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Research article

Anthropization impacts the selection of resting sites and their centrality in movement networks: wild boar across Europe as an example

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For many animal species, resting and activity happen at distinct sites. As animals are limited in how far they can travel between resting and foraging sites, the spatial layout of those sites may constrain animal movements across the landscape. In anthropized landscapes, suitable resting sites are often scarce and dispersed, and movements between them are generally more constrained than in natural landscapes. In this context, animals may not be able to travel between any pair of resting sites in one single phase of activity. Thus, it is likely that in anthropized landscapes, some resting sites have a central position in the movement patterns of animals, serving as 'stepping-stones' allowing them to travel between different sectors of their home range. We tested this hypothesis by investigating the resting site selection and movement patterns of wild boars *Sus scrofa* along wide gradients of anthropization and forest cover across Europe. First, we characterized the dynamics of resting site utilization by the wild boar in response to anthropization, on a continental scale. Then, using network analysis applied to animal movements, and betweenness centrality as a metric, we investigated the relative contribution of resting and activity sites in connecting different parts of the home range. We found that the importance of resting sites in structuring movement patterns depended on the characteristics of the landscape, and notably on the level of anthropization. Our results suggest that in anthropized landscapes, where resting sites are sometimes a limiting resource for many animals, their spatial layout may play an often unnoticed yet important role in allowing animal movements across the landscape.

Keywords: betweenness centrality, human footprint, *Sus scrofa*, tree cover

Introduction

All animals need to rest regularly, either to sleep, or because times of the day are not suitable for activity, and thus alternate between active and resting phases on a regular basis (Korstjens et al. 2010, Riede et al. 2017). Activity and resting generally happen in different places. Although some animals always rest in the same exact location, and others may rest opportunistically about anywhere, many species – including a diversity of fishes (Pickholtz et al. 2018), squamates (Mohanty et al. 2022), birds (Conklin and Colwell 2007), and mammals such as mustelids (Zalewski 1997, Wang and Fuller 2003), bats (Rollinson et al. 2013), primates (Franklin et al. 2007, José-Domínguez et al. 2015, Fei et al. 2022), elephants (Wittemyer et al. 2017), and suids (Fradin and Chamaillé-Jammes 2023) – select a resting site per day from a limited availability of suitable options, returning regularly to previously used sites. For these animals, the choice of a daily resting site is a crucial and recurring decision. When they make this decision, they determine the environmental conditions, including the level of predation risk, that they will face while in their most vulnerable state (Lima et al. 2005). The location of a resting site influences the probability of any disruption of resting – including anthropogenic disturbances – to occur, thus affecting the level of vigilance required during the resting phase, which generally lasts many hours (Campbell and Tobler 1984). Increased vigilance over long periods of rest can be energetically detrimental and reduce rest and sleep quality, with potential physiological drawbacks (Tisdale et al. 2018, Ferretti et al. 2019, Olejarz et al. 2023). As a consequence, animals usually seek resting sites that are sheltered and where disturbance is unlikely.

In addition to the above, resting sites are also selected for their spatial situation relative to the sites used during activity (Brividoro et al. 2019, Mohanty et al. 2022). Animals are constrained, both in terms of navigation and movement capacity (Nathan et al. 2008), and a suitable resting site may not be reachable if located far away from the sites visited previously during activity. Likewise, the location of a resting site may impose restrictions on where the subsequent active phase may occur, and where the next resting site to be used may be (Génin 2010, Janmaat et al. 2014). Landscape characteristics, such as permeability to movement and resting sites' availability, are key drivers of the distances and paths animals may move across during the active phase. Consequently, the resting sites and the sites used for activity, such as the preferred foraging grounds, are interconnected through movement, in ways that may depend on motion capacity and environmental features. A resting site might thus have a more or less important position in an animal's movement pattern, depending on how it connects to other sites within the home range.

As anthropization intensifies worldwide, many large and medium-sized animals increasingly struggle to find where to rest, both because altered physical environments often provide fewer suitable resting sites (Brotcorne et al. 2014, Llaneza et al. 2016, Weinberger et al. 2019, Bradsworth et al. 2021), and because the risk of disturbance by people and domestic animals reduces their suitability (Wam et al. 2012, Wittemyer et al. 2017, Bojarska et al. 2021). Animals must adjust how they select resting sites to cope with these conditions. Some reuse the same resting sites more frequently (Wittemyer et al. 2017, Fradin and Chamaillé-Jammes 2023), while others learn to use anthropic structures as shelters (Bateman and Fleming 2012). Such flexibility in resting behavior is an essential, yet sometimes overlooked quality to live in human-altered environments (Candolin et al. 2023). However, where human footprint is high, animal movements are generally constrained (Tucker et al. 2018), and transiting

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between resting and foraging sites should thus prove harder. Besides, the spatial layout of potential resting sites – i.e. their distribution in the landscape in relation to each other and to activity sites – may also be altered in anthropized landscapes. As a result, the opportunities for movement between resting sites and activity sites may be an understudied obstacle to life in anthropized landscapes. Yet, to our knowledge, the influence of anthropization on how animals move between activity sites and resting sites, and how it may affect the relative role of these sites in connecting different parts of the home range, remains to be investigated. When anthropization is low, animals should be able to travel quickly and relatively linearly between activity sites. In this context, resting sites should only be selected for their intrinsic qualities (notably for their safety), and animals should travel from and to resting sites in a rather unstructured way (as illustrated in Fig. 1a). As anthropization increases and constrains movements, animals should increasingly struggle to move across the landscape. As a result, they could select resting sites not only for their safety, but also to use them as 'stepping-stones', to move across their home range (Fig. 1b). In anthropized landscapes, well-situated resting sites could thus become important in connecting home ranges' sectors together.

We tested this hypothesis by leveraging a continental-scale movement database of a species that is found to thrive across the full gradient of anthropization: the wild boar *Sus scrofa*. We used telemetry data collected throughout Europe by members of the collaborative Euroboar initiative (https://euromammals.org/; Urbano et al. 2021). In its native range, the wild boar occupies a wide diversity of landscapes, along the widest possible gradient of anthropization. It equally thrives in remote forests, swamps and mountains, across agricultural areas, at the fringes of cities and even within them (Massei et al. 2015, Stillfried et al. 2017a). The success and current geographic and demographic expansion of the wild boar is in great part attributed to its impressive behavioral flexibility, and capacity to cope with anthropogenic constraints (Stillfried et al. 2017a). Wild boars have been shown to modify their displacement rate and home range size as anthropization increases (Podgórski et al. 2013, Stillfried et al. 2017a). They are also known to adjust both their temporal patterns of activity (Podgórski et al. 2013, Johann et al. 2020) and where they rest (Maillard and Fournier 1995) to avoid encounters with humans, although they sometimes rest very near infrastructures like houses or roads (Brogi et al. 2023). Specific needs in terms of resting site selection are low in this species, but sufficient vegetation cover is required for concealment (Spitz and Janeau 1995, Allwin et al. 2016). Their resting behavior is thus constrained by the spatial distribution of densely vegetated patches. Individuals frequently revisit resting sites that they have previously visited (Boitani et al. 1994, Brogi et al. 2023) and often reutilize the same paths and areas for transit and foraging (Morelle et al. 2015). As a result, their movement patterns may be structured by important resting sites, foraging sites and/or corridors used for transit (Brogi et al. 2023).

In a first step, we assessed the effect of anthropization on the use of resting sites by wild boars across Europe. To do this, we described where in the landscape resting sites were selected, and we calculated how often previously used resting sites were revisited. We accounted for the amount of tree cover, as forest patches are favorable to wild boars and influence resting site selection (Allwin et al. 2016). Although an increase in anthropization generally comes with a reduction of tree cover, both variables were considered, as human activities are susceptible of affecting resting behavior through other mechanisms, such as direct disturbances or infrastructure (Sodeikat and Pohlmeyer 2007, Fradin and Chamaillé-Jammes 2023, Olejarz et al. 2023). Besides, both forested areas with high human activity and natural areas with low tree cover do exist, and are inhabited by wild boars, further justifying the distinction between anthropization and tree cover in the analysis. Given their well-known behavioral flexibility, we expected wild boars to be able to find where to rest in all kinds of habitats, including the most anthropized (Brogi et al. 2023). We predicted that they would adjust to highly anthropized areas by resting more specifically in forested patches, and by revisiting more often the same resting sites, to compensate for a lower availability of suitable resting sites (Fradin and Chamaillé-Jammes 2023).

In a second step, we evaluated the influence of anthropization on how resting site utilization may shape wild boars' movements across their home ranges. Network-based tools are efficient to evaluate the importance of sites critical to animals' movements across their ranges (Shimazaki et al. 2004), and are adapted to the study of daily resting sites (Wittemyer et al. 2017, Lenormand et al. 2021). We thus constructed movement networks in which resting and activity sites formed nodes connected to each other through movement. In each wild boar's movement network, we evaluated the centrality of each node with the betweenness, a classic networks' metric measuring the usefulness of a node to circulate across the whole network (Jacoby et al. 2012). We expected that in more anthropized (but also in less forested areas), where suitable resting sites are fewer and movements are generally constrained, resting sites would contribute more to the connectivity of movement networks, as wild boars would be using some of them as 'stepping-stones', to circulate across their home range. The wild boar is a highly dimorphic species, and sexes differ in their movement patterns. Males roam, mostly solitarily, over larger home ranges than females, which live in family groups (Cavazza et al. 2023). Larger home ranges may provide more suitable resting sites, and resting solitarily may allow the selection of smaller shelters, in which several individuals could not hide to rest. We thus expected males to be less influenced by anthropization and tree cover than females, in both their selection of resting sites and their revisitation rate. We also predicted that anthropization would affect how resting sites contribute to the connectivity of movement networks more strongly in females than in males.

Overall, our study aimed at providing a unique view on how anthropization impacts the selection of resting sites and their centrality in movement networks, using a ubiquitous mammal, emblematic of human–wildlife co-existence, as a model species.

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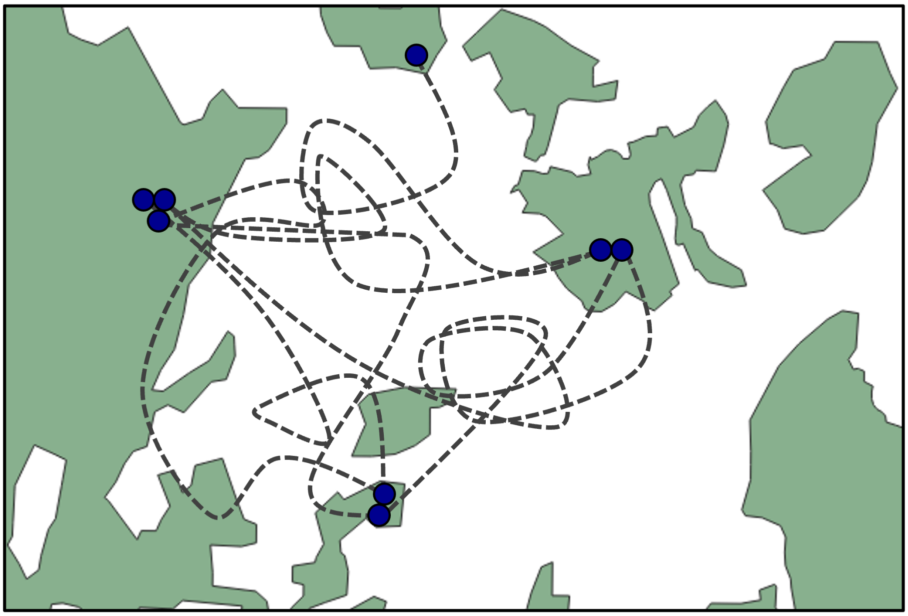
(a) Low anthropization



(b) High anthropization

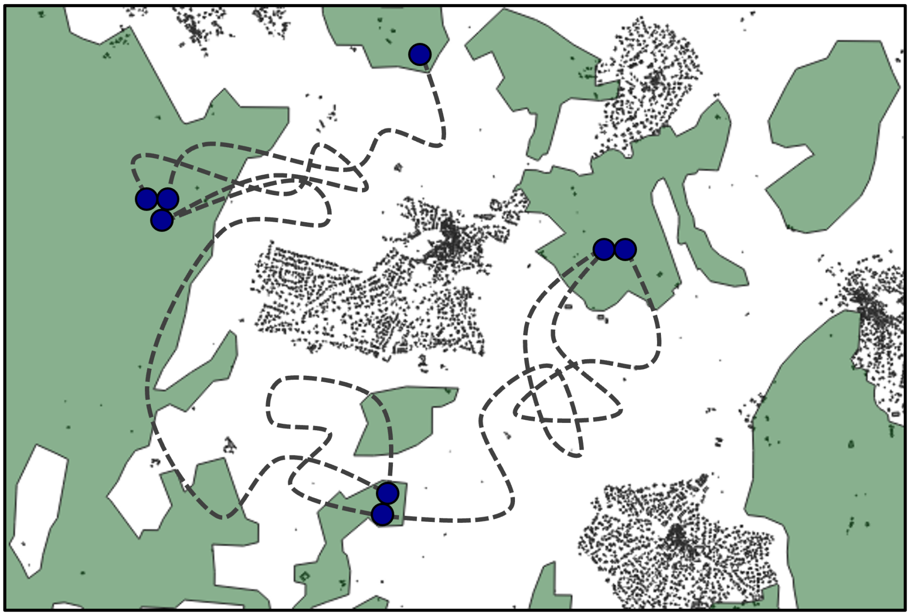


Figure 1. Illustration of the expected movement pattern of an animal using one type of habitat (green patches) for resting (dark blue circles), and another type of habitat (white patches) for activity (dashed lines). The pattern of movements between resting sites is expected to be less structured in a little anthropized landscape (a), than in a highly anthropized landscape (b). Villages and isolated buildings are added in (b), compared to (a).

Material and methods

Data preparation

GPS data preparation

Movement data were collected through Euroboar, the European collaborative initiative for research on wild boars' movement ecology, as part of the Euromammals initiative (https://euromammals.org/; Urbano et al. 2021), and supplemented with some additional data from southern France. The dataset was composed of GPS locations collected across Europe, at various sampling frequencies, which we subsampled to one location every 60 or 120 min, according to availability. First, we interpolated the tracking records to

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infer isolated missing locations and improve track continuity. Second, as the tracking durations of individual wild boars were extremely variable (from one month to three years), we standardized the data by splitting each wild boar's GPS track per month, to extract variables of interest at the level of each 'individual-month', thus facilitating comparisons. Incomplete months of tracking were discarded. Third, as pairs of individuals sometimes moved together as parts of the same social group, we discarded one individual-month per dyad that had spent more than 10% of their tracking period in close proximity (< 50 m), to avoid any pseudo-replication of the data. Finally, as we expected any range shift to mechanically structure the dynamics of resting sites' utilization, thus biasing our study, we excluded the individual-months that had durably relocated away from their initial range. More details on the preparation of the data are available in the Supporting information.

When did the wild boars rest?

To identify when the wild boars were at rest each day, we classified the GPS data between two behavioral states: activity and resting. To do so, we used the succession of step lengths and turning angles calculated from the GPS tracks to associate a behavioral state to each GPS location, using a hidden Markov model (HMM; Michelot et al. 2016). We did this independently for the data sampled every 60 min, and for the data sampled every 120 min, so that whenever 60 min-sampled data were lacking, we could use the categorization obtained from the data sampled every 120 min to fill the gaps. The relevance of the categorization of the GPS location between activity and resting was visually validated using actigraphy data, which were available from Euroboar for 41% of the individual-months (Supporting information).

Where did the wild boars rest?

As revealed by both the output of the HMM and the actigraphy data, while a non-negligible proportion of the individuals were not exclusively nocturnal, all of them consistently exhibited monophasic activity patterns (Supporting information). This means that they organized each 24-h cycle between one active phase and one resting phase, even though these phases were sometimes scattered with short bouts of respectively inactivity and activity. For each animal and each day, we identified a single resting site (hereafter RS), that corresponded to the location where the animal had been spending most (if not all) of its resting phase (Supporting information).

Summary of the data available

After this process, we were left with ~ 1 236 000 GPS locations (respectively ~ 1 144 000 and ~ 92 000 with the sampling frequencies of 60 and 120 min) from 1854 individual-months. These corresponded to 409 wild boars (269 females and 140 males), distributed between 50 populations from 13 countries (Fig. 2a), and tracked between 2007 and 2022. The median, lower, and upper quartiles of the number of individual-months per population were respectively 28, 7, and 49 (Supporting information).

Environmental variables

We used Copernicus' high-resolution layer on tree cover density (TCD; https://land.copernicus.eu/pan-european/high-resolution-layers/forests), a freely available geographic layer derived from satellite imagery, at the European scale. TCD gives a percentage of tree cover with a resolution of 100 m, thus accounting for even small patches of forest, where wild boars may select RSs (Salvatori et al. 2022). We matched the tracking data with the temporally closest TCD layer available (years 2012, 2015 and 2018). We also assessed the level of anthropization at a spatial resolution of 1 km, by using the human footprint index (HFI) map of 2009, downloaded from the NASA/SEDAC website (Venter et al. 2018). This global proxy of the cumulative human pressure on the environment accounts for multiple factors including human population density, infrastructures, and landscape modification by agriculture, and is given as a value ranging from 0 (untouched habitat) to 50 (heavily anthropized habitat; Venter et al. 2016).

Spatial analysis of resting site selection

Habitat selection for resting

We explored how the wild boars' RS selection was influenced by the TCD and the HFI. Each day, we sampled one RS and one active GPS location (as classified by the HMM, and randomly selected among daily active locations to avoid autocorrelation) to summarize landscape use during resting and activity ('used' set of locations). We then simulated landscape availability by generating 10 random locations per used location, within the home range of each individual-month ('available' set of locations). These monthly home ranges were defined as the contour of the 95% utilization distribution, estimated using a standard kernel density approach, and enlarged with a 1 km buffer to account for habitats that would be accessible but avoided. We then used a resource selection function (RSF), fitted using a generalized linear mixed model (GLMM) with a binomial error distribution. The binary response variable coded whether each location was part of the 'used' or 'available' set of locations. In our model, the predictors were the HFI, the TCD, the behavioral state (resting or active), and the sex of the animal. We expected the individuals to respond to TCD and HFI differently during resting and activity, and depending on their sex, so we considered the predictors in a four-way interaction. Correlations between predictors were low, as even the most correlated pair, HFI and TCD, had a Pearson's product-moment correlation of -0.35. The individual's identity and the population were included as nested random intercepts. Selection ratios were then calculated (Chamaillé-Jammes 2020), to quantify habitat selection (selection ratio above one) and avoidance (selection ratio below one). We used the k-fold cross-validation method described by Boyce et al. (2002) for model fit assessment. This method uses the Spearman-rank's correlation as the performance metric. We reported the average Spearman-rank's correlation and standard error obtained for 20 model replications, with 5 folds, and 10 bins of RSF scores.

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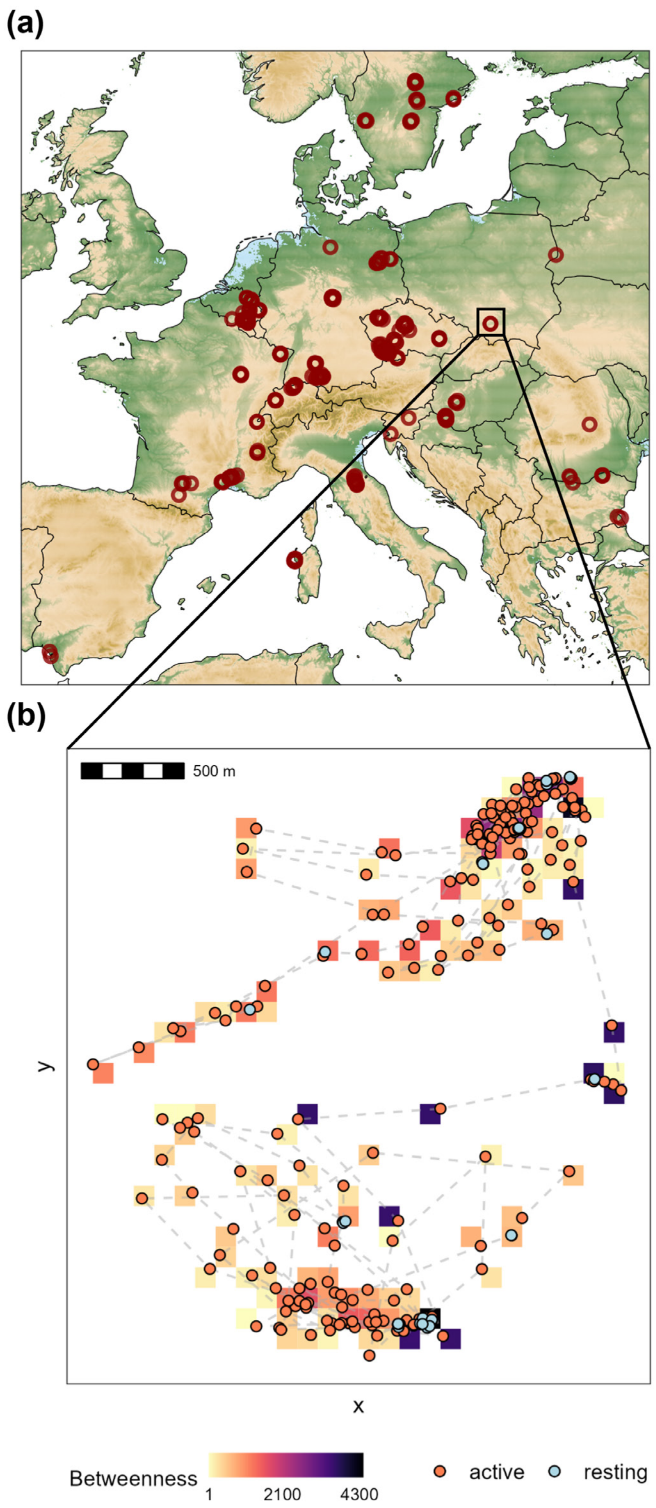

Figure 2. (a) Sampling location of individual wild boars (red circles) considered in the study. (b) Illustration of a movement network built from the GPS tracking of a wild boar over one month. Blue dots represent resting sites' locations while orange dots represent the GPS locations corresponding to activity. The dashed grey lines represent the animal's movement path. The tiles correspond to the nodes in the movement network obtained by laying the animal's trajectory over a raster grid, as described in Bastille-Rousseau et al. (2018). Each tile is a square (100 m per side), and is colored according to the betweenness of the node, as calculated with the R package 'moveNT' (Bastille-Rousseau 2023).

Resting sites' revisitation rate

We laid out the RSs of each individual-month over a raster grid of a resolution of 100 m to describe RSs' revisitation behavior. We identified clusters of RSs that were revisited over time by counting the number of RSs within each cell. For each individual-month, the RSs' revisitation rate was defined as the total number of revisits to previously visited cells over the number of resting phases after the first one. The use of raster grids was preferred over other clustering method, as these would be further useful to build movement networks (see the following section 'Contribution of resting sites to the connectivity of movement networks'). The resolution of 100 m was chosen to fit the scale of RSs' clustering across individuals (Supporting information). We fitted a GLMM on the RSs' revisitation rate, using a binomial regression to evaluate the effect of landscape characteristics. As predictor variables, we used the overall levels of anthropization and tree cover experienced by each individual-month. These were expressed as the mean value of HFI and TCD, respectively, within the monthly home range (as defined above). The mean HFI and the mean TCD did show a moderate correlation (Pearson's product-moment correlation = −0.56; different from the value given in the previous section 'Habitat selection for resting', as calculated at the scale of the monthly home range rather than locally), but we assumed both to be likely to affect RSs' revisitation through distinct mechanisms (Supporting information). We considered these two variables in interaction with the sex. Monthly home range size was also expected to affect revisitation rate, as large home ranges impose more travelling to revisit RSs. Visual exploration of the data suggested a non-linear effect, and we thus added the logarithm of monthly home range size (calculated without accounting the 1 km buffer mentioned above) as a predictor variable, as it seemed to provide better fit than alternative non-linear formulations. Individuals' identities nested within populations were incorporated as random intercepts. Model fit was evaluated using the marginal Nakagawa's R² (Nakagawa and Schielzeth 2013).

Contribution of resting sites to the connectivity of movement networks

Construction of the movement networks

For each individual-month, we constructed a movement network using the framework developed by Bastille-Rousseau et al. (2018). We laid out each trajectory over a raster grid of a resolution of 100 m, and considered each cell containing a GPS location as a node in the movement network. The raster grid resolution was chosen according to the scale of spatial clustering of RSs (Supporting information). We considered two types of nodes: the resting nodes,

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containing at least one RS, and the activity nodes, not containing any RS. In these movement networks, the edges between nodes were defined by the steps between GPS locations in the tracking data (see one example in Fig. 2b). We used the R-package ‘moveNT’ (Bastille-Rousseau 2023) to calculate the betweenness of each node. This node-level metric corresponds to the number of shortest paths between two nodes passing through the node of interest. It measures the importance of this node in the overall connectivity of the network (Jacoby et al. 2012), and can be used to identify nodes that may act as bottlenecks in movement patterns (Wittemyer et al. 2019). We then assessed the relative importance of the RSs, compared with activity sites, in the connectivity of movement networks. To do this, we calculated the ratio of the mean betweenness of the resting nodes over the mean betweenness of the activity nodes, in each network. This resulted in an index of contribution of the RSs to movement networks’ connectivity (hereafter called RSs’ contribution to connectivity).

Analysis of the drivers of resting sites’ contribution to connectivity

We tested the influence of the landscape characteristics on the RSs’ contribution to connectivity by using a GLMM with a Gaussian distribution. As in the model on revisitation rate, predictor variables were the sex, in interaction with the mean values of HFI and TCD within the monthly home range. Once again, the size of the monthly home range was expected to influence RSs’ contribution to connectivity, and visual exploration of the data revealed a strong non-linear relationship. As before, we incorporated the logarithm of the monthly home range size (calculated without accounting for the 1 km buffer mentioned above) as an additive predictor in the model. Finally, we considered the population and individual identities as nested random intercepts. We evaluated the fit of the model by using the marginal Nakagawa’s R^2 (Nakagawa and Schielzeth 2013).

Results

Selection of resting sites

All the range and possible combinations of HFI and TCD were represented in at least some of the monthly home ranges considered in the study, and the wild boars made some use of this wide diversity of habitats, both for resting and activity (see details in the Supporting information). As expected, the RSF showed that the strength of selection for TCD was highly dependent on the level of HFI (Fig. 3, Table 1). At low HFI, wild boars only showed a slight selection of sites with greater TCD (selection ratio close to one). At high HFI, however, wild boars strongly selected areas with high TCD. The selection for high TCD was always stronger during the resting phase compared to the active phase, and equal or greater in males compared to females (Fig. 3, Table 1). The 5-fold cross-validation performance score (Spearman-rank correlation) of the model was 0.99 ± 0.01 SE.

Resting sites’ revisitation rate

Across all individual-months, the mean RSs’ revisitation rate was 0.58 (SD = 0.17), which means 58% of the resting phases happened in a site that had already been used for resting earlier in the same month. As expected, this revisitation rate was highly dependent on the size of the monthly home range, animals with larger home ranges being less prone to revisit RSs over time (Table 2, Supporting information). The RSs’ revisitation rate was also dependent on the mean TCD and HFI in the monthly home range (Fig. 4, Table 2). In monthly home ranges with low mean TCD, the RSs’ revisitation rate slightly decreased with increasing mean HFI,

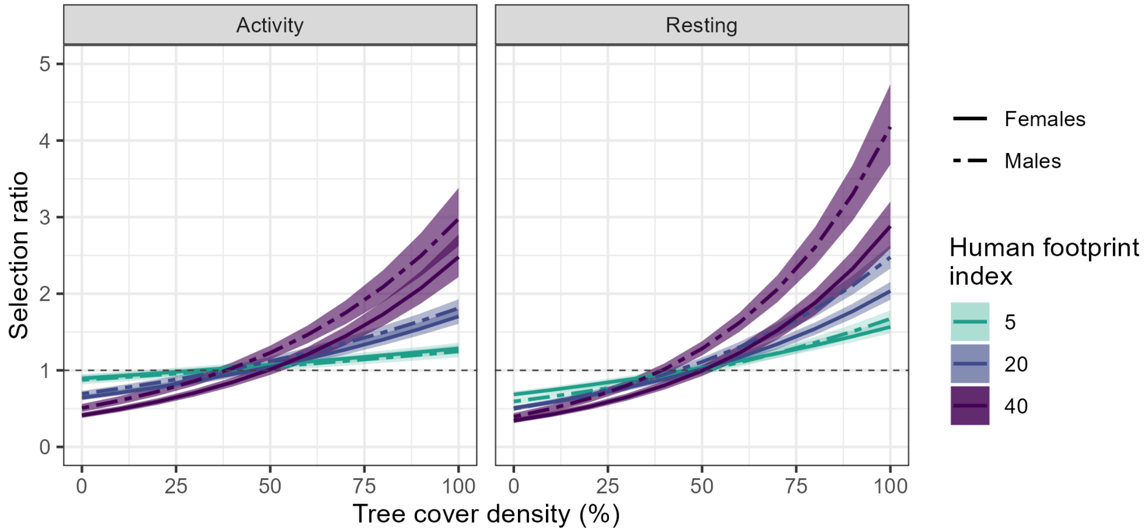

Figure 3. Selection ratio for areas of increasing tree cover density as a function of the human footprint index, for female (solid lines) and male (dashed lines) wild boars, during resting and activity. Sites are selected for when the selection ratio is above one, and avoided when it is below one. Color ribbons show the 95% confidence intervals.

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Table 1. Parameters and statistics of the model estimating the selection ratio for areas of varying levels of tree cover density (TCD) and human footprint index (HFI).

Variable	β	SE	z-value	p-value
Intercept	−2.3033	0.0337	−68.2637	< 0.001
Male	−0.0543	0.0440	−1.2340	0.22
Resting	−0.2790	0.0309	−9.0213	< 0.001
HFI	−0.0221	0.0014	−15.9750	< 0.001
TCD	0.0016	0.0004	4.2317	< 0.001
Male × Resting	−0.1303	0.0530	−2.4573	0.01
Male × HFI	0.0065	0.0024	2.7433	< 0.01
Resting × HFI	0.0023	0.0017	1.3501	0.18
Male × TCD	−0.0001	0.0007	−0.0919	0.93
Resting × TCD	0.0048	0.0005	10.1433	< 0.001
HFI × TCD	0.0004	0.0000	16.3635	< 0.001
Male × Resting × HFI	0.0016	0.0028	0.5745	0.57
Male × Resting × TCD	0.0021	0.0008	2.6032	< 0.01
Male × HFI × TCD	0.0000	0.0000	−0.0922	0.93
Resting × HFI × TCD	0.0000	0.0000	−1.1730	0.24
Male × Resting × HFI × TCD	0.0000	0.0000	0.2106	0.83

'Female' and 'Active' are the default sex and behavioral state. 'Male' and 'Resting' are the alternatives.

while in monthly home ranges with high mean TCD, the RSs' revisitation rate slightly increased with increasing mean HFI. The most contrasted revisitation rates were observed at low HFI, where it increased with decreasing mean TCD. Note, however, that the predictor variables included in the model explained only a very small proportion of the variability of the RSs' revisitation rate (marginal $R^2 = 0.05$; conditional $R^2 = 0.11$; Table 2). We observed no notable effect of the sex of the animals on the RSs' revisitation rate (Table 2, Supporting information).

Contribution of the resting sites to movement network's connectivity

RSs' contribution to connectivity averaged 2.5 (SD = 1.3), and was always above one, indicating that RSs serve as connectivity hotspots to travel within home ranges, more than activity sites. As expected, this index was significantly lower for animals with larger monthly home ranges compared to animals with smaller ones (Table 3, Supporting information). The RSs' contribution to connectivity also depended on the combination of mean HFI and mean TCD (Table 3), despite the correlation between these variables (Pearson's product-moment correlation = −0.56; Supporting information), which inflated the standard errors of the estimates. Wild boars in monthly home ranges with a high mean TCD had a greater RSs' contribution to connectivity if the mean HFI was also high (Fig. 5). Conversely, wild boars in monthly home ranges with a low mean TCD had a greater RSs' contribution to connectivity if the mean HFI was also low (Fig. 5). We observed no notable effect of the sex of the animals on the RSs' contribution to connectivity (Table 3, Supporting information).

Discussion

In this study, we proposed a conceptual framework (Fig. 1) and derived the prediction that the use of resting sites as 'stepping-stones' to navigate through the landscape should increase with anthropization. Our analysis of wild boar movement data collected across a wide range of conditions at a continental scale allowed us to simultaneously study the effects of human pressures, as aggregated in the commonly used human footprint index (HFI), while accounting for tree cover density (TCD), a key variable to consider given the ecology of the species, and the diversity of landscapes it occupies across Europe (Barrios-Garcia and Ballari 2012, Lewis et al. 2017). This allowed us to decipher the reduction of tree

Table 2. Parameters and statistics of the model estimating the resting sites' revisitation rate with varying mean tree cover density (TCD) and human footprint index (HFI). The conditional R^2 is 0.11 and the marginal R^2 is 0.05.

Variable	β	SE	z-value	p-value
Intercept	3.1338	0.2045	15.3216	< 0.001
Male	−0.2620	0.2500	−1.0481	0.29
mean HFI	−0.0194	0.0092	−2.1165	0.03
mean TCD	−0.0132	0.0031	−4.3073	< 0.001
log(monthly home range size)	−0.3632	0.0118	−30.6850	< 0.001
Male × mean HFI	0.0009	0.0136	0.0689	0.95
Male × mean TCD	0.0019	0.0048	0.3850	0.7
mean HFI × mean TCD	0.0005	0.0002	2.3201	0.02
Male × mean HFI × mean TCD	0.0002	0.0003	0.6412	0.52

'Female' is the default sex. 'Male' is the alternative.

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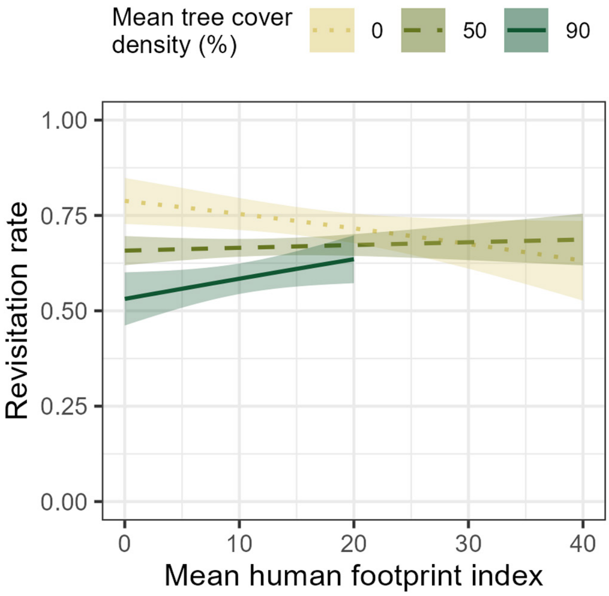

Figure 4. Rate of revisitation of resting sites as a function of the mean human footprint index (HFI) and tree cover density (TCD) in monthly home ranges. The predictions are illustrated for a female wild boar and a typical monthly home range size of 150 ha (predictions for males were similar; Supporting information). We did not make predictions for the combinations of mean HFI and TCD that were not represented in the data. Color ribbons show the 95% confidence intervals.

cover through the destruction and fragmentation of natural habitats from other effects of anthropization (Haddad et al. 2015, Rutten et al. 2019). Our results supported some of our predictions, but overall provide a more complex picture than anticipated, suggesting new research avenues.

Our first element of hypothesis (Fig. 1a) was that in the most untouched landscapes, wild boars would not use resting sites as ‘stepping-stones’ to travel across their home ranges. This prediction was only supported if tree cover was highly available, as resting sites’ contributions to connectivity were among the lowest, in these conditions (Fig. 5). Interestingly, in the least anthropized landscapes, a decrease in tree cover density drove an increase in resting sites’ contribution to connectivity, up to the highest values we observed (Fig. 5). We believe that the wild boars with undisturbed forested home ranges likely have an almost unlimited availability of sites providing enough cover for resting, as selection for cover during resting always remains quite low, at low HFI (Fig. 3). This low yet still significant selection may however impose strong constraints for wild boars in little forested landscapes, where sites with sufficient cover may be rare, and thereby almost mandatory to use when travelling across the home range. This would also explain why, among low HFI landscapes, the revisitation rate of resting sites increased with decreasing tree cover availability (Fig. 4). We conclude that if resting must occur in a habitat that is locally rare, the need for suitable resting sites may represent a constraint for animals to travel across their home ranges, even where anthropization is low. Species relying on specific structures for resting, like those using tree holes and other cavities, could be particularly affected (Du Plessis 1992, Lutermann et al. 2010, Le Roux et al. 2014).

Our second element of hypothesis (Fig. 1b) was that resting sites’ contribution to connectivity would increase with anthropization, as wild boars should be more and more constrained in where they can rest and how they can travel across the landscape, thus amplifying the importance of certain resting sites in connecting different parts of movement networks. This prediction was only supported where tree cover was highly available (Fig. 5). In a densely forested landscape, an increase in HFI may result from an increased road density, and/or a growing exposure to forestry and leisure activities (Venter et al. 2018). Roads are known to generally constrain wildlife movements (Bischof et al. 2017, Soanes et al. 2024), and road crossings by wild boars are highly restricted in time and space (Thurfjell et al. 2015, Bastianelli et al. 2024). Likewise, animals exposed to human disturbances are generally constrained in their movements (Doherty et al. 2021), and this certainly applies to wild boars, although empirical evidence is scarce (Petit et al. 2020). We therefore conclude that in forested landscapes exposed to increasing human pressure, more constrained movement patterns cause resting sites to become increasingly central in wild boars’ movements. Besides, resting sites availability and quality may also decrease in such conditions (Bojarska et al. 2021, Olejarz et al. 2023), forcing animals to rely repeatedly on fewer resting sites. This prediction was only slightly supported as wild boars in

Table 3. Parameters and statistics of the model estimating the resting sites’ contribution to connectivity for monthly home ranges with varying mean tree cover density (TCD) and human footprint index (HFI). The conditional R^2 is 0.37 and the marginal R^2 is 0.11.

Variable	B	SE	z-value	p-value
Intercept	5.4844	0.4290	12.7846	< 0.001
Male	−0.5526	0.4954	−1.1156	0.26
mean HFI	−0.0458	0.0187	−2.4524	0.01
mean TCD	−0.0193	0.0065	−2.9852	< 0.01
log(monthly home range size)	−0.3637	0.0286	−12.7223	< 0.001
Male × mean HFI	0.0354	0.0273	1.2996	0.19
Male × mean TCD	0.0101	0.0098	1.0286	0.3
mean HFI × mean TCD	0.0013	0.0004	3.2274	< 0.01
Male × mean HFI × mean TCD	−0.0008	0.0007	−1.2629	0.21

‘Female' is the default sex. 'Male' is the alternative.

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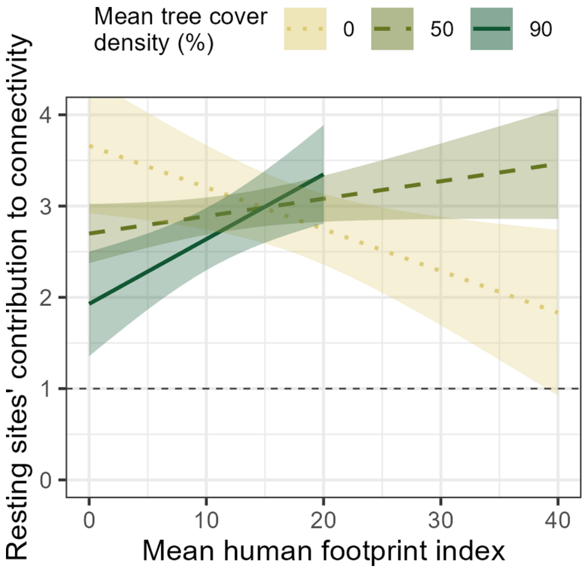

Figure 5. Resting sites' contribution to connectivity as a function of the mean human footprint index (HFI) and mean tree cover density (TCD) in monthly home ranges. The predictions are illustrated for a female wild boar and a typical monthly home range size of 150 ha (predictions for males were similar; Supporting information). We did not make predictions for the combinations of mean HFI and TCD that were not represented in the data. Color ribbons show the 95% confidence intervals.

forested landscapes tended to revisit resting sites only slightly more frequently when anthropization increased (Fig. 4). Note, however, that environmental variables only explained a tiny proportion of revisitation rates variability. This suggests that in landscapes with high TCD and high HFI, the higher centrality of resting sites in movement networks must have resulted mostly from more constraints on movement, rather than from a reduction of resting sites availability and quality. In species less flexible in their selection of resting sites, like mustelids or primates for instance (Lutermann et al. 2010, Larroque et al. 2015, Fei et al. 2022), the spatial layout of available resting sites should be more influential on how individuals navigate the landscape. This could be particularly meaningful for species whose resting sites get scarcer when anthropization increases (Le Roux et al. 2014, Nimmo et al. 2019, Cowan et al. 2024).

In little forested and highly anthropized landscapes, we assumed that suitable resting sites would be very rare, and movements highly constrained. We thus expected resting sites to be often revisited and to greatly contribute to movement connectivity. Surprisingly, however, we observed the opposite, as both the revisitation rate (Fig. 4) and the resting sites' contribution to connectivity (Fig. 5) tended to *decrease* with increasing HFI, in unforested landscapes. The very high selection for tree cover when resting in high HFI areas (Fig. 3) indicates that the few well-concealed sites occurring in these environments are most often used, but sites with less tree cover will also be used for resting (see the Supporting information). In urban and suburban areas (HFI > 30), wild boars may feed on anthropogenic food resources (Hafeez et al. 2011, Stillfried et al. 2017b, Castillo-Contreras et al. 2018), which are highly predictable in space (Murray et al. 2015, Davidson et al. 2022), and thus may revisit regularly the same sites for foraging (Cahill et al. 2012), which could rebalance the contribution of activity sites and resting sites to movement connectivity. This could explain the decreased contribution of resting sites to connectivity in unforested and highly anthropized areas, as movement patterns could be more influenced by the reutilization of foraging sites in these landscapes (Brogi et al. 2023). Besides, in urban and suburban landscapes, where hunting generally does not occur (Carpio et al. 2021), wild boars sometimes become habituated to people (Cahill et al. 2012, Stillfried et al. 2017a), which could challenge our predictions. Habituation may enhance wild boars' ability to find resting sites in risky areas (Brogi et al. 2023), as it does in other species found to thrive in urban landscapes (Bateman and Fleming 2012, Lowry et al. 2013). Habituated wild boars may also be surprisingly little constrained in their movements by people and infrastructure (Toger et al. 2018). We could not test this hypothesis here because habituated and non-habituated individuals may coexist in the same population (Cahill et al. 2012), and assessing habituation from tracking data on such a large scale is difficult, if not impossible. However, we believe that a better understanding of the wild boar's movement behavior and its drivers in high HFI areas such as urban and suburban landscapes is a critical next step for future research, which could illuminate how anthropization is affecting wildlife.

All the results discussed above were qualitatively similar between males and females, but also surprisingly similar quantitatively. Contrary to our prediction, the strength of selection for tree cover when resting increased with anthropization more rapidly in males than in females (Fig. 3). Tentatively, we suggest that males could sometimes venture into more anthropized areas than whole social groups with females do, at a scale lower than we could measure with the HFI (computed at a resolution of 1 km). There, concealed resting sites are rarer than anywhere, and their use for resting, which could be detected as we measured TCD at a resolution of 100 m, could explain the strong selection observed. Other results did not differ statistically between sexes. Males and females only responded differently to anthropization through the size of their monthly home range, which is larger in males (Morelle et al. 2015, Cavazza et al. 2023; see also the Supporting information). Therefore, although our analyses demonstrate that both sexes respond similarly to anthropization in general, the raw values of the metrics studied here would differ between the male and female samples.

In our attempts to predict how much wild boars would revisit their resting sites, and how central their resting sites would be in movement networks, based on the environmental characteristics of their home ranges, we could only explain a small share of the variability we observed (Table 2, 3). Some explanation might be looked for in our continental-scale characterization of the landscape: 1) the HFI is an aggregated index whose relevance to wild boars' ecology is not direct,

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although most factors it encompasses, such as human population and road densities, are expected to affect wild boars quite directly (Olejarz et al. 2023, Bastianelli et al. 2024). Also, HFI has previously been shown to be related to various aspects of ungulates' ecology (Mumme et al. 2023); 2) we had to leave aside some possibly relevant factors, such as hunting practices (Sodeikat and Pohlmeyer 2007, Morelle et al. 2015), because we were unable to gather and synthesize the data needed on such a large scale and with enough detail. Therefore, our models may have had a low explanatory power in part because of the predictors used. We however argue that the large unexplained variability is likely a consequence of the behavioral flexibility of the wild boar. Individuals in similar situations may respond in a great variety of ways, influenced by their own experience and personality (Brogi et al. 2022, Mortlock et al. 2024). As a result, knowing the environmental context could hardly be enough to predict how an animal would behave. Yet, by mobilizing a large amount of data along a wide gradient of environmental conditions, we were able to identify some trends, emerging from the great variability observed in the data. Although the flexibility of the wild boar makes predicting its behavior with coarse, large-scale models, difficult, this flexibility is also what allows it to exploit habitats spread across a wide anthropization gradient, offering the opportunity to conduct the study presented here.

Overall, our results show that anthropization may restrict animals' movements patterns, through the increased constraints imposed on resting site selection, and movements between them. While animal movements in general are known to be reduced in anthropized (Tucker et al. 2018) and fragmented landscapes (Gehring and Swihart 2003, Fahrig 2007, Jayadevan et al. 2020, Mumme et al. 2023), due to reduced permeability to movement, we argue that degraded resting opportunities may play an underestimated role in this global pattern. In all animal species that select one resting site every day from a limited availability of suitable choices, the utilization of anthropized landscapes is likely limited by the spatial layout of suitable resting sites. The wild boar is particularly adaptable, and the great flexibility of its resting behavior allowed us to evidence these constraints on the widest possible gradient of anthropization. We suggest that more investigation on the importance of resting sites in structuring movement networks is needed, in particular on less flexible species, more reliant on specific structures or conditions for resting. Well-located resting sites acting like 'stepping-stones' could be necessary to allow animal movements, with potential applications in species conservation and management. To understand and predict how animals move across anthropized landscapes, we must not overlook the spatial flexibility of resting behavior (Candolin et al. 2023).

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Permits – The wild boars from the numerous study areas considered in this study were captured and handled in compliance with the applicable national and regional laws, and following ethical guidelines for the use of wild animals in research. Belgium: captures and handling procedures were approved by the regional governments. Order of the Walloon Government authorising the Laboratoire de la Faune sauvage et de Cynégétique of the DEMNA (SPW) to immobilise game animals for scientific research purposes (Moniteur belge. Numac: 2011203564 Publication du 14 juillet 2011). Authorisation from the Agency for Nature and Forest for the Flemish Research Institute for Nature and Forest (INBO) to capture and handle game animals (licences #ANB/BL-FF/V12-00352, #ANB/BL-FF/V12-00354, #ANB/BL-FF/V12-00355, #ANB/BL-FF/V15-00232, #ANB/BL-FF/V15-00233, #ANB/BL-FF/V15-00234, #ANB/BL-FF/V15-00235). Czech Republic: captures and handling procedures were approved by the Ethics Committee of the Ministry of the Environment #MZP/2019/630/361 for studies involving animals. France: captures and handling procedures were in line with the French Environmental Code (Art.R421-15 to 421-31 and R422-92 to 422-94-1) and duly approved by the ethical committee of the French Ministry of Research (APAFIS#20279-2019041522576537v3 and APAFIS #40911-2023021311395166 v2) and by legislation from the Prefecture of Paris (Prefectural Decree #2009-014 and #2015-020). Germany: captures and handling procedures were approved in the respective states, by the

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ethics committee of the federal state Baden-Württemberg for animal welfare (permit #WFS1/12), by the ethics committee of the Upper Bavaria government (permit #ROB-55.2-2532.Vet-02-20-149), by the animal welfare licensing committee of Berlin ("Landesamt für Gesundheit und Soziales": permit #Reg 0383/12), by the animal welfare licensing committee of Brandenburg ("Landesamt für Umwelt, Gesundheit und Verbraucherschutz": permit #V3-2347-40-2012), and by the regional Veterinary Authorities of the Federal State of Lower Saxony (permit #33.14-42502-04-12/0767) and the Free State of Thuringia (permit #15-109.16). Hungary: captures and handling procedures were carried out in the presence of representatives of the managers of hunting grounds, using authorized traps, following Hungarian laws, aligned explicitly with "Act LV of 1996 on the Protection of Game, Game Management, and Hunting", as well as its implementing regulation, "Decree 79/2004 (V. 4.) of the Ministry of Agriculture and Rural Development". Italy: captures and handling procedures were approved by Sardinia Regional Administration (#4753 REP N 74 DEL 07/03/ 2017) and Tuscany Regional Administration (#103/5936/152e13/03/2002). Poland: captures and handling procedures were approved by the Local Ethical Commission for Experiments on Animals in Białystok and Cracow. Romania: captures and handling procedures were carried out in the presence of representatives of the managers of hunting grounds, using authorized traps, following the Romanian law 407 from 9 November 2006, art. 1. point 32.ad on hunting and the protection of the game fund, and art. 22. point 1). Slovenia: captures and handling procedures were conducted with authorization from the Ministry of Agriculture, Forestry, and Food of the Republic of Slovenia (#V4-0498). Spain: captures and handling procedures followed a protocol designed and developed in accordance with EC Directive 86/609/ EEC for animal handling and experiments, and approved by the Animal Experiment Committee of Castilla-La Mancha University and by the Spanish Ethics Committee. Sweden: captures and handling procedures were approved by the Ethical Committee in Animal Research, Uppsala, Sweden (permit C 80/9, C 77/10, C 5.2.182830/16, and 5.8.18-00845/2017). Switzerland: captures and handling procedures were approved by the Direction générale de la Nature et du Paysage of the canton of Geneva, the Service des Forêts de la Faune et de la Nature of the canton of Vaud, the Federal Office for the Environment, and the cantonal ethics committee on animal experiments of the canton of Berne (permission Nr. 75662).

Author contributions

Gustave Fradin: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Resources (equal); Writing – original draft (lead); Writing – review and editing (lead). **Tsviatko Alexandrov**: Resources (equal). **Marco Apollonio**: Resources (equal). **Janosch Arnold**: Resources (equal). **Grzegorz Baś**: Resources (equal). **Eric Baubet**: Resources (equal); Writing – review and editing (supporting). **Francesca Brivio**: Resources (equal); Writing – review and editing (supporting). **Rudy Brogi**: Resources (equal); Writing – review and editing (supporting). **Jim Casaer**: Resources (equal). **Attila Farkas**: Resources (equal). **Claude Fischer**: Resources (equal). **József-Tamás Fodor**: Resources (equal). **Stefano Grignolio**: Resources (equal); Writing – review and editing (supporting). **Justine Güldenpfennig**: Resources (equal); Writing – review and editing (supporting). **Marco Heurich**: Resources (equal). **Klemen Jerina**: Resources (equal). **Miloš Ježek**: Resources (equal). **Oliver Keuling**: Resources (equal). **Petter Kjellander**: Resources (equal). **Alisa Klamm**: Resources (equal). **Stephanie Kramer-Schadt**: Resources (equal); Writing – review and editing (supporting). **Alain Licoppe**: Resources (equal). **Kevin Morelle**: Data curation (lead); Writing – review and editing (supporting). **András Náhlik**: Resources (equal). **Tomasz Podgórski**: Resources (equal); Writing – review and editing (supporting). **Johan Roy**: Resources (equal). **Sonia Saïd**: Resources (equal); Writing – review and editing (supporting). **Thomas Scheppers**: Resources (equal). **Stefan Suter**: Resources (equal). **Tamás Tari**: Resources (equal). **Joaquín Vicente**: Resources (equal). **Simon Chamaillé-Jammes**: Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Resources (equal); Supervision (lead); Writing – review and editing (supporting).

Data availability statement

Data and code are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.15792089 (Fradin et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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