

ORIGINAL RESEARCH

Behavioural responses to temporal variations of human presence: Insights from an urban adapterR. Brogi¹ , M. Apollonio¹, S. Grignolio^{1,2} , A. Cossu¹, S. Luccarini¹ & F. Brivio¹ ¹Department of Veterinary Medicine, University of Sassari, Sassari, Italy²Department of Life Science and Biotechnology, University of Ferrara, Ferrara, Italy**Keywords**

behaviour-specific; human-dominated environments; wildlife management; behavioural plasticity; resource selection; *Sus scrofa*; fear; urban wildlife.

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Abstract

Human-dominated environments are growing worldwide, forcing animals to adapt to new conditions characterized by increased risks and/or anthropogenic resources availability. While numerous studies have compared behavioural patterns of rural and urban populations, little is known about plastic behavioural responses to temporal variations in human presence. We modelled the behaviour-specific resource selection of 15 wild boars (*Sus scrofa*) GPS-tracked between 2017 and 2019 in a tourist area in Italy characterized by high seasonal variability of human presence. By means of activity sensor data, we differentiated between two behavioural states with different ecological needs: resting (safe shelter) and activity (food intake). We investigated the variability of selection/avoidance of infrastructures and beaches, across seasons and behavioural states. We expected human-built landscape features to be avoided for resting and selected for activity, with a strength proportional to the seasonal level of human presence. Instead, wild boars selected locations near infrastructures and away from beaches, both for resting and while being active. We showed that the similarity of behavioural patterns exhibited during the resting and active phases was accountable to the wild boar activities being spatially constrained by the proximity with their previous resting location. As expected, the selection for infrastructure proximity and avoidance of beaches peaked in summer (maximum human presence) and was negligible in winter (least human presence), showing that a variable human presence elicits intra-individual plastic responses in animal populations. Our results suggest the behavioural flexibility of wild boars as a key factor enabling them to rapidly colonize human-dominated environments.

Introduction

Human presence and activities have an increasing impact on animal behaviour worldwide (Wilson et al., 2020), forcing animals to either adapt or be excluded from the growing human-dominated portion of the global surface (Lowry et al., 2013). The most prominent consequences include modifications of spatial and temporal patterns of risk perception, triggering major changes in animal behavioural ecology (Gaynor et al., 2019; Suraci et al., 2019). Humans can, indeed, induce fearful responses even stronger than those induced by natural predators in a wide variety of ecosystems (Ciuti et al., 2012; Suraci et al., 2019; Wilson et al., 2020). Human activities can also affect the availability and distribution of food sources. This is the case with anthropogenic food subsidies such as human waste exploited by animal populations inhabiting urban and suburban areas (Murray et al., 2015; Stillfried et al., 2017). The increased risks and availability of resources in human-dominated

environments can disrupt natural risk-foraging trade-offs, altering the selective pressures to which animals are exposed.

Several studies have investigated the behavioural adaptations of animals to human presence by comparing the behavioural patterns of rural populations with those of their urban counterparts (e.g., Breck et al., 2019; Miranda et al., 2013; Ritzel & Gallo, 2020; Stillfried et al., 2017). Specifically, comparisons between urban and rural populations have highlighted diet shifts to anthropogenic food (Castillo-Contreras et al., 2021; Traut & Hostetler, 2003), alterations of activity rhythms (Tigas et al., 2002), and changes in resource selection and movement patterns (Ngcobo et al., 2019; Stillfried et al., 2017). However, it remains largely unexplored whether and how animals respond to seasonal variations in human disturbance. Understanding the mechanisms that allow a population to deal with temporal changes of anthropogenic presence might shed light on the factors driving the behavioural responses to human presence. Behavioural differences between rural and urban populations may

indeed be accounted to both phenotypic plasticity or intrinsic differences (Lowry *et al.*, 2013; Miranda *et al.*, 2013), whereas behavioural responses of individuals to a temporally variable human presence could only be the result of phenotypic plasticity, which is indeed 'the change in the expressed phenotype of a genotype as a function of the environment' (Scheiner, 1993).

Fitting the description of both urban adapter (Castillo-Contreras *et al.*, 2021; Stillfried *et al.*, 2017) and phenotypically plastic species (Brogi *et al.*, 2021; Podgórski *et al.*, 2013), wild boars (*Sus scrofa*) can be used as a particularly appropriate case study for exploring possible behavioural adaptations of large mammals to a temporally variable human presence. Wild boar is an omnivorous generalist species that is expanding globally (Brook & van Beest, 2014; Keuling *et al.*, 2016; Massei *et al.*, 2015) increasingly present in urban areas where it mostly relies on anthropogenic food (Cahill *et al.*, 2012; Castillo-Contreras *et al.*, 2021; Podgórski *et al.*, 2013; Stillfried *et al.*, 2017). Its presence in urban habitats is the cause of a wide variety of conflicts with humans, including damage to public and private properties, traffic accidents, disease transmission, and even attacks on pets and humans (Castillo-Contreras *et al.*, 2022; Hagemann *et al.*, 2022). As a consequence, comparisons between rural and urban populations of wild boar are increasingly present in literature, highlighting behavioural (Castillo-Contreras *et al.*, 2021; Podgórski *et al.*, 2013; Stillfried *et al.*, 2017) and even genetic differentiations (Hagemann *et al.*, 2022; Zsolnai *et al.*, 2022). Nonetheless, to the best of our knowledge, no study investigated the behavioural responses exhibited by wild boar individuals facing strong temporal variations in human presence and disturbance (excluding hunting).

To test the hypothesis of wild boars plastically adapting their behaviour to the temporal variations in human presence, we collected high-resolution spatial data on wild boar movements in a seaside area, characterized by a marked seasonal variation in human presence because of a huge tourist frequentation highly variable across seasons: high in summer, moderate in spring and fall, weak in winter. We modelled the wild boar resource selection across two behavioural states, resting and activity, which can be expected to differ in the sensitivity of wild boar towards human disturbance and attraction for anthropogenic food resources. We predicted that:

- Since resting requires a safe shelter while activity is intended to acquire resources, resting wild boars avoid areas close to infrastructures and beaches. Conversely, wild boars are attracted by human-built landscape features to exploit anthropogenic resources during their active state;
- The strength of the selection/avoidance patterns to the proximity of infrastructures and beaches is consistent with tourist flow (i.e., high in summer, moderate in spring and fall, and low in winter).

Materials and methods

Study area

We collected animal spatial data in a seaside tourist area located in north-western Sardinia, a large island in Italy, specifically in

the municipality of Alghero (40°35'50" N, 8°15'9" E, Fig. 1). According to the 2019 Italian National census, this area hosted 42 589 human residents (190 residents/km²). Tourist flow was markedly seasonal, with the number of incoming tourists being minimum in winter (10 776 ± 1216, mean ± SD), maximum in summer (149 135 ± 9606) and moderate in spring and fall (66 306 ± 2749 and 79 010 ± 2466, respectively), during the years of monitoring (Morandi F. unpublished data). The altitude ranges between 0 and 424 m a.s.l. and the climate is characterized by very hot and dry summers, and windy and cold winters. Monthly average temperatures range from 9.8°C (January) to 24.3°C (August) and an average rain precipitation of 495 mm is recorded annually. Evergreen forests and Mediterranean garrigue cover 29 and 21% of the study area, respectively, while a further 7% of the study area once occupied by open pastures is now being recovered by sparser, regrowing garrigue. Agricultural areas (mostly cereals, vineyards, and olive groves) occupy 40% of the study area. Human infrastructures (mainly small villages and paved roads) cover the remaining 3%.

A protected area of 54 km² (Porto Conte Regional Park) was included in the study area. Outside the protected area, wild boar is hunted by means of drive hunt from October to January, while non-human predators are totally absent.

Wild boar spatial data

Wild boars were captured by means of baited traps, between 2017 and 2019 ($n = 15$, 8 females and 7 males). Following the protocol described by Brogi *et al.* (2019), each captured wild boar was sedated and equipped with a Global Positioning System collar (Vertex Lite collar, Vectronic Aerospace), configured to record one spatial position every 2 h (12 GPS spatial positions/day). An average of 4077 valid spatial positions (i.e., recorded with at least four satellites and with dilution of precision smaller than 10) per individual were recorded. Each collar included a two-axis accelerometer which measured activity every 5 min, recording it along a continuous range (0–255, for more details see Brivio *et al.*, 2017). For more details on animal welfare during capture, manipulation, and collar fitting, see Brogi *et al.* (2022). This study complies with all national and regional laws dealing with ethics and animal welfare. Protocols for capture and manipulation were approved by Sardinia Regional Administration (no. 4753 REP N 74 DEL 07/03/2017). The research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research (Guidelines for the treatment of animals in behavioural research and teaching, 2020).

Identification of resting and activity locations

Since we aimed to consider the behavioural state of wild boars when modelling their resource selection, we first identified the locations used for resting and those used for activities, by merging the information on spatial positions with data recorded by the activity sensors.

First of all, each raw activity record was transformed into a binary variable (0 inactive, 1 active) according to the protocol described by Brivio *et al.* (2021). Then, we averaged the

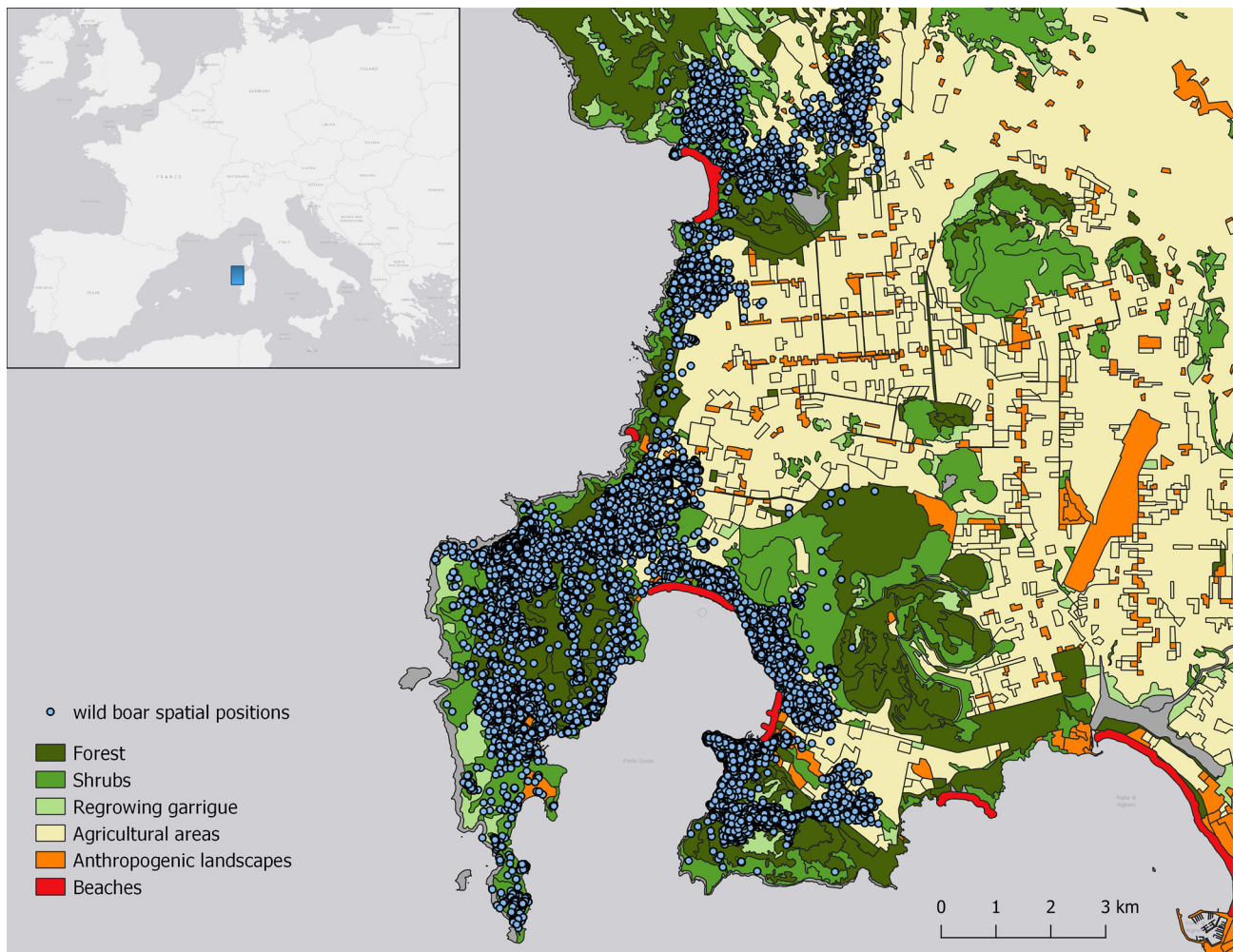


Figure 1 Map of the wild boars' locations collected by means of GPS telemetry from 2017 until 2019 in Sardinia, insular Italy, and the landcover features used for the resource selection analysis (see the text for more details). Top-left panel shows the localization of the study area in Southern Europe.

activity recorded during the 2 h preceding every recorded spatial position, and we classified as 'active' those spatial positions with an average activity ≥ 0.1 (i.e., at least 10% of time spent moving) and as 'inactive' those with an average activity < 0.1 (Brogi *et al.*, 2022). However, by using this classification method, some resting locations may be wrongly classified as active locations, because every first spatial position recorded during a resting event is likely to be preceded by an intense activity (i.e., animal's movements to reach the resting location). Consequently, to use a conservative approach, we identified as 'active locations' (ALs) only those active spatial positions that were followed by at least a further active spatial position and discarded those that were followed by an inactive spatial position.

We adopted a rigorous and conservative spatio-temporal criterion also to identify resting locations (RLs). Firstly, we identified a RL as the centroid of a series of at least two consecutive inactive spatial positions. In so doing, we could:

- (1) avoid the inclusion of short inactive periods possibly accountable to external factors rather than to a real resting event;
- (2) correctly identify one single RL for every resting event avoiding pseudoreplications (i.e., different inactive spatial positions at the same RL). As a further precautionary measure, for each RL, we calculated the average distance between the inactive spatial positions and their centroid and dropped from our dataset specific RLs characterized by an average distance between spatial positions and centroid higher than 15 m (roughly, the GPS precision). Hence, we considered as resting events only those characterized by null or negligible spatial movements. Finally, we generate a unique dataset putting RLs and ALs together adding a binary variable 'behavioural state' assuming 'resting' and 'activity' for RLs and ALs, respectively. This dataset was used for subsequent Resource Selection Function analysis.

For each wild boar, we additionally identified the 'resting sites' (RSs), that is, sites repeatedly used by each individual

for resting during different resting events. RSs were identified by using a clustering approach: we used the QGIS algorithm 'DBScan' (Density-Based Spatial Clustering of Applications with Noise, Sander *et al.*, 1998) to identify the spatial clusters of RLs, setting to 1 the minimum number of RLs per cluster and to 100 m the maximum distance between RLs to be included in the same cluster. We then calculated the number of RSs repeatedly used by each individual for resting and the number of consecutive days the same RS was used by each wild boar.

Generation of available points and spatial covariates extraction

We modelled wild boar selection of spatial features by adopting a presence/availability design (Manly *et al.*, 2002) and matched locations where wild boars were actually observed (presence data) to randomly selected locations (hereafter referred to as available locations). We sampled available locations within monthly home ranges of each wild boar, calculated by using the *hr_locoh()* function from the 'amt' R package (Signer *et al.*, 2019) with the Local Convex Hull (LoCoH) method. For each observed RL and AL, we generated a set of available locations randomly placed within the individual monthly home range, by means of the *random_point()* R function. To prevent the instability of the resource selection parameters, we defined the optimal number of random available locations to be associated with each observed location by running a sensitivity analysis (e.g., Brivio *et al.*, 2019), which suggested the use of 11 available locations per observed location. Available locations were thus paired to observed ones and to each pairing (ratio 1:11) was assigned a unique identification code (stratum-ID). The individual identity of each monitored wild boar, its behavioural status (resting/active), and date and time of observation were assigned to each observed location, as well as to its corresponding available locations. We added a new binary variable 'used' to each location, assuming 0 for available and 1 for observed locations. We generated a further categorical variable referred to the season of the year according to the location date, following the rule: 'spring' between March and May, 'summer' between June and August, 'fall' between September and November, and 'winter' between December and February.

We used a rasterized CORINE Land Cover database (resolution of 10 m) to assign all locations (either observed or available) to one of the following habitat categories: forest, shrub, regrowing garrigue (sparser shrubs), agricultural area (cereal fields, vineyards, olive groves), or anthropogenic landscape (villages, urban areas, paved roads). We assigned to each location two continuous variables related with human presence: the linear distance (m) from the nearest human infrastructure (house, urban areas and factory) and that from the nearest beach (hereafter 'distance.infrastructure' and 'distance.beach', respectively). We also calculated the distance from the nearest paved road of each location, but since it was collinear with distance.beach and had a worse ranking in a random forest calculation ('random.Forest' R package), we dropped it from the subsequent analyses. Finally,

we used a digital surface model online database (EU-DEM v1.0, <https://land.copernicus.eu/>) to assign to all locations three further continuous covariates: altitude (m a.s.l.), slope index (0 = vertical terrain, 250 = horizontal terrain), and surface orientation (sine of North degrees, -1 = South, 0 = East and West, 1 = North).

Resource selection functions

We estimated the effect of human presence on wild boar resource selection by running a binomial GLMM (Generalized Linear Mixed Model) with the 'glmer' function ('lme4' R package), with 'used' as response variable and the individual identity included as random intercept to account for unbalanced sample sizes across individuals. The input datasets comprised the whole set of observed and available locations for both resting and activity, for a total of 332 548 entries. Since our hypotheses were that (1) the proximity to infrastructures and beaches is selected for being active but avoided for resting, and (2) the strength of these effects follows the seasonality of tourism presence, we included into the models the third-order interaction terms distance.infrastructure: behavioural state: season of the year and distance.beach: behavioural state: season of the year. To achieve a meaningful model, besides these third-order interactions we also included the main effects of distance.infrastructure, distance.beach, the behavioural state, the season of the year, and the second-order interactions distance.infrastructure: behavioural state, distance.infrastructure: season, distance.beach: behavioural state, distance.beach: season, and behavioural state: season. To control for the effect of the behaviour-specific wild boar preference for different habitat types, we included into the model the habitat type and its interaction with the behavioural state. Finally, we controlled for the possible effects of the terrain morphology on wild boar resource selection by adding altitude, slope index, and surface orientation as control predictors. Since the model already included third-order interactions, we decided not to add further non-spatial predictors (e.g., individual characteristics, such as sex and age); this, in fact, would have entailed including even higher order interactions with an increase in model complexity, without providing useful information to the topic of this study (population-level plastic responses to human presence). Prior to fitting the model, we screened all numeric predictors for collinearity (Pearson coefficient $|r_p| < 0.7$) and multicollinearity (Variance Inflation Factor, VIF < 3 , Zuur *et al.*, 2009), but no issues arose. After this, we *z*-transformed all numerical predictors (distance.infrastructure, distance.beach, altitude, slope, and surface orientation) to a mean of zero and a standard deviation of one to get comparable estimates and easier interpretable model results (Schielzeth, 2010).

As an overall test on the effect of infrastructures and beaches proximity significantly changing across behavioural states and seasons and to avoid 'cryptic multiple testing' (Forstmeier & Schielzeth, 2011) we compared the fit of the full model as described above with that of a null model lacking all third- and second-order interactions involving the behavioural state and the season but comprising all other terms included in the full model,

including distance.infrastructure and distance.beach. This comparison was based on a Chi squared test (R function ‘anova’).

Resource selection function validation and visualization of predictions

Since the presence/available data characterizing RSFs cannot be really assimilated to the presence/absence data, we validated the full model by means of a five-fold cross-validation (Boyce *et al.*, 2002). This process entailed calculating a Spearman rank correlation between RSF ranks and area-adjusted frequencies for a withheld sub-sample of data (i.e., 1/5 of the data, see Boyce *et al.*, 2002; Brivio *et al.*, 2019 for more details on the analytical approach). Good predictive performance models would be expected to have a strong positive correlation (Wiens *et al.*, 2008).

Finally, we followed the protocol described by Brivio *et al.* (2019) to correctly visualize wild boar resource selection predictions by means of RSF scores which are proportional to the probability of selection (Lele *et al.*, 2013).

Spatial constraints between RLs and ALs

To evaluate possible spatial constraints between RLs and ALs, we calculated the linear distance (m) between each AL (either observed or available) and the last observed RL of the same individual. Then, we tested whether the distance from the previous RL significantly differed between observed and available ALs. We performed a *t*-test by means of the ‘*t.test*’ R function to compare the distance from the previous RL of observed ALs with that of available ALs.

Results

We identified 4 888 RLs and 23 558 ALs. Wild boars used a limited set of different RSs, with an individual average of 2.65 ± 1.07 RSs/month of monitoring (mean \pm SE), changing them every 4.09 ± 2.29 days (Table S1). We generated available locations within 168 individual monthly home ranges, whose sizes averaged 102 ± 118 ha, 49 ± 21 ha, 180 ± 127 ha, and 114 ± 110 ha in spring, summer, fall, and winter, respectively (see Table S2 for monthly averages of home range size).

Resource selection functions

Overall, the full model was highly significant as compared with the null model ($\chi^2 = 1776.275$, $P < 0.001$) and had outstanding predictive ability on withheld data (Spearman correlation coefficients: $\rho_{\text{fold1}} = 0.964$, $\rho_{\text{fold2}} = 0.988$, $\rho_{\text{fold3}} = 0.964$, $\rho_{\text{fold4}} = 0.985$, $\rho_{\text{fold5}} = 0.988$; Fig. S2).

The estimated effects of the predictors related to the human presence (distance.infrastructures and distance.beach) across different seasons and behavioural state are shown in Fig. 2 (see also Table 1 for an overview of the estimated effects for all predictors included in the full model). The interaction between the distance from the nearest infrastructure and the behavioural state was not significant, and the same holds for the distance from the nearest beach (Table 1), rejecting our

prediction on the proximity with human infrastructures and beaches being avoided for resting and selected for being active. Consistently, the seasonal effects of distance.infrastructures and distance.beach did not substantially differ between the two behavioural states (Fig. 2).

Conversely, both the effects of the distance from the nearest infrastructure and from the nearest beach significantly varied across different seasons (Table 1). Wild boars selected locations close to human infrastructures in all seasons, irrespectively to the behavioural state (resting/activity), with this effect being the strongest in summer and spring, less pronounced but still significant in fall, and not significant in winter (Table 1, Fig. 2a). The nearest beach had an opposite effect but with an analogous seasonal variation, with wild boars avoiding the proximity to beaches in summer (strongest effect) and spring, while this effect became not significant in fall and winter (Table 1, Fig. 2b), consistently with our second prediction. As regards the habitat types, the relative probability of selection of habitats characterized by a dense vegetation cover (forest, regrowing garigue, and shrubs) was higher during the resting phase. Conversely, the selection of anthropogenic landscapes was higher for active wild boars (Fig. 3).

Spatial constraints between RLs and ALs

When active, wild boars selected locations close to their last RL, with a linear distance from the last RL being significantly shorter for observed (592 ± 163 m) than for available (1083 ± 348 m) ALs ($t = -74.95$, d.f. = 46 170, $P < 0.001$).

Discussion

The effect of human presence on wild boar resource selection did not differ between resting and activity, but significantly changed across seasons, consistently with the touristic flow. Therefore, our results showed that even populations exposed to a seasonally variable human presence can exhibit adaptations to humans, analogous to those observed in wild boars living in urban areas and thus constantly exposed to human activities (e.g., Stillfried *et al.*, 2017). Moreover, we provided evidence that wild boars exhibit a plastic response to seasonal variations in perceived risks and resource availability. Since only investigating a population exposed to a varying level of human presence may inform about the intra-individual plasticity of behavioural responses to humans, we can consider this study as one of the first confirmations of this phenomenon.

In partial accordance with our first prediction, wild boars selected areas close to human infrastructures when active, likely revealing their habit of exploiting anthropogenic food resources. In this context, the selection of locations situated away from beaches could be attributed to their relatively low availability of anthropogenic food in comparison to urban areas. The scarcity of food might have negated the benefits of tolerating the high levels of disturbance commonly found on beaches. The use of anthropogenic food by the monitored individuals was further confirmed by the selection for the habitat category of anthropogenic landscapes observed during the

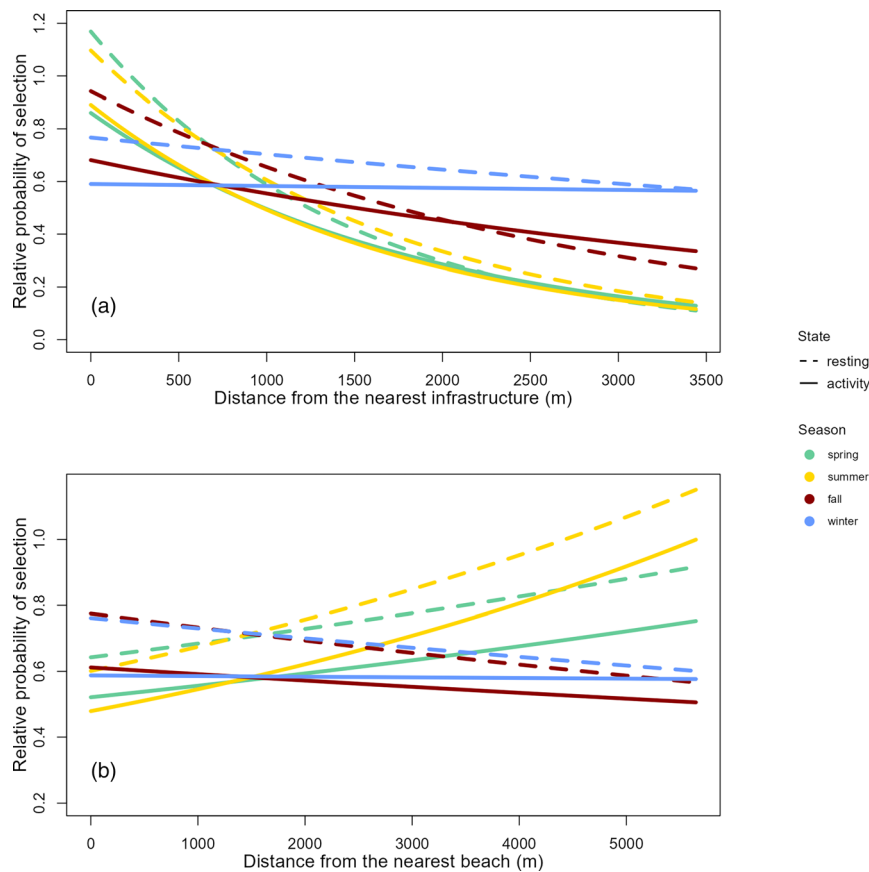


Figure 2 Seasonal effects of the distance from the nearest infrastructure (a) and from the nearest beach (b) on the relative probability of selection of a spatial position, as predicted by the best Generalized Linear Mixed Models on the resource selection by wild boar in Sardinia (Italy, see the text for more details). Dashed lines depict the pattern of the resting state, while solid lines that of the active state. Green, yellow, brown, and light blue lines represent the probability of selection in spring, summer, fall, and winter, respectively.

active states and it is consistent with previous reports on wild boars living at the edge of large European cities (Cahill *et al.*, 2012; Castillo-Contreras *et al.*, 2021; Stillfried *et al.*, 2017). Nonetheless, wild boars may have approached infrastructures only when active, that is, when they could effectively utilize anthropogenic food resources while facing lower levels of disturbance (as the monitored individuals were predominantly nocturnal, see Fig. S1), avoiding these high-perceived risk areas for resting. Similarly, wild boars may have selected locations situated away from beaches solely for resting. Surprisingly, the selection for areas close to infrastructures and away from beaches was observed during both resting and active states, contrary to our first prediction. Such unexpected evidence may be accounted to the non-mutual independence of resting and active locations, as shown by wild boars implementing their activities close to the location they used for resting, at an observed average distance of 592 m. Wild boars thus chose to rest close to human infrastructures to be able to use these areas for their subsequent activities. This interpretation is consistent with the set of results obtained for the habitat categories, as wild boars selected anthropogenic landscapes for being active but not for resting. This behavioural pattern may

be explained by the spatial constraint between resting and activity as highlighted by our data, which probably forced wild boars to rest within the surroundings of the foraging areas, not necessarily within them. Therefore, wild boars attempted to cope with the different main requirements of resting (safety) and activity (food intake) through different habitat selection patterns, but they were unable to avoid the proximity to human infrastructures and beaches for resting, possibly due to their limited spatial mobility (Morelle *et al.*, 2015). In this context, the evidence of wild boars trading the safety of their resting locations for a higher intake of anthropogenic resources confirmed their tendency to favour food acquisition over the avoidance of risks (Brogi *et al.*, 2020). If evaluated together with the RS use patterns, this result suggests that wild boars rested in the same site for a few days to forage within its immediate surroundings (possibly searching for anthropogenic food), then moved to another resting site to use another sub-portion of the home range, and cyclically repeated this routine moving across a limited set of resting sites (an average of 2.65 ± 1.07 per month in the monitored individuals).

Consistent with our second prediction, the strength of human infrastructures' effect on wild boar resource selection varied in

Table 1 Full model output of the Resource Selection Function of the 15 wild boars GPS-tracked in Sardinia (Italy) between 2017 and 2019

Term	Estimate	SE	P
Intercept	-2.709	0.074	<0.001***
season (fall)	-0.004	0.022	0.860
season (spring)	-0.030	0.021	0.149
season (summer)	-0.015	0.023	0.506
behavioural state (resting)	0.220	0.031	<0.001***
slope	0.065	0.010	<0.001***
surface orientation	0.024	0.007	<0.001***
altitude	0.068	0.011	<0.001***
habitat type (agricultural lands)	0.543	0.023	<0.001***
habitat type (anthropogenic)	0.819	0.033	<0.001***
habitat type (regrowing garigue)	0.503	0.035	<0.001***
habitat type (other habitats)	-1.754	1.006	0.081
habitat type (shrubs)	0.379	0.022	<0.001***
habitat type (agricultural lands): behavioural state (resting)	-2.088	0.094	<0.001***
habitat type (anthropogenic): behavioural state (resting)	-0.937	0.095	<0.001***
habitat type (regrowing garigue): behavioural state (resting)	0.305	0.073	<0.001***
habitat type (other habitats): behavioural state (resting)	-12.927	1745	0.994
habitat type (shrubs): behavioural state (resting)	0.299	0.048	<0.001***
distance.infrastructure	-0.005	0.018	0.760
distance.infrastructure: season (fall)	-0.110	0.022	<0.001***
distance.infrastructure: season (spring)	-0.312	0.022	<0.001***
distance.infrastructure: season (summer)	-0.334	0.026	<0.001***
distance.infrastructure: behavioural state (resting)	-0.067	0.037	0.067
distance.infrastructure: season (fall): behavioural state (resting)	-0.033	0.054	0.548
distance.infrastructure: season (spring): behavioural state (resting)	-0.028	0.051	0.577
distance.infrastructure: season (summer): behavioural state (resting)	0.064	0.058	0.269
distance.beach	-0.003	0.017	0.842
distance.beach: season (fall)	-0.025	0.022	0.248
distance.beach: season (spring)	0.057	0.022	<0.01**
distance.beach: season (summer)	0.134	0.028	<0.001***
distance.beach: behavioural state (resting)	-0.051	0.034	0.138
distance.beach: season (fall): behavioural state (resting)	0.020	0.053	0.706
distance.beach: season (spring): behavioural state (resting)	0.079	0.048	0.096
distance.beach: season (summer): behavioural state (resting)	0.023	0.057	0.687

The levels of the categorical predictors are shown in brackets as 'predictor (level)', and their effect is expressed as the comparison with the reference level. Season, behavioural state, and habitat type had winter, forest, and activity as reference levels, respectively. Slope (slope index of the terrain), surface orientation (sine of North degree), altitude (meters above the sea level), distance.infrastructure (spatial distance from the nearest infrastructure), and distance.beach (spatial distance from the nearest beach) are continuous numerical variables, z-transformed to a mean of zero and a standard deviation of one. Second- and third-order interactions are indicated as 'predictor1:predictor2' and 'predictor1:predictor2:predictor3'. "Estimate" and "SE" refer to the β coefficients and their standard errors, respectively.

***Refers to P values <0.001, **To P values comprised between 0.001 and 0.01. See the Methods section for more details.

accordance with the seasonality of the touristic flow. In summer, with more people in the area, the selection for locations close to infrastructures was stronger, likely to take advantage of the increased availability of anthropogenic resources. This effect progressively decreased in other seasons characterized by a lower human presence until becoming negligible in winter. This result depicted a change in the expressed phenotype (i.e., a behavioural pattern) in a set of individuals as a function of the environment, thus fitting the formal definition of plasticity (Scheiner, 1993; Sih *et al.*, 2004). The same was observed for beach proximity avoidance, with wild boars keeping away from crowded beaches in summer and then gradually adapting this behavioural pattern to the tourist presence variation in the other seasons. This striking

behavioural flexibility may be a key factor enabling wild boar populations to rapidly colonize human-dominated environments (Castillo-Contreras *et al.*, 2021; Stillfried *et al.*, 2017).

Besides shedding light on the reasons behind wild boar's success in anthropized areas, our set of results also provided useful information for managing human-wild boar conflicts. The selection of areas surrounding infrastructures, both during resting and foraging phases, suggests that a broader environmental management would be more effective than a generalized culling. In addition to reducing the availability of anthropogenic food resources to decrease the attractiveness of inhabited areas for active wild boars, removing vegetation, such as shrubs and regrowing garrigue in the present study,

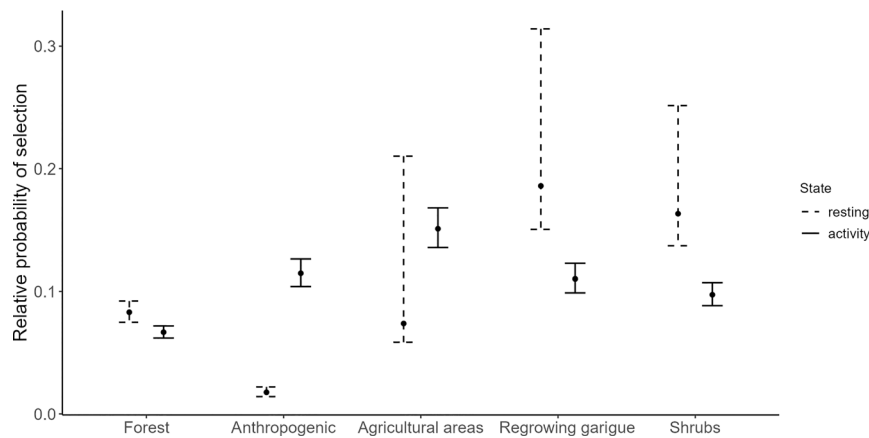


Figure 3 Relative probability of selection of the habitat categories included in the best Generalized Linear Mixed Models on the resource selection by wild boar in Sardinia (Italy, see the text for more details). Dots represent the mean probability of selection, dashed and solid bars represent the estimated confidence intervals for the resting and the active states, respectively.

located near roads, infrastructures, and urban areas, might prevent wild boars from finding suitable resting sites, substantially hindering their persistence in human-dominated environments.

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Conflict of interest

The authors declare they have no competing interests.

Author contributions

RB, FB, SG, and MA conceived the idea and designed methodology. FB, SG, AC, and SL collected the data. RB analysed the data. RB and FB wrote the first draft of the manuscript. SG and MA commented on previous versions of the manuscript. FB supervised all steps of the manuscript preparation. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

All data generated or analysed during this study are deposited on the Mendeley Data repository and are publicly available at <https://data.mendeley.com/datasets/z54hcs3yvz/1>.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure A1. Activity rhythms of the monitored Sardinian wild boars in the four seasons. Each colored line represents an individual (purple: females; blue: males), while vertical dashed lines represent the seasonal averages of local UTC time of sunrise (left) and sunset (right). Spring included dates from 1st of March to 31st of May, summer those from 1st of June to the 31st of August, fall those from 1st of September to the 31st of November, and winter those from 1st of December to the 28th of February, respectively.

Figure A2. Resource selection function (RSF) evaluation: area-adjusted frequency of categories (bins) of RSF scores. The evaluation implied calculating the correlation between RSF ranks and area-adjusted frequencies for a withheld sub-sample of data, e.g. 1/5 of the data in a 5-fold crossvalidation scheme. We investigated the pattern of predicted RSF scores for partitioned testing data (presence-only) against categories of RSF scores (10 bins). A Spearman rank correlation between area-adjusted frequency of cross-validation points within individual bins and the bin rank was calculated for each cross-validated model. A model with good predictive performance would be expected to be one with a strong positive correlation, as more use locations (area-adjusted) would progressively fall into higher RSF bins. In this case, the 5-fold cross-validation showed that the resource selection model had outstanding predictive ability on withheld data (Spearman correlation coefficients: $\rho_{\text{fold1}} = 0.964$, $\rho_{\text{fold2}} = 0.988$, $\rho_{\text{fold3}} = 0.964$, $\rho_{\text{fold4}} = 0.985$, $\rho_{\text{fold5}} = 0.988$).

Table A1. Description of the use of resting sites by the 15 wild boars GPS-tracked in Sardinia from 2017 to 2019.

Table A2. Mean size of monthly home ranges of male and female Sardinian wild boars along the year.