnal habits of wild boar in our study area (Brivio et al., 2017) and the fact that hunting is permitted only during daytime, diurnal locations were expected to be influenced exclusively by the need for shelter while nocturnal ones mainly by the spatial distribution of food resources. Thus, we predicted a stronger reserve effect during daytime.

2. Materials and methods

2.1. Study area

The study area was in the Casentino valley, in the Tuscan Apennine (Province of Arezzo, central Italy, 43°48′N, 11°49′E, Fig. 1). Climate is temperate-continental, with hot and dry summers and cold and wet winters. Occasional snowfalls occur between October and April. Temperature reaches its highest and lowest values in July and January, respectively. A rich ungulate community inhabits the study area, with wild boar showing a homogeneous distribution and a high population density. Roe deer, red deer (*Cervus elaphus*), and fallow deer (*Dama dama*) are also present with heterogeneous distribution and density throughout the study area. The area is characterised by a high density of wolf (*Canis lupus*), with 1.21 ± 0.27 packs/100 km^2 estimated during the data collection period (Mattioli et al., 2018). Wild boar resulted to be the main component of wolf diet (Mattioli et al., 2011; Bassi et al., 2012). The study area hosts two protect areas of different sizes. The large one, Foreste Casentinesi National Park (FCNP), covers a total surface of 362 Km^2, with a perimeter of about 187 Km (surface/perimeter ratio = 1.936). The study was conducted around its southern border, with elevation ranging from 500 to 1289 m a.s.l.. Inside this part of the FCNP, the habitats are composed of 55% of highly seed-productive deciduous forests (oaks, *Quercus* spp., chestnuts, *Castanea sativa*, and beeches, *Fagus sylvatica*, both as high stand or coppice), 25% of coniferous forests (silver fir, *Abies alba*, black pine, *Pinus nigra*, and Douglas fir, *Pseudotsuga menziesii*), 5% of mixed forests of all the above mentioned species, 3% of shrubs, and 12% of agricultural lands and pastures. Outside the protected area borders, landscape composition shifts to 40% of deciduous forests, 3% and 2% of coniferous and mixed forests, respectively, 3% of shrubs, and 52% of agricultural lands and pastures. The small protected area, Oasi Alpe di Catenaia (OAC), covers a total surface of 27 km^2, with a perimeter of 43 Km (surface/perimeter ratio = 0.628). The area including the reserve and the hunting districts in proximity of its boundaries has an elevation range of 300-1414 m a.s.l.. Deciduous forests account for 68% of the OAC protected surface, with coppices of oaks and chestnuts and high stands of beech; 18% is composed of coniferous forests of black pine and Douglas fir, 3% of mixed deciduous-coniferous forests, 6% of shrubs, and the remaining 5% agricultural lands and pastures. Outside the protected area, hunting lands have a similar habitat composition, with 71% of deciduous forests, 8% of coniferous forests, 3% of mixed forests, 6% of shrubs, and 12% of agricultural lands and pastures.

Any form of hunting is strictly forbidden inside both protected areas, while wild boar hunting reaches high intensity levels in their surroundings. It is performed with drive hunts involving 25—50 hunters and tens of dogs, three times a week from October to December only during daytime (see Grignolio et al., 2011 for further details).

2.2. Data collection and analysis

We captured wild boar by means of baited traps and vertical dropping nets from June 2013 to October 2017, following the protocol detailed by Brogi et al. (2019). Captured individuals were first immobilized and sedated with a mixture of zolazepam — tiletamine or zolazepam — tiletamine — xylazine, alternatively. Each wild boar was weighted, aged based on teeth eruption and abrasion (Heck and Raschke, 1980), and finally equipped with a GPS collar (GPS PRO Light collar, Vectronic Aerospace). Such devices were configured to record 12 GPS locations/day, with a regular 2-h interval. To obtain a uniform sampling of protected area potential use, all captures were performed in a buffer of 1700 m from the reserve boundary inside both FCNP

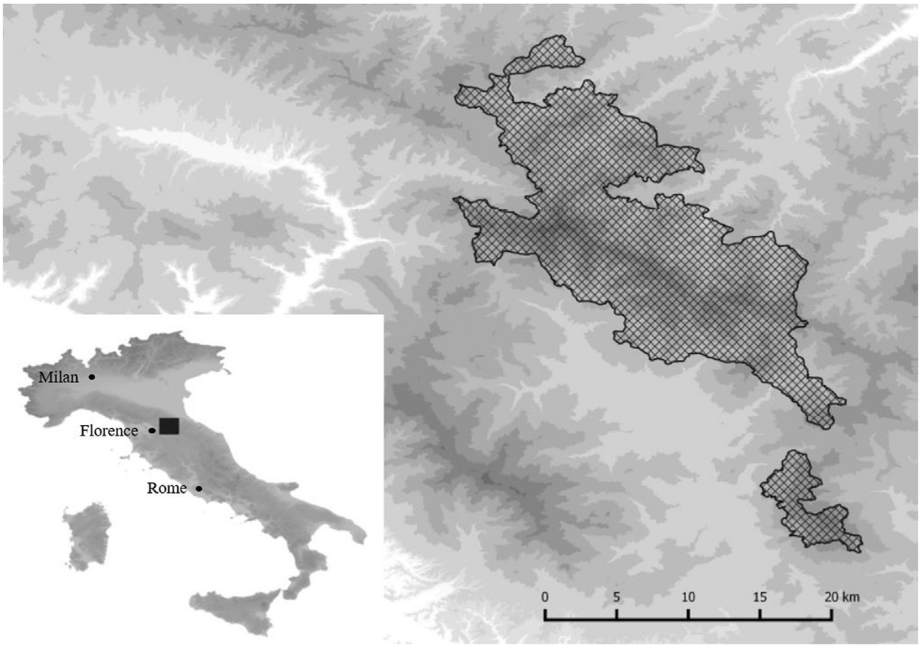

Fig. 1. Map of Italy (down-left), with the black rectangle showing the location of the study area and its relative enlargement in which the northern and southern reticulated areas represent FCNP (large) and OAC (small) protected areas, respectively. The greyscale represents the altitudinal gradient (dark: higher altitudes; light: lower altitudes).

and OAC. The distance between the capture site and the nearest reserve boundary averaged a mean of 409 ± 410 m (mean ± SD) in FCNP and 455 ± 433 m in OAC. In order to avoid capture site related bias, we checked for correlation between such distance and the external/total location proportion at an individual level by means of a Pearson correlation coefficient calculation.

Regional Hydrological Service of Tuscany kindly provided weather data (mean air temperature, mean air humidity, and rain precipitation), hourly recorded in the weather station of Poppi (Arezzo province, 43°44′09″ N, 11°45′42″ E). We used CORINE Land Cover database (2013) to assess study area habitat composition.

2.2.1. Identification of commuters and residents

Unverified locations, i.e., with dilution of precision (DOP) higher than 10 or obtained with less than 4 satellites, were discarded from our analysis. Each of the remaining locations was assigned an “In-Out” value based on its relative position in respect to reserve boundaries, which was 0 for locations inside the protected areas and 1 for locations outside of them.

Based on the individual average of “In-Out”, we subdivided wild boar into “residents” (less than 5% of locations outside the reserve) and “commuters” (more than 5% of locations outside the reserve). We chose a relatively low threshold value, consistent with the conservative approach we aimed to adopt, in order to also take into account external locations of individuals which seldom left the protected areas. In fact, even few locations outside the reserve can produce a high impact on agricultural crops, especially when they are concentrated in a certain period of the year and time of the day. By using a 5% threshold, we avoided underestimating any potentially important use of unprotected lands by discarding individuals which rarely left the reserve from the commuter group. Thereafter, since hunting land use was negligible for the resident group, we restricted advanced statistical analysis only to the commuter group for both protected areas.

We assigned each location to either daylight or nightlight by comparing recording date and time with local sunrise and sunset times.

2.2.2. Models on protected area use by commuter wild boar

In order to assess the relation between reserve use and environmental predictors in each protected area, we divided our dataset into 4 sub-datasets with a spatial (FCNP vs OAC) and temporal (daylight vs nightlight) criterion. For each sub-dataset, the “In-Out” variable was modelled by means of Generalised Additive Mixed Models (GAMMs) with a binomial distribution, which were implemented by means of the *mgcv* package in R 3.2.2 (R Core Team, 2015). To account for the nested nature of data, we used individual wild boar identity as random factor. Such biological factors as sex, age, and body weight were added as predictors. Julian date was included in our models as explanatory variable to check for potential intra-annual patterns of variation in reserve use. We also inserted the environmental variables which resulted to significantly affect wild boar behavioural ecology (Brivio et al., 2017), i.e., mean air temperature, mean air humidity, and total rain precipitation, calculated on the 2-h interval preceding each location. Finally, to take into account the potential effect of resource availability, we assessed the home range (Minimum Convex Polygon – MCP - 90%) for each month/wild boar and calculated the relative percentage of the 3 most important habitat types (forest, shrubs, and open areas) by using Corine Land Cover (2013) database and the QGis 2.12.2 software (QGIS Development Team, 2016). These percentage values were assigned to all locations according to the month of recording and used as predictors in our models.

For each sub-dataset discretely, we performed a variable selection process to choose only explanatory variables unaffected by collinearity, following Zuur et al. (2009). Firstly, we calculated Pearson correlation coefficients among all possible predictor variable pairs and then ran a multicollinearity test by using the corvif function (*AED* package). In case of variables affected by not-negligible multicollinearity (VIF≥3), we performed a random forest calculation (*random.Forest* package) and excluded the worst variable of each collinearity condition affecting two or more variables. In the FCNP sub-datasets, we detected a not-negligible collinearity between age, weight, and sex. In accordance with the random forest results, we excluded weight from the daylight sub-dataset and both age and sex from the nightlight sub-dataset. Habitat composition variables contained a couple of predictors affected by collinearity in all four sub-datasets (forest-open areas and forest-shrubs for FCNP and OAC sub-datasets, respectively): as we preferred not to exclude any habitat composition predictor in this phase, we built alternative models with one or the other collinear variable.

In the final step, for each sub-dataset, we built a GAMM with a full model structure including the explanatory variables selected during the previous steps (Table 1). The effect of Julian date was modelled as a cyclic cubic regression spline in order to consider its circularity, while the effect of all the other variables was modelled as natural cubic spline functions. For each sub-dataset, we subsequently ran a set of models with all possible combinations of the predictor variables included in the full model (Table 1) by means of the dredge function (*MuMln* package). We selected the 4 best models following the minimum AIC criterion (Symonds and Moussalli, 2011). In case of models with ΔAIC<2, we selected the most parsimonious in terms of number of predictor variables included (Symonds and Moussalli, 2011). If two or more models had ΔAIC<2 and the same number of predictors, we considered the minimum AIC model as the best model, accepting any ΔAIC value.

3. Results

We captured and monitored 18 and 8 wild boar in FCNP and OAC, respectively. The distance between the capture site and the nearest reserve boundary resulted to be poorly correlated with the external/total location proportion at an individual level in both FCNP and OAC (FCNP: r = 0.102, P = 0.038; OAC: r = 0.041, P = 0.001): individuals whose capture site was located

Table 1
Summary of explanatory variable sets used for the four sub-datasets in random forest, full model, and best model, respectively.

		age	sex	weight	J date	temp	humidity	rain	forest	open areas	shrubs
FCNP day	Random forest	x	x	x	x	x	x	x	x	x	x
	Full model	x	x		x	x	x	x	x	x	x
	Best model				x	x	x		x		x
FCNP night	Random forest	x	x	x	x	x	x	x	x	x	x
	Full model			x	x	x	x	x	x	x	x
	Best model				x	x	x	x	x		x
OAC day	Random forest	x	x	x	x	x	x	x	x	x	x
	Full model	x	x	x	x	x	x	x	x	x	x
	Best model	x			x	x	x		x	x	
OAC night	Random forest	x	x	x	x	x	x	x	x	x	x
	Full model	x	x	x	x	x	x	x	x	x	x
	Best model	x			x	x	x		x	x	

x = the explanatory variable was included; empty cell = the explanatory variable was not included; age = individual age expressed in years; weight = individual body weight; J date = Julian date; temp = mean air temperature; humidity = mean air humidity; rain = total rain precipitation; forest = forest cover availability; open areas = open area availability; shrubs = shrub cover availability; FCNP = Foreste Casentinesi National Park; OAC = Oasi Alpe di Catenaia; Random forest = explanatory variables selection process; Full model = GAMM including all the explanatory variables selected; Best model = best alternative model selected following the minimum AIC criterion.

further in the protected areas showed slightly higher proportions of external locations. We identified 9 commuters and 9 residents in FCNP and 6 commuters and 2 residents in OAC. In FCNP, commuters had an external/total location proportion of 0.52 ± 0.15 (mean ± SE) during daylight and 0.51 ± 0.12 during nightlight, while in OAC the proportion was 0.29 ± 0.06 and 0.35 ± 0.05 during daylight and nightlight, respectively.

3.1. Models on protected area use by commuter wild boar

3.1.1. Large protected area (FCNP)

The two best models explaining the likelihood of being outside FCNP included the predictor variable sets summarized in Table 1 (daylight $R^2_{adj} = 0.442$; nightlight $R^2_{adj} = 0.381$). For the diurnal sub-dataset, Julian date had a significant but weak effect with a slightly lower proportion of external locations falling from the 250th (7th September) to the 350th day of the year (16th December, Fig. 2a). Conversely, the effect of Julian date on the likelihood of being outside during the night was strong and significant, with wild boar being predominantly outside for most of the year and then increasing their stay inside the protected area boundaries from around the 250th day of the year (7th September) until the 334th day (30th November), with a sharp minimum peak around the 290th day of the year (17th October) and a gradual increase until the 30th day of the subsequent year (30th January, Fig. 2b). Mean air temperature affected the response variable with a positive but almost flat pattern during the day (Fig. A1a). On the other hand, it had a positive, not-negligible effect on the likelihood of being outside the protected area during the night, with wild boar external locations raising at higher environmental temperatures (Fig. A1b).

During both daylight and nightlight, wild boar resulted to have generally more external locations when the shrub cover availability was lower: the maximum likelihood of being outside was recorded with shrubs covering about 5% of their monthly home range, then progressively decreasing as shrub cover increased (Fig A2a and A2b). Monthly forest cover availability affected both diurnal and nocturnal likelihood of being outside in a similar way: the likelihood was high with high forest cover availability and sharply decreased with forest cover below 68% and 65% for daylight and nightlight, respectively (Fig. A3a and A3b). Although statistically significant, the other predictor variables (mean air humidity and rain precipitation) had biologically negligible effects on the response variable (Fig. A4 and A5).

3.1.2. Small protected area (OAC)

Best models explaining the variation of the likelihood of wild boar being outside OAC included the same set of explanatory variables for diurnal and nocturnal sub-datasets, as summarized in Table 1 (daylight: $R^2_{adj} = 0.529$; nightlight: $R^2_{adj} = 0.366$). Older wild boar tended to locate outside the reserve more frequently than younger individuals during both the day and the night (Fig. A6a and A6b). Julian date affected the diurnal likelihood of being outside the reserve with a complex pattern, which fluctuated during the first half of the year and became quite stable in the second half (Fig. 2c). Wild boar use of the reserve during the night did not vary markedly during the year, showing three weak positive peaks of the likelihood of being outside the protected area around the 80th, 190th and 330th day of the year (21st March, 9th July, and 26th November, respectively) characterized by wide confidence intervals (Fig. 2d). The likelihood of being outside resulted to be lower with higher air temperature, although this effect was strong and significant for the diurnal sub-dataset but relatively weak for the nocturnal one (Fig. A7a and A7b). During the day, the relationship between forest cover and the likelihood of being outside estimated by the best model was complex and its biological significance difficult to disentangle (Fig A8a). During the night, the likelihood of being outside was high when monthly forest cover availability was higher than 70% and decreased when it was smaller (Fig

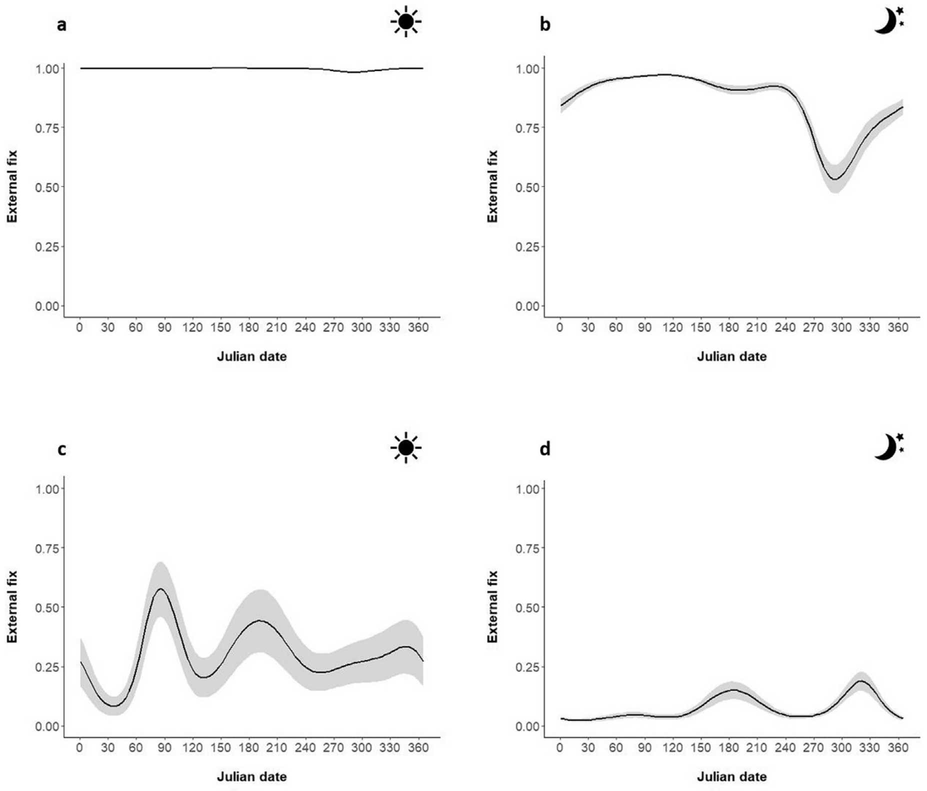

Fig. 2. Effect of Julian date on the likelihood of wild boar being outside the FCNP protected area during daylight (a) and nightlight (b) and the OAC protected area during daylight (c) and nightlight (d), respectively. The values reported were predicted by the best generalised additive mixed model, separately for each sub-dataset (see the text for more details). The predictions are given according to the mean of all other covariates in the model. In the graphs the gray-shaded areas represent the estimated standard errors.

A8b). As in the case of FCNP models, the other explanatory variables included in best models (mean air humidity and open area cover) had a biologically negligible effect on the likelihood of being outside OAC (Fig. A9 and A10).

4. Discussion

Our study investigated reserve effect patterns in two contiguous protected areas of different size. The results highlighted the importance of using detailed information on both animal behaviour and environmental resources in evaluating reserve effect. Although biologically negligible, the positive correlation between the distance separating the capture site from the nearest reserve boundary and the proportion of external locations clearly excluded the possibility that our samples were biased by the opportunistic choice of capture sites. As expected, a relevant number of individuals had a negligible use of unprotected lands. We showed that this portion of “resident” wild boar was two times higher in the large protected area (FCNP) in respect to the small one (OAC), as a wider surface is likely to sustain a higher number of individuals all-year round. The use of the protected lands was neither limited to nor concentrated in a specific part of the day, thus pointing out a lack of use of both the large and the small protected areas as refuge during hunting activities.

We did not detect variations in the likelihood of wild boar being outside the small protected area during both daylight and nightlight, whereas a clear decrease was observed in the large protected area in autumn, though surprisingly only during nightlight. This finding completely refutes our second prediction, since the likelihood of wild boar being inside the protected area in autumn did not increase when hunting activities were actually performed (that is, during daylight). Conversely, it increased during nightlight, when any kind of human disturbance was either minimal or absent. In fact, though statistically significant, the intra-annual variation of the likelihood of being outside the large protected area during daylight was biologically negligible (Fig. 2a). In the light of a recent research in the same study area showing that wild boar is strictly nocturnal (Brivio et al., 2017), we can argue that wild boar homogeneously used resting areas located outside the protected area throughout the year. Conversely, in the same area, the likelihood of wild boar being outside during the night sharply decreased from 7th September until 30th November, with a negative peak around 17th October and a gradual increase until 30th January (Fig. 2b). It is worth noting that any form of hunting is strictly forbidden during the night and that any other source of human disturbance is also expected to be minimal if compared with daylight. Moreover, the temporary decrease of the likelihood of being outside did not exactly correspond to the hunting season (lasting from around 1st October until 31st December), which began and ended after such decrease. In conclusion, we can speculate that wild boar increased their use of the large protected area in autumn to implement their foraging activities and not to find refuge from hunting. This explanation is supported by the fact that chestnuts are known to be a key food resource for wild boar in our study area during autumn (Cutini et al., 2013; Bisi et al., 2018) and chestnut forests are abundant inside the large protected area boundaries and quite scarce outside. The lack of reaction to hunting we observed is consistent with previous studies showing that human activities had minimal impacts on the behaviour of this species (Sodeikat & Pohlmeyer 2002, 2004; Keuling et al., 2008; Brivio et al., 2017; Melletti and Meijaard, 2017). Moreover, it indicates that, on account of their behavioural plasticity, wild boar can use environmental resources regardless of human disturbance. Although we are unable to provide any biological explanation of the complex variation pattern of the likelihood of wild boar being outside the small protected area throughout the year, we clearly did not detect any increase in its use throughout the hunting season during both daylight and nightlight (Fig. 2c and d). Though offering total shelter from hunting disturbance, we can argue that the small reserve lacked in satisfying other requirements because of its limited extension, thus making stays for medium-long periods unfeasible for wild boar. Thurfjell et al. (2013) reported that wild boar, fleeing into refuge areas owing to hunting disturbance, were negatively affected by the intra-specific competition with resident individuals. Similarly, in our case-study, competition with resident wild boar for the limited resources of the small protected area may have played a major role in discouraging commuter individuals to seek refuge inside the reserve during the hunting season. This effect was likely to concern wild boar diurnal resting as well as their nocturnal foraging activities, as both secure resting sites and food availability may act as limiting resources. It is worth nothing that, even though our results showed the absence of reserve effect, protected areas may still act as reservoir for wild boar in a sources-sinks system. Nevertheless, as commuter wild boar and individuals outside the protected area have the same likelihood to be culled during hunting, this phenomenon would only concern the resident group. Our findings are consistent with a previous study on white-tailed deer (Root et al., 1988), though they are in contrast with the results of Tolon et al. (2009) on another wild boar population and Grignolio et al. (2011) on roe deer. Root et al. (1988) showed that white-tailed deer did not move inside the protected area when intensive hunting started. Notably, their protected area covered only 7 Km^2. Conversely, Tolon et al. (2009) highlighted a marked displacement of wild boar home ranges from hunting lands to a protected area when hunting started, though this only affected the individuals whose home ranges were already “in contact” with the protected area. It is worth noting that our wild boar sample was entirely captured inside the protected areas. Thus, we could not have overestimated reserve effect by monitoring individuals which were not in contact with the protected areas. Finally, the study conducted by Grignolio et al. (2011) found that hunting with hounds (targeting wild boar and hares, *Lepus europaeus*) forced roe deer to select safe but sub-optimal areas. By comparing their results with ours, we can suggest that different species and populations may tend to prioritise either predation avoidance (i.e., roe deer) or resource supply (i.e., wild boar). Nevertheless, while the aforementioned studies focused on home ranges, our finer-scale approach (based on the likelihood of single locations being inside the protected areas and high resolution spatial data) is necessary to detect the occurrence of reserve effect on a local scale. Moreover, our study points out the need to consider the activity rhythms of species and the temporal distribution of anthropic sources of disturbance in order to fully understand the drivers affecting behavioural patterns.

Since both protected areas are located on the top of mountainous ridges, we expected a negative effect of mean air temperature on the likelihood of wild boar being outside both reserves, as individuals can compensate environmental temperature variations by moving across the altitudinal gradient (Lamberti et al., 2004; Mason et al., 2014; Brivio et al., 2019). Such supposition was verified in the small protected area (relevant only during daylight, Fig A7), while the relation between mean air temperature and the likelihood of being outside was positive in the large protected area (relevant only during nightlight, Fig A1). We can suppose that this unexpected result is another consequence of the peculiar resource distribution of this area, in which the main food resources are concentrated inside its boundaries (that is, at higher altitudes) in the cold seasons. However, it is to note that we included in our analysis this and other environmental and biological variables to take into consideration their influence on wild boar behaviour, i.e., to enhance the robustness of our results and not to properly investigate their effect on the use of the protected areas.

5. Conclusions

We showed that a relevant portion of wild boar living along the borders of the protected areas was composed of resident individuals permanently located inside the reserves and that this number was positively related to the size of the protected area. Therefore, pest species population control practices performed inside protected areas to limit damages on neighbouring unprotected lands may lack effectiveness, as their effort would be partially wasted on the control of harmless resident individuals. This consideration is especially valuable for the management of large protected areas. As we aimed to evaluate the intra-annual variation of individual likelihood to be located outside protected areas, we only included in our advanced analysis individuals showing a not-negligible use of both the protected and the unprotected areas, that is, the commuter group. Nevertheless, further investigations are needed to evaluate which factors affect the likelihood of individuals to act either as inside resident, commuter or outside resident.

We did not detect any increased use of protected areas during wild boar hunting period. Thus, the effectiveness of management practices ordinarily performed on unprotected surfaces is unlikely to be negatively affected by the presence of protected areas. Moreover, in our study area, abnormal concentrations of individuals inside the protected areas during the hunting season are unlikely to occur.

Variability of results of the few studies on reserve effect (Root et al., 1988; Tolon et al., 2009; Grignolio et al., 2011; this paper) suggests that this phenomenon is not as widespread as thought. Moreover, in the case of wild boar, its known behavioural variability can play a major role in producing even more variable reserve effect patterns. The case-dependence of reserve effect clearly highlights the necessity to verify its occurrence on a local scale. To better understand its complexity, researchers should base further investigations on fine-scale information on animal movements and activity rhythms, such as those obtained from GPS tracking.

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Ethical standards/permits

This study complies with all national and regional laws dealing with ethics and animal welfare. Capture and manipulation protocols were approved by Tuscany Regional Administration (no. 103/5936/152–13/03/2002). The research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research.

Author contributions

MA, RB, SG originally formulated the idea. RB conducted fieldwork. RB, SG and FB collaborated in imaging analysis. RB, FB and SG performed statistical analyses. RB, SG and FB wrote the original draft of the manuscript. MA provided editorial advice. MA provided materials tools and contributed to funding acquisition.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix

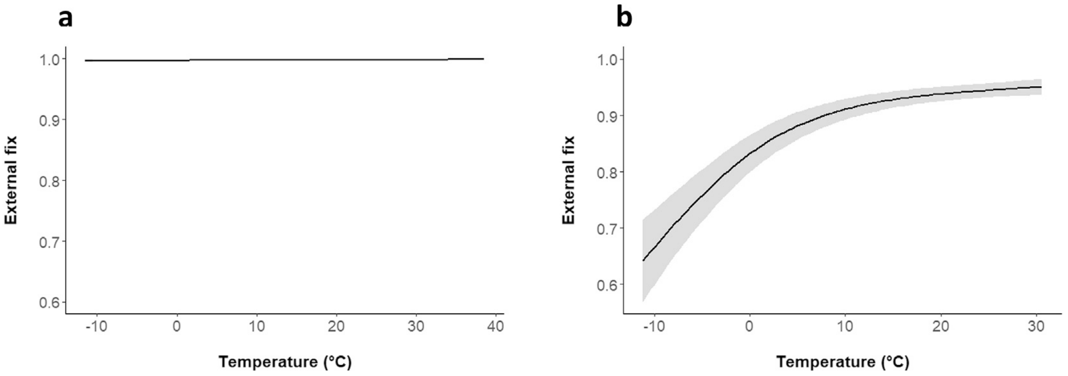

Fig. A1Effect of mean air temperature on the likelihood of wild boar being outside the FCNP protected area during daylight (a) and nightlight (b). The values reported were predicted by the best generalised additive mixed models (see the text for more details). The predictions are given according to the mean of all other covariates in the model. In the graphs the gray-shaded areas represent the estimated standard errors.

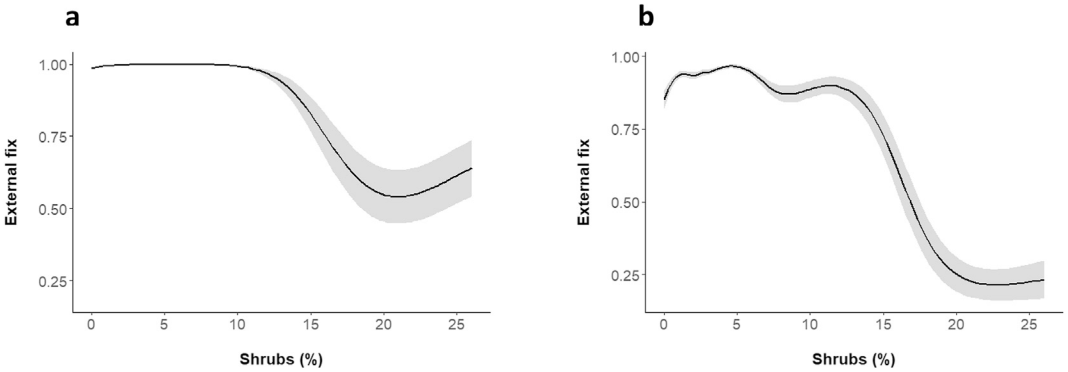

Fig. A2. Effect of shrub cover monthly availability on the likelihood of wild boar being outside the FCNP protected area during daylight (a) and nightlight (b). The values reported were predicted by the best generalised additive mixed models (see the text for more details). The predictions are given according to the mean of all other covariates in the model. In the graphs the gray-shaded areas represent the estimated standard errors.

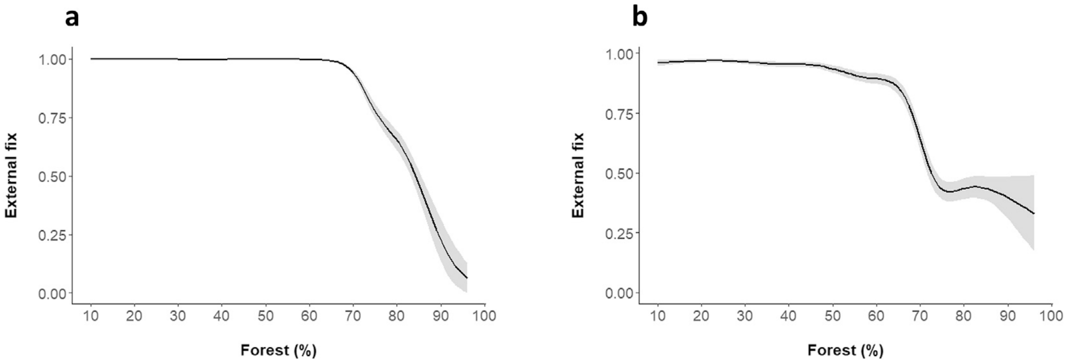

Fig. A3. Effect of forest cover monthly availability on the likelihood of wild boar being outside the FCNP protected area during daylight (a) and during nightlight (b). The values reported were predicted by the best generalised additive mixed models (see the text for more details). The predictions are given according to the mean of all other covariates in the model. In the graphs the gray-shaded areas represent the estimated standard errors.

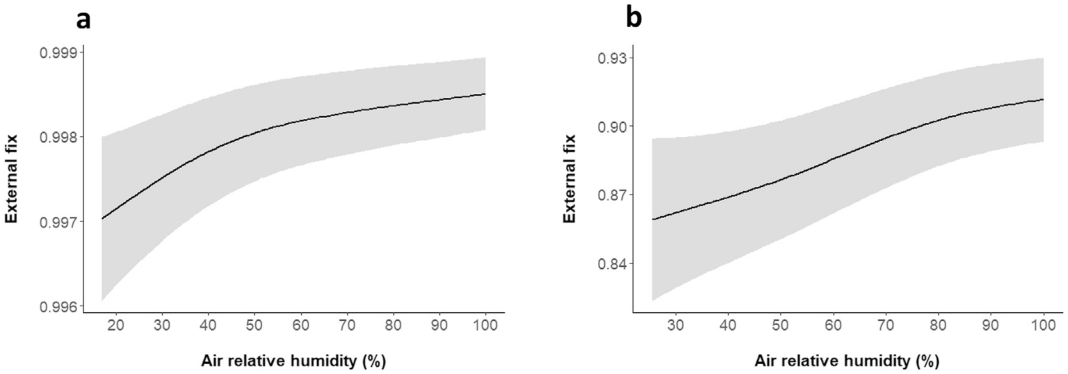

Fig. A4. Effect of air relative humidity on the likelihood of wild boar being outside the FCNP protected area during daylight (a) and nightlight (b). The values reported were predicted by the best generalised additive mixed models (see the text for more details). The predictions are given according to the mean of all other covariates in the model. In the graphs the gray-shaded areas represent the estimated standard errors.

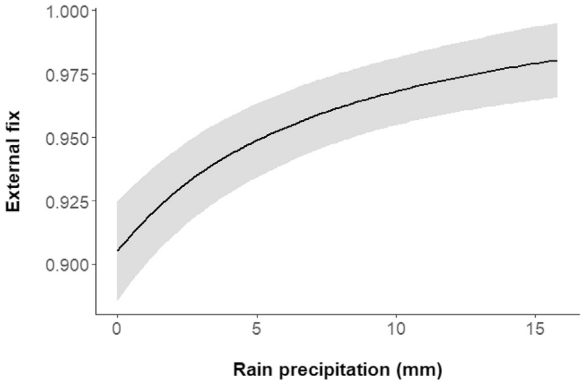

Fig. A5. Effect of rain precipitation on the likelihood of wild boar being outside the FCNP protected area during nightlight. The values reported were predicted by the best generalised additive mixed model (see the text for more details). The predictions are given according to the mean of all other covariates in the model. In the graphs the gray-shaded areas represent the estimated standard errors.

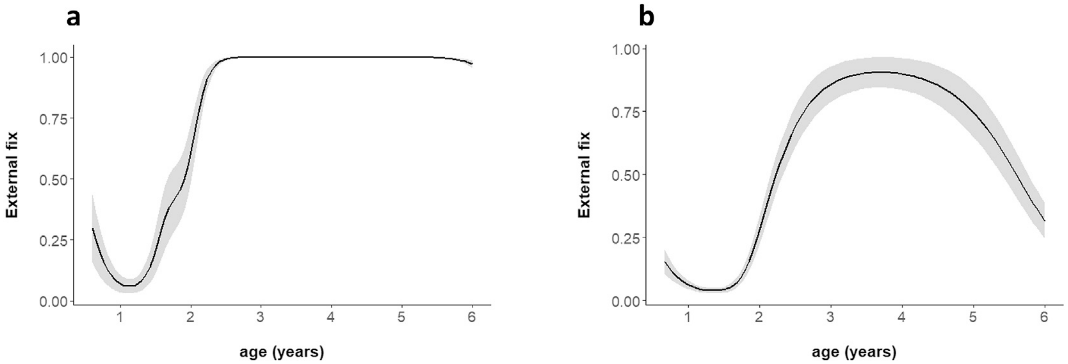

Fig. A6. Effect of individual age on the likelihood of wild boar being outside the OAC protected area during daylight (a) and nightlight (b). The values reported were predicted by the best generalised additive mixed models (see the text for more details). The predictions are given according to the mean of all other covariates in the model. In the graphs the gray-shaded areas represent the estimated standard errors.

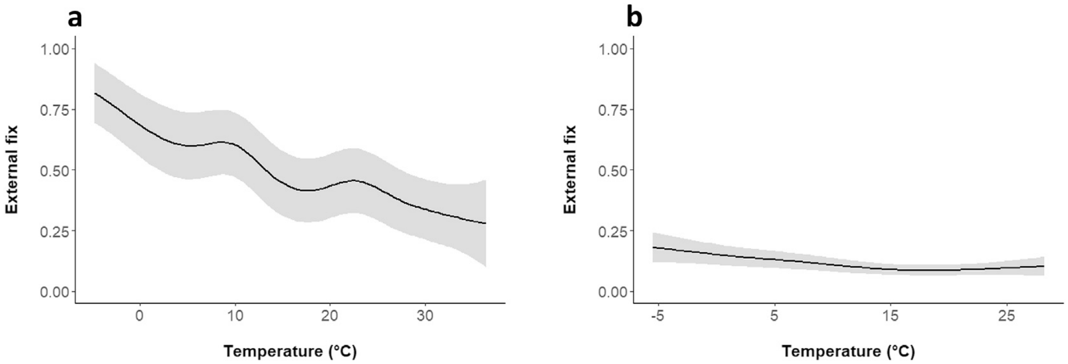

Fig. A7. Effect of mean air temperature on the likelihood of wild boar being outside the OAC protected area during daylight (a) and nightlight (b). The values reported were predicted by the best generalised additive mixed models (see the text for more details). The predictions are given according to the mean of all other covariates in the model. In the graphs the gray-shaded areas represent the estimated standard errors.

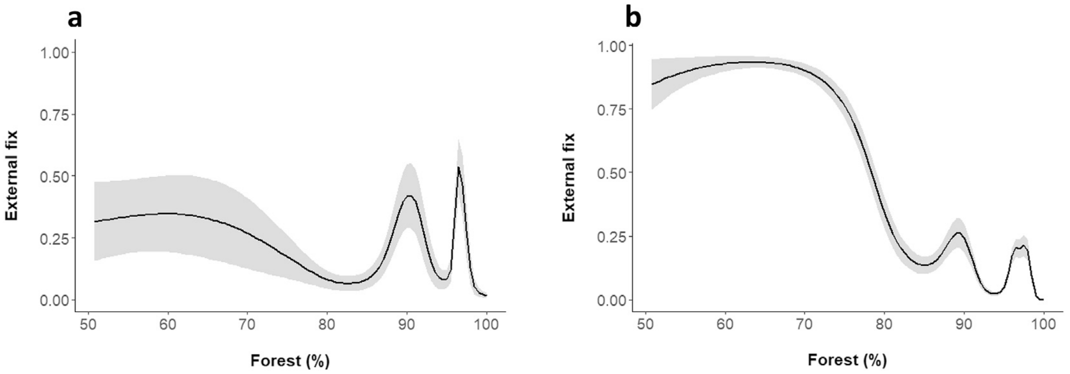

Fig. A8. Effect of forest cover monthly availability on the likelihood of wild boar being outside the OAC protected area during daylight (a) and nightlight (b). The values reported were predicted by the best generalised additive mixed models (see the text for more details). The predictions are given according to the mean of all other covariates in the model. In the graphs the gray-shaded areas represent the estimated standard errors.

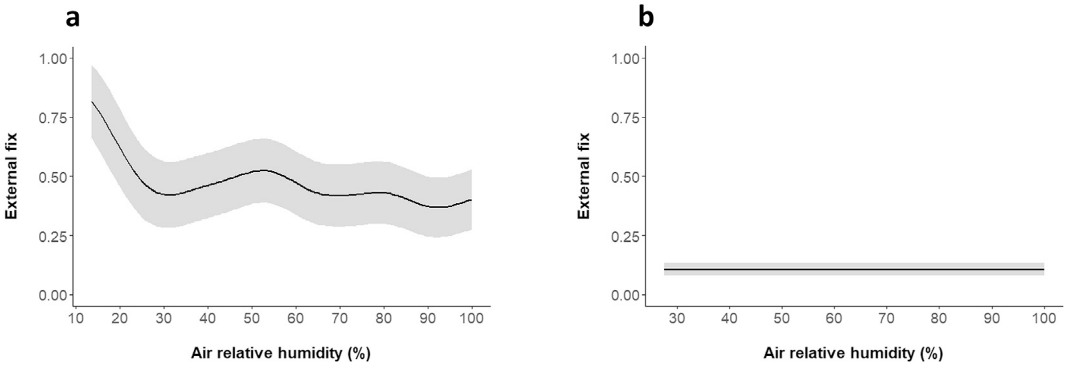

Fig. A9. Effect of air relative humidity on the likelihood of wild boar being outside the OAC protected area daylight (a) and nightlight (b). The values reported were predicted by the best generalised additive mixed models (see the text for more details). The predictions are given according to the mean of all other covariates in the model. In the graphs the gray-shaded areas represent the estimated standard errors.

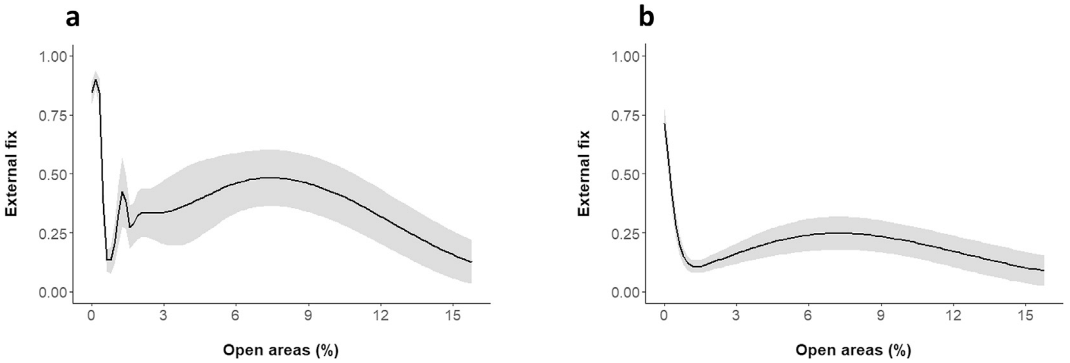

Fig. A10. Effect of open area monthly availability on the likelihood of wild boar being outside the OAC protected area during daylight (a) and nightlight (b). The values reported were predicted by the best generalised additive mixed models (see the text for more details). The predictions are given according to the mean of all other covariates in the model. In the graphs the gray-shaded areas represent the estimated standard errors.

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