When and where? Day-night alterations in wild boar space use captured by a generalized additive model

Martijn Bollen Corresp., 1, 2, 3 , **Jim Casaer** 2 , **thomas Neyens** 3, 4 , **Natalie Beenaerts** 1

1 Centre for Environmental Sciences, Hasselt University, Hasselt, Flanders, Belgium
2 Research Institute for Nature and Forest (INBO), Brussels, Brussels, Belgium
3 Data Science Institute, Hasselt University, Hasselt, Flanders, Belgium
4 Leuven Biostatistics and statistical Bioinformatics Centre, University of Leuven, Leuven, Flanders, Belgium

Corresponding Author: Martijn Bollen
Email address: martijn.bollen@uhasselt.be

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Wild boar, an abundant species across Europe, is often subjected to management in agro-ecosystems in order to control population size, or to scare them away from agricultural fields to safeguard crop yields. Wild boar management can benefit from a better understanding on changes in its space use across the diel cycle (i.e. diel space use) in relation to variable hunting pressures or other factors. Here, we estimate wild boar diel space use in an agro-ecosystem in central Belgium during four consecutive “growing seasons” (*i.e.* April-September). To achieve this, we fit generalized additive models (GAMs) to camera trapping data of wild boar aggregated over 1h periods.

Our results reveal that wild boar use different sites throughout the diel cycle. At day time, wild boar utilize sites in the centre of the forest. During the night, they forage near (or in) agricultural fields. We do not find a statistical effect of hunting on wild boar diel space use. Finally, our work reveals the potential of GAMs to model variation in space across 24h periods from camera trapping data; an application that will be useful to address a range of ecological questions.

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Martijn Bollen[1,2,3*], Jim Casaer[2], Thomas Neyens[3,4] and Natalie Beenaerts[1]

[1]Centre for Environmental Sciences, Hasselt University, Hasselt, Flanders, Belgium
[2]Research Institute for Nature and Forest (INBO), Brussels, Brussels, Belgium
[3]Data Science Institute, Hasselt University, Hasselt, Flanders, Belgium
[4]Leuven Biostatistics and statistical Bioinformatics Centre, University of Leuven, Leuven, Flanders, Belgium

Corresponding Author:
Martijn Bollen[1,2,3]
Agoralaan, Building D, Diepenbeek, Flanders, 3590, Belgium
Email address: martijn.bollen@uhasselt.be

Abstract

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Introduction

Species distribution models are widely applied to study biotic and abiotic factors, including the impacts of hunting, that influence animal space use (Di Bitetti et al. 2008; Guisan & Thuiller 2005). Many of these studies have relied on camera trapping data (Burton et al. 2015; O'Connell et al. 2010). Species distribution models typically require that the user defines a time period (*i.e.,* the time of a single "survey" or "temporal replicate") over which species records are aggregated. In camera trapping studies, it is common to define survey durations of 24h or coarser to increase the probability of detection (Bassing et al. 2023; Caruso et al. 2018; Crunchant et al. 2020; Rich et al. 2017; Shannon et al. 2014). Consequently, any changes in spatial patterns that occur within 24h periods are typically obscured in camera trapping studies investigating animal space use. However, variation in space use across the diel cycle (henceforth referred to as "diel space use") is widespread among animals and has been observed in, for example, tropical riverine fish (Crook et al. 2021), voles (Grácio et al. 2017) and zebras (Klappstein et al. 2023). Diel space use patterns can hold critical information about the ecology of a species. For instance, within one 24h cycle many animals use different habitats for foraging and resting, which has been linked to a trade-off between meeting energetic requirements and avoiding predation risk (Campanella et al. 2019; De Groeve et al. 2023; Kohl et al. 2018). In general, changes in habitat preferences within 24h occur because behavioural needs also change with time of the day and a single habitat that fulfils all of these needs usually does not exist (Erdtmann & Keuling 2020; Hut et al. 2012). Thus, being able to obtain diel space use patterns from camera trap data would enable the evaluation of a new suite of ecological questions.

Wild boar (*Sus scrofa*), a species with high population densities across Europe (Carpio et al. 2021; Massei et al. 2015), is known to use different habitats during different parts of the diel cycle. For instance, it has been suggested that wild boar prefer deciduous forests during the first half of the night, when they are typically foraging, and select for coniferous forests when resting (Erdtmann & Keuling 2020). In forested areas with nearby agricultural fields (henceforth referred to as “agro-ecosystems” cfr. Fattebert et al. (2017)), a part of the wild boar population tends to spend its active time (night time) inside the fields, during growing season when crops are ripe (need for food), while staying inside the forest during day time (need for cover) (Keuling et al. 2009; Kramer et al. 2022). Others may permanently stay inside agricultural fields or in forests (Keuling et al. 2009). Since, wild boar can cause considerable damage to agricultural crops (Amici et al. 2012; Schley et al. 2008), they are typically under moderate to high hunting pressure in an attempt to safeguard crop yields. In this context, hunting regimes serve two main goals: population control through increased mortality (Keuling et al. 2013) and creating a “landscape-of-fear” near agricultural fields in order to prevent wild boar from using them as foraging ground (Tolon et al. 2009). Indeed, it appears that wild boar shift their space use in response to hunting in some cases (Colomer et al. 2021; Tolon et al. 2009), but not in others (Brogi et al. 2020; Reinke et al. 2021). At the same time, hunting can cause wild boar to shift their activities towards increased nocturnality (Keuling et al. 2008; Podgórski et al. 2013). Hence, it is possible that fear effects induced by hunting in agro-ecosystems are short-lived, such that wild boar may safely exploit agricultural fields during the night when they are less vulnerable due to night cover. A similar type of dynamic spatiotemporal responses to predation risk is observed in an elk-wolf system (Kohl et al. 2018). Investigating, these kind of dynamics for a wild boar-hunter system could contribute to improve the effectiveness of hunting strategies in agro-ecosystems.

Hence, the main objective of our study is to bridge the knowledge gap related to diel space use of wild boar in relation to hunting pressure in an agro-ecosystem. We hypothesize that that the space use pattern of wild boar in an agro-ecosystem is different between day and night. Moreover, we expect wild boar to use to centre of the forest during the day for resting, while preferring areas close to or in agricultural fields during the night for foraging. Finally, we believe that the outcomes of these ecological hypotheses are of interest to managers and hunters working in agro-ecosystems as they provide information about the effectiveness of hunting efforts in changing the spatiotemporal behaviour of wild boar.

Materials & Methods

Study area

The study area (longitudes: 4.650◦W - 4.750◦W; latitudes: 50.788◦N - 50.824◦N) is situated in a Natura 2000 reserve called "Meerdaal" in central Belgium (**Fig. 1**). It has a total surface area of ~16 km^2, consisting of a mosaic of coniferous (mainly *Pinus sylvestris*) and broadleaved (mainly *Quercus sp.*, *Fagus sylvatica* and *Carpinus betulus*) forest stands. The forested area in Meerdaal is surrounded by a rich mosaic of croplands, with crops growing predominantly during April-September. Meerdaal has altitudes ranging from 35 to 103 m above sea-level, and is characterised by locally steep slopes. The study area has a cool temperate and moist climate, with a mean annual temperature of 11◦C and 773.2 mm rainfall (KMI 2021). The study area is subdivided into three hunting management zones, with different (intensities of) hunting pressure. In the year-round hunting zone ('HY'; ~9 km^2), hunting on wild boar is allowed during the entire year. In the winter hunting zone ('HW'; ~4 km^2), hunting is restricted to the time period from November until March. In the hunting-free core zone ('C'; ~2 km^2), hunting is prohibited the year round (with the exception of a limited number of drive hunts (1 or 2) and joint hunting efforts from high seats (4), both during winter) (**Fig. 1**). Hunting in Meerdaal is restricted to fixed locations (*i.e.* high seats), and can only take place between 19:00 and 9:00 during Daylight Saving Time, and from 16:00 until 10:00 during Winter Time (note that hunting during the night is also allowed). Wild boar density in and around Meerdaal, in the context of an European observatory of wildlife project by *ENETWILD*, has been estimated at 7.88±3.50 individuals/km^2 using the random encounter model (Guerrasio et al. 2023; Rowcliffe et al. 2008).

Data

Wild boar

As part of a larger monitoring framework, a subset of 13 cameras has been deployed in Meerdaal, since March 2018 (**Fig. 1**). Cameras are placed at the centre of a subset of randomly selected 250 m x 250 m grid cells (0.0625 km^2) from a grid overlaying the study area. All cameras are relocated monthly to a new grid cell location. Annually, the same set of grid cells is visited twice: a first time during the summer (April-September) and a second time during winter (October-March). All cameras are mounted ~50 cm above ground, facing North, on the tree nearest to the middle of the selected grid cell. None of the cameras was baited to lure animals, or placed along a trail. Each camera trigger was followed by a sequence of ten consecutive photos, with a 0s recovery time between triggers. We considered sequences (10 photos/trigger) to be independent if they were a least 2 min apart. Non-independent sequences were aggregated and annotated as a single sequence of >10 photos. We considered each independent sequence to display an independent group of wild boar, and defined the raw counts as the number of unique individuals in these groups. Annotation was done using the Agouti software platform (www.agouti.eu). For our analysis, we only considered images from a six months growing seasons (April – October), for the years 2018 until 2021. This yields a total of 10086 24h observation periods from 303 camera deployments, in which 1873 independent groups of wild boar were captured (total count: 4505, average group size of 2.34).

Hunting

Within Meerdaal it is mandatory for hunters to record their activities in a hunting diary. From 2018 until 2021 we have information from 3460 different hunting activities at 60 high seats (**Fig. 1**), of which 1131 occurred during the study period. After removing observations without information on the hunting effort (duration in hours) or high seat used, we retain 1114 records (98.5%). To reliably represent the total hunting effort in hunter activity patterns, we created "new" hunting records every 10 minutes between the start and end time of a hunting activity recorded in the diary. This yields 8868 time records for hunting activity, which we use to model the spatiotemporal hunting pressure in Meerdaal.

Statistical model

Wild boar data

Each unique camera deployment $i = 1, 2, \ldots, R$ produces pictures of wild boar that are tagged with information on their coordinates $\{lon(i), lat(i)\}$, the survey day $j = 1,2, \ldots, J_i$ and the "solar hour" of observation $t = 0, \frac{2\pi}{24}, \ldots, 2\pi$. We first obtain (continuous) solar times t^* by mapping clock times to $[0, 2\pi]$ and anchoring these radian times to sunrise ($t_1 = \frac{\pi}{2}$) and sunset ($t_2 = \frac{3\pi}{2}$) on the day and location of the observation (Nouvellet et al. 2012). This ensures that wild boar behaviour is studied relative to solar events that are considered important regulators of cyclic patterns recurring each day, rather than exact clock times (Nouvellet et al. 2012; Vazquez et al. 2019). Secondly, we define the lower bound of one of 24 evenly spaced intervals of $\frac{2\pi}{24}$ between 0 and 2π that holds the solar time t^* as the (discrete) solar hour t.

To explore our data, we estimate wild boar activity patterns and overall activity levels (using conventional methods) for the three hunting management zones. More specifically, we fit a circular kernel density function $c(t^*)$ to solar times t^* using the *fitact()* function from the R package *activity* (Rowcliffe et al. 2014). In order to obtain accurate density functions from this kernel estimator, a minimum of 100 time records is recommended (Lashley et al. 2018; Rowcliffe et al. 2014). For the management zones, we collected a total of 1073 (HY), 259 (HW) and 541 (C) time records of wild boar during the study period. Hence, we are confident that these activity patterns accurately represent the true underlying wild boar activity. By default *fitact()* also calculates the absolute overall activity levels ($\frac{1}{2\pi c_{max}}$) as the area under the curve (Rowcliffe et al. 2014). To assesses the significance between pairwise differences in overall activity levels, we perform a Wald test on each pairwise comparison using the *compareAct()* function from *activity*. Finally, we identify the solar times t^* at which the two strongest peaks (local maxima) in $c(t^*)$ occur.

To obtain diel space use of wild boar, we adopt a generalized additive model (GAM), a type of regression model that allows the relationship between the outcome and one or more predictors to be smooth curves (Hastie & Tibshirani 1986; Wood 2017). We assume that counts y_{ijt} captured by camera i on day j, resulting from aggregating all observations with solar hours t follow a negative binomial distribution:

$$y_{ijt} \sim NegBin(\lambda_{ijt}, \theta),$$

with λ_{ijt} the expected capture rate at camera i on day j, for a given solar hour t and θ an overdispersion parameter. We explicitly choose a negative binomial distribution as initial inspection of our data suggested that wild boar counts are overdispersed relative to a Poisson distribution, but we also explore the goodness-of-fit statistics from the latter. Note that a zero-inflated (hurdle) Poisson would be another sensible choice for our data, but this did not lead to convergence of our model. We model λ_{ijt} flexibly through a GAM using the R package *mgcv* (Wood 2011). We consider the following information to be used as fixed and/or random effects potentially affecting λ_{ijt}: solar time, survey day, week, longitude and latitude of the observation. Using this information we evaluated nine candidate models based on their AIC, percentage of model deviance explained and the model degrees of freedom (**Supplemental file S1**). The remainder of this section describes the best-ranking model. This model includes a global smoothing term for the solar times $f_1(t)$ based on a cyclic cubic regression spline ('bs = cc' in *mgcv*) since solar events are inherently periodic. It also includes a cyclic cubic regression spline $f_2(week(j))$ to capture a periodic trend in wild boar encounters across weeks of the year. Thirdly, it includes a 3d smoother for solar times, longitude and latitude $f_3(t,lon(i),lat(i))$, which is approximated by the superposition of three simpler basis functions $f_1(t)$, $f_{lon}(lon)$ and $f_{lat}(lat)$. In *mgcv*, this is done by taking the tensor products of these components using the function *te()*. For $f_{lon}(lon)$ and $f_{lat}(lat)$ we use thin plate regression splines ('bs = tp' in *mgcv*) as they are considered a general purpose spline (Wood 2003). A grid search to determine the optimal number of knots k based on the Akaike information criterion (AIC; (Akaike 1974)) indicated that $k = 10$ was optimal. However, this yielded smooth functions that overfitted the data. Hence, we explored a progressively smaller number of knots until this overfitting behaviour disappeared. Eventually, $k = 5$ was used for all terms. Given the combination of smoothers, the encounter rate λ_{ijt} is expressed as:

$$log(\lambda_{ijt}) = (\beta_0 + \beta_{0,j}) + f_1(t) + f_2(week(j)) + f_3(t,lon(i),lat(i)),$$

where β_0 represents the general intercept and $\beta_{0,j}$ are random intercepts for the survey days. Finally, we test if adding the total duration (in radians) of hunting on day j at solar time t as a fixed effect (*i.e.,* $\beta_1 Hunt_{jt}$) improves this model. Note that the data y_{ijt} is typically very sparse, which may lead to poor goodness-of-fit. Therefore, we present an information-reduced approach in the **Supplemental file S2** that increases the signal in y by summation of counts across J_i survey days on which the i^{th} camera was active.

Hunting data

For data on hunting activities which occurred at hunting location (high seat) $s = 1, 2, ..., S$ and at solar hour t, we adopt a similar strategy as for wild boar observations: we use exact solar times of hunting attempts t_h^* to obtain and compare activity peaks, as well as overall activity levels using *fitact()* and *compareAct()*. After mapping clock times of observations to solar hours t, we use a GAM to estimate hunter space use across the diel cycle, where we assume hunter counts h_{st} at high seat s at solar hour t to follow a negative binomial distribution:

$$h_{st} \sim NegBin(\lambda_{st}^h, \theta^h),$$

and,

$$log(\lambda_{st}^h) = log(J) + f_1^h(t) + f_2^h(lon(s),lat(s)).$$

Note that we use the total number of survey days J as an offset term, such that the hunting rate λ_{st}^h represents the expected number of hunters at high seat s during solar hour t of any given day (instead of the expectation across all days). Moreover, for hunting records we do not model the full (3d) tensor product as before, since there is too little data available at many solar hours t. Instead, we model f_1^h as a separate cubic cyclic regression spline and f_2^h as the superposition of $f_{lon}^h(lon)$ and $f_{lat}^h(lat)$, again with the number of knots $k = 5$ for each of these terms. To test correlations between wild boar activity and hunting activity, we first average $\widehat{\lambda_{ijt}}$ across all days J and then calculate Pearson correlations $corr(\overline{\lambda_{it}}, \widehat{\lambda_{st}^h})$ for solar hours t with at least one hunting record.

Results

Wild boar activity and space use

During the growing season, wild boar dispaly a bimodal activity pattern across all of the management zones in Meerdaal, with peaks at sunrise (π/2) and just after sunset (3π/2) (**Fig. 1**). Timing of the peaks between zones are well aligned both at sunrise and after sunset (**Tables 1 and 2**). Additionally, hunting activity peaks coincide with maximum wild boar activity only at sunrise. Human recreational activity largely occurs when boars are inactive (**Fig. 1; Table 2**). Overall, wild boar are active during 46%, 35% and 48% of the day in the zones HY, HW and C respectively. Differences between overall activities are significant for HY vs. HW (W = 12.99, p < 0.001) and HW vs. C (W = 8.63, p = 0.003), but not for HY vs. C (W = 0.21, p = 0.64). The QQ plots in **Figs. S3.1 and S3.2** suggest that a negative binomial model fits the wild boar counts better than a Poisson GAM. However, the distribution of the deviance residuals is dominated by small negative values and observed versus fitted values resemble a funnel (**Fig. S3.1**). The negative binomial GAM reveals that wild boar encounter rate randomly varies from day-to-day, with some months having consistently lower or higher encounter rates, *e.g.*, April-

June 2020 (**Fig. 2a**). Moreover, it shows that wild boar encounter rate during the growing season peaks at the end of June/ beginning of July, *i.e.,* week 26 (**Fig. 2b**). At a daily scale, the encounter rate displays a bimodal curve with peaks at sunrise and sunset (**Fig. 2c**, cfr. activity patterns obtained by kernel density estimation in **Fig. 1**), and that relevant spatiotemporal variations in activity exist (**Fig. 2d**).

Specifically, wild boar space use during active times (around activity peaks) is mostly restricted to the south of Meerdaal (*i.e.* lower part of HY), while boar select for the centre (*i.e.* HW and C) of the study area during day time (**Fig. 3**; **Figs. S4.1-2**). Including hunting duration per day per solar hour did not improve our GAM, *i.e.,* its effect was nonsignificant.

Hunting intensity – Landscape of fear

Similar to wild boar observations, a negative binomial model fits the hunter data better than a Poisson GAM (**Figs. S3.3-4**). According to the negative binomial GAM, hunters are predominantly active in the periphery of Meerdaal, except for small regions in the southwest and northeast of the study area (**Fig. 3**). During times of wild boar activity, Pearson correlations between the activity pattern of hunters and boars are significant for solar hours between (3/24) 2π and (6/24) 2π (**Table 3**).

Discussion

The objective of this study was to estimate diel space use – space use patterns across the diel cycle – of wild boar from camera trapping data in the context of an agro-ecosystem where hunting occurs. For this purpose, we applied a GAM as they allow the construction of a single smoother in function of a set of coordinates and time of the day (solar time), while at the same time specifying different types of smoothing for each variable (Pedersen et al. 2019).

The percentages of daily activity for wild boar in our study area (35% - 48%), estimated from the kernel density function (*activity* package), are similar with those observed by Johann et al. (2020) (46%) during a similar period of the year based on GPS-telemetry. There appear to be more days with low wild boar encounter rate during the period of April-June 2020 as compared to other months in the study period (**Fig. 2a**). This is exactly the period during which the most stringent Covid-19 related lockdown was enforced in Belgium (*i.e.,* all non-essential travel was prohibited). Both positive and negative impacts of Covid-19 related suppression of human activity on the detectability of a species have been observed (Anderson et al. 2023; Procko et al. 2022), and hence depend on the context. In our study, strongly reduced human activity (hunting and recreational) during the lockdown of April-June 2020 may have led to wild boar roaming outside the forested area (where no cameras were deployed) or to a reduction of the number of escape responses. This could explain the lower number of wild boar detected at that time.

Regardless of the year, we find that wild boar encounter rate tends to peak at the beginning of July, which is consistent with the increased percentage of wild boar activity during the summer observed in other studies (Brivio et al. 2017; Johann et al. 2020). Increased encounter rates around July could be a consequence of cereals, such as wheat, being ripe at that time resulting in more commutes between the forest and surrounding agricultural fields in Meerdaal (Keuling et al. 2008; Keuling et al. 2009; Kramer et al. 2022). In addition, females which typically have high energetic requirements in the summer in order to nurse their piglets (3-8 months old) may also contribute to more detections during this period of the year (Keuling et al. 2008).

Based on circular kernel densities, wild boar seem to be almost exclusively nocturnal across all three management zones (**Fig. 1**). Activities inferred from our GAM yield similar insights in the activity periods of wild boar (**Fig. 2c**). The almost exclusively nocturnal activity that we observe for wild boar is consistent with activity patterns reported in other studies (Brivio et al. 2017; Keuling et al. 2008; Wevers et al. 2020), and has been linked to human disturbance (Gaynor et al. 2018; Podgórski et al. 2013). However, we observe strong peaks at sunset and sunrise typical of crepuscular activity, with reduced activity during the rest of the night (**Fig. 1**; **Fig. 2c**). This is in conflict with studies that report continuous activity of wild boar during short summer nights at high latitudes, which even extend after sunrise or before sunset in order to meet their energetic requirements (Keuling et al. 2008). Other studies even observed a unimodal activity pattern with a peak in wild boar activity around midnight (Caruso et al. 2018; Johann et al. 2020). There are several hypotheses that could have led to the crepuscular-like activity pattern that we observe for wild boar in our study area. Possibly, lower probability of detection by cameras during the night, as observed by Palencia et al. (2022), compared to sunrise and sunset could explain the apparent reduction in activity across the night. Alternatively, it could be that wild boar stay within the forest during the night (*i.e.,* available for detection), but that they are engaged in comfort-related behaviour (*i.e.,* not moving and thus not generating detections) (Erdtmann & Keuling 2020). Another possibility is that wild boar move into adjacent agricultural fields around sunset and return at sunrise (Keuling et al. 2009). This would lead to more detections clustered at sunset/sunrise, while also leading to fewer night time detections in the forest (*i.e.,* the area monitored in our study), simply because wild boar are temporarily unavailable in this area. This hypothesis seems to be supported by the diel space use of wild boar estimated by our GAM, showing that they stay in centre of the forest during the day, but that they roam into the periphery of (and beyond?) the study area at night time (**Fig. 2d**; **Fig. 3**). The diurnal activity that we observe in the centre of the forest (HW and C), but not in its periphery (HY) (**Fig. 1**; **Fig. 3**) could also be a consequence of the lower hunting pressure in this zone (Johann et al. 2020). De Groeve et al. (2023) observed a similar day-night alteration in the selection of habitats during the fall hunting season by migrating Elk, which preferred safer habitats with a high cover during the day, and riskier foraging habitats with a low cover at night. Similarly, wild boar may prefer resting sites in the centre of the forest because the hunting risk during the growing season is almost fully restricted to HY. A possible avoidance for this zone at times of human activity could be exacerbated by the combination of hunting (lethal) and recreational (non-lethal) activities (Paton et al. 2017).

In our study area, wild boar do not seem to temporally avoid hunters when active (**Fig. 1**; **Tables 1 and 2**), as observed elsewhere (Ohashi et al. 2013). Therefore, we also assessed whether wild boar avoided hunters spatiotemporally *in sensu* Kohl et al. (2018). However, the landscape-of-fear that we infer from a GAM based on hunting visits is significantly (positively) correlated with wild boar diel space use between (3/24) 2π and (6/24) 2π (**Table 3**; **Fig. 3**). Moreover, adding the effect of hunting to the GAM modelling diel space of wild boar did not improve this model substantially (*i.e.,* the effect of hunting was nonsignificant). This suggests that wild boar do not avoid hunters spatiotemporally, or that hunters preferentially visit locations and times with the highest wild boar encounter rates in Meerdaal. However, the absence of a statistical effect of hunting does not necessarily mean that a biological effect is not present. Possibly, wild boar trade off their need for food intake with the risks induced by hunters that show substantial spatiotemporal overlap with wild boar (Ferrari et al. 2009). This is in accordance with some other studies, which found that wild boar space use is primarily driven by food resources and that they are seemingly insensitive to predation risk (Bubnicki et al. 2019; Wevers et al. 2020). Furthermore, wild boar in Meerdaal may also trade off avoidance of human recreational activity, with the risks induced by hunters. Alternatively, the hunting pressure in Meerdaal may be too low (**Table S5**) to effectively modulate the spatial behaviour of wild boar. In summary, we find inconclusive evidence for effects of hunting on the spatial behaviour of wild boar, which is in line with other studies on this subject (see Keuling & Massei (2021) for a recent review).

Finally, our study has some important limitations and future prospects. First, we stress that in order to produce reliable diel space use maps, the sampling effort should be relatively high (*i.e.* here 10086 trapping days for all cameras combined), since few photo-captures will typically be produced during times of inactivity (**Table 1**). This may make our approach unsuitable for short-term camera trapping studies, and for rare or conspicuous species. Even with a large number of data points, the errors associated with spatiotemporal predictions of diel space use are substantial (**Figs. S4.2-3**). Furthermore, our GAM has problems predicting the rare encounters of a large number of individuals that occur from time to time, since most solar hours have a zero-count (99.52%). This behaviour is reflected in the residual plots (**Figs. S3.1-2**). One solution is to fit a GAM to counts aggregated over all survey days, hence only retaining information on the solar hours and spatial locations (see **Supplemental file S2**). This lowers the percentage of solar hours having a zero-count considerably (72.00%) at the cost of losing information about calendar dates of the observations. Nevertheless, we find that this GAM preserves the typical diel space use of wild boar in our study area (**Fig. S3.2**). So when the only goal is to obtain diel space use, without acknowledging other sources of variation (between days, weeks, months or years) this reduced information approach can be adopted. Another option that may improve the goodness-of-fit, without needing to aggregate across survey days is to apply a piecewise exponential additive model (a GAM for exponentially-distributed responses) to time-to-event data (Bender et al. 2018). Essentially, this would be an extension of the time-to-event model in Moeller et al. (2018) that permits the modelling of smooth predictor-response relationships. We have not explored this approach yet, but encourage future research in this direction. The implementation of Gaussian processes, a parametric alternative to spline approaches, could be another interesting development in the modelling of diel space use (KI Williams 2006). Regarding the effects of hunting, landscape-of-fear maps that we inferred from hunting pressure could have been distorted by missingness not at random in or underreporting of hunter visits (~10-20% of hunter visits is missing/not reported). Treating hunter visits and wild boar counts as two correlated processes, analyzed through a joint modelling approach for preferentially sampled data, may improve inference on hunting effects (Diggle et al. 2010). Last but not least, we only sample the forested area in Meerdaal, yet we observe wild boar gradually moving towards the forest edge during the night. Hence, it would be interesting to also monitor wild boar beyond the forest edge, *i.e.*, in the agricultural fields adjacent to the current study area.

Conclusions

The main objective of our study was to infer the diel space use pattern of wild boar in an agro-ecosystem, where hunting occurs, from camera trap data. We hypothesized that wild boar space use differs between day and night. More specifically, we expected wild boar to use the centre of the forest during the day for resting and areas close to agricultural fields for foraging during the night. Regardless of its limitations (see Discussion), we have shown that GAMs can be useful tools to model diel space use from photo-captures. We revealed that wild boar in Meerdaal adjust their space use pattern throughout the diel cycle in an agro-ecosystem during the growing season, most likely to avoid human activities during day time. During the night, we estimated space use patterns that reveal wild boar activity close to agricultural field. Thus, our hypothesis that day-night alteration in wild boar space use are driven by a timely need for safety (to rest) and food seems to be confirmed. In the future, our approach may yield relevant insight in other ecological settings as well.

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Ethics statement

Our study makes use of data, collected through non-invasive monitoring methods (*i.e.* camera traps). Hence, animal subjects are minimally disturbed and approval from an animal ethics committee was not mandatory. Camera traps also collect images of human subjects. However, raw images are unavailable to the data user, and all human observations are anonymized (only the tag "human" is retained). Therefore, approval of an ethics committee was not mandatory.

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Table 1(on next page)

The number of wild boar and the number of hunters counted during the entire study period within each solar hour.

Wild boar counts/day obtained by dividing counts through the total number of trapping days of all cameras combined (10086). Hunter visits/day obtained by dividing visits through the total number of days in the study period (732).

Solar hour	Wild boar		Hunters	
	Counts	Counts/Day	Visits	Visits/Day
$({}^{0}/24) \cdot 2\pi$	121	0.012	1	0.001
$({}^{1}/24) \cdot 2\pi$	97	0.010	1	0.001
$({}^{2}/24) \cdot 2\pi$	109	0.011	1	0.001
$({}^{3}/24) \cdot 2\pi$	257	0.025	12	0.016
$({}^{4}/24) \cdot 2\pi$	272	0.027	110	0.150
$({}^{5}/24) \cdot 2\pi$	313	0.031	226	0.309
$({}^{6}/24) \cdot 2\pi$	496	0.049	254	0.347
$({}^{7}/24) \cdot 2\pi$	255	0.025	184	0.251
$({}^{8}/24) \cdot 2\pi$	219	0.022	15	0.020
$({}^{9}/24) \cdot 2\pi$	84	0.008	1	0.001
$({}^{10}/24) \cdot 2\pi$	17	0.002	0	0.000
$({}^{11}/24) \cdot 2\pi$	35	0.003	0	0.000
$({}^{12}/24) \cdot 2\pi$	30	0.003	0	0.000
$({}^{13}/24) \cdot 2\pi$	10	0.001	0	0.000
$({}^{14}/24) \cdot 2\pi$	18	0.002	0	0.000
$({}^{15}/24) \cdot 2\pi$	31	0.003	9	0.012
$({}^{16}/24) \cdot 2\pi$	28	0.003	256	0.350
$({}^{17}/24) \cdot 2\pi$	239	0.024	416	0.568
$({}^{18}/24) \cdot 2\pi$	442	0.044	377	0.515
$({}^{19}/24) \cdot 2\pi$	443	0.044	96	0.131
$({}^{20}/24) \cdot 2\pi$	372	0.037	23	0.031
$({}^{21}/24) \cdot 2\pi$	232	0.023	11	0.015
$({}^{22}/24) \cdot 2\pi$	188	0.019	7	0.010
$({}^{23}/24) \cdot 2\pi$	197	0.020	3	0.004
Total	4505	0.447	2003	2.736

Table 2(on next page)

The timing and magnitude of the first and second activity peaks for different populations.

Population	1st peak		2nd peak	
	Solar time (rad)	Density	Solar time (rad)	Density
Human	3.632	0.473	NA	NA
Hunters	1.694	0.718	4.602	1.201
Year-round hunting zone	1.534	0.345	5.301	0.338
Winter hunting zone	1.620	0.446	5.019	0.457
Core zone	1.681	0.286	5.031	0.330

Table 3(on next page)

Pearson correlations and their significance between wild boar activity and hunting activity for solar hours with >1 hunting record.

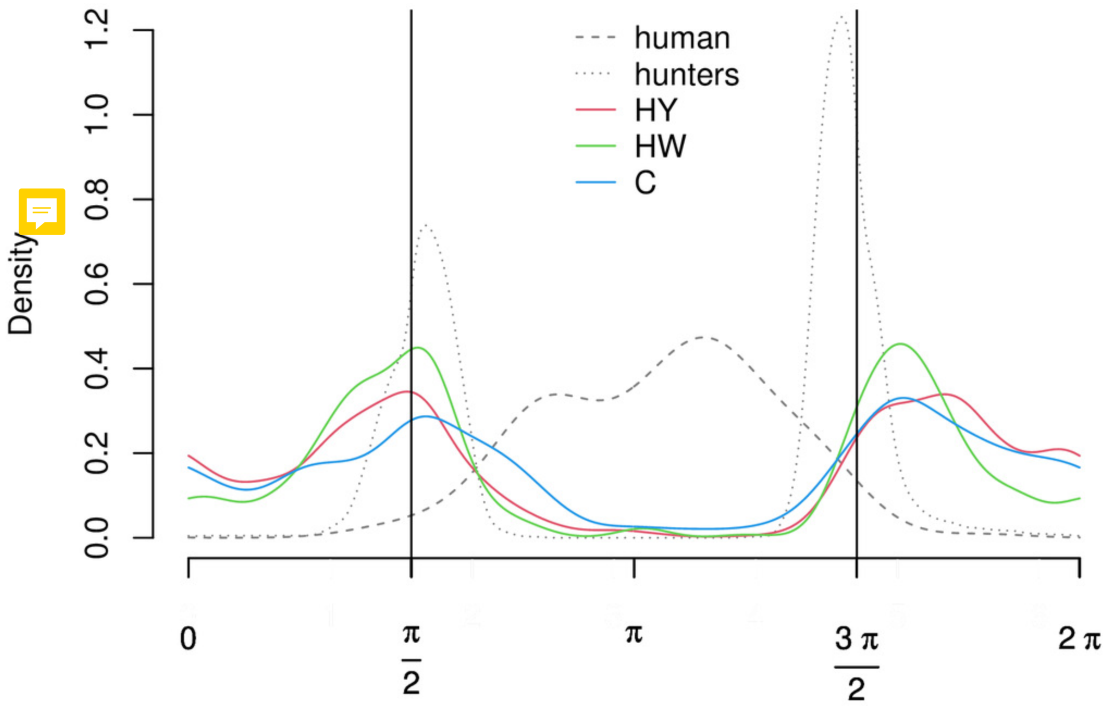
p-value > 0.05 (ns); 0.05 ≥ p-value > 0.01 (*); 0.01 ≥ p-value > 0.001 (**); and 0.001 ≥ p-value (***).

Solar hour	statistic	ρ	p-value	significance
$({}^{3}/24) \cdot 2\pi$	2.492	0.150	0.013	*
$({}^{4}/24) \cdot 2\pi$	2.617	0.160	0.009	**
$({}^{5}/24) \cdot 2\pi$	2.621	0.160	0.009	**
$({}^{6}/24) \cdot 2\pi$	2.328	0.140	0.021	*
$({}^{7}/24) \cdot 2\pi$	1.526	0.093	0.128	ns
$({}^{8}/24) \cdot 2\pi$	0.547	0.034	0.585	ns
$({}^{15}/24) \cdot 2\pi$	-1.124	-0.069	0.262	ns
$({}^{16}/24) \cdot 2\pi$	-0.716	-0.044	0.475	ns
$({}^{17}/24) \cdot 2\pi$	-0.176	-0.011	0.861	ns
$({}^{18}/24) \cdot 2\pi$	0.442	0.027	0.659	ns
$({}^{19}/24) \cdot 2\pi$	0.994	0.061	0.321	ns
$({}^{20}/24) \cdot 2\pi$	1.388	0.085	0.166	ns
$({}^{21}/24) \cdot 2\pi$	1.614	0.099	0.108	ns
$({}^{22}/24) \cdot 2\pi$	1.729	0.110	0.085	ns
$({}^{23}/24) \cdot 2\pi$	1.844	0.110	0.066	ns

Figure 1

Map of the study area (lower panel) and activity patterns of wild boar, humans and hunters (upper panel).

Management zones: year-round hunting zone (HY - red), winter hunting zone (HW - green) and core zone (C - blue). In the upper panel, vertical lines indicate sunrise and sunset. In the lower panel, hunting locations (“high seats”) and camera locations are indicated by respectively dots and crosses.


Density
0.0
0.2
0.4
0.6
0.8
1.0
1.2
human
hunters
HY
HW
C
0
π/2
π
3π/2
2π

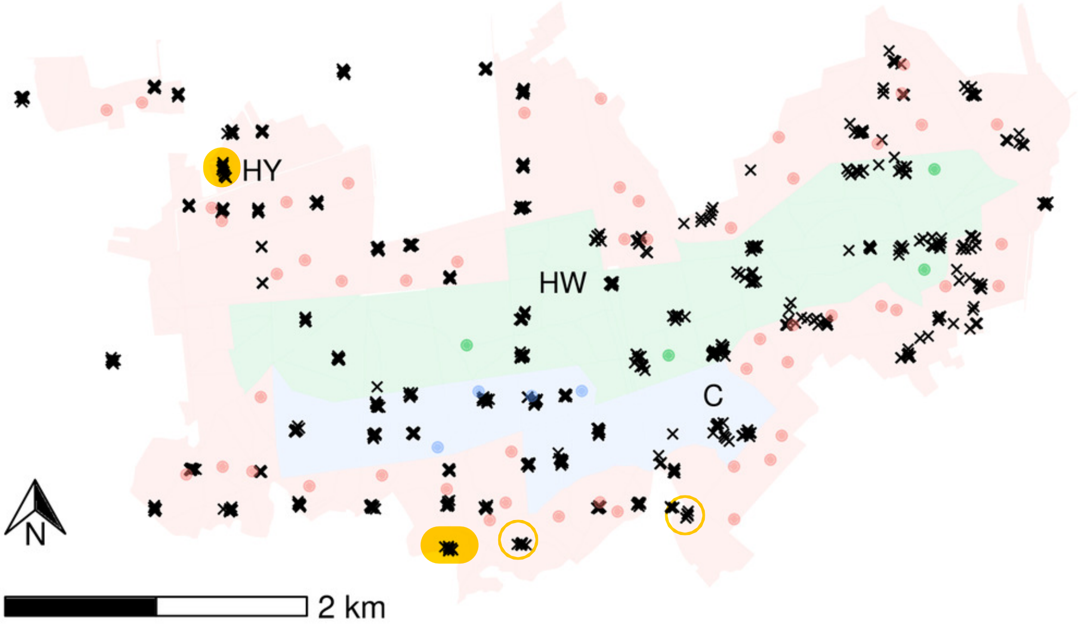

HY
HW
C
N
2 km

Figure 2

Partial effects of the elements in the GAM modelling diel space use of wild boar.

(a) Random effects per day (dots) and the corresponding averages per month (full line). (b) Effects of the week of the year. (c) Effects of the solar time in radians. (d) Effects of the tensor product of longitude, latitude and solar time in radians. Facets represent solar times. Color scale: partial effect < 0 (blue), partial effect = 0 (white), partial effect > 0 (red).

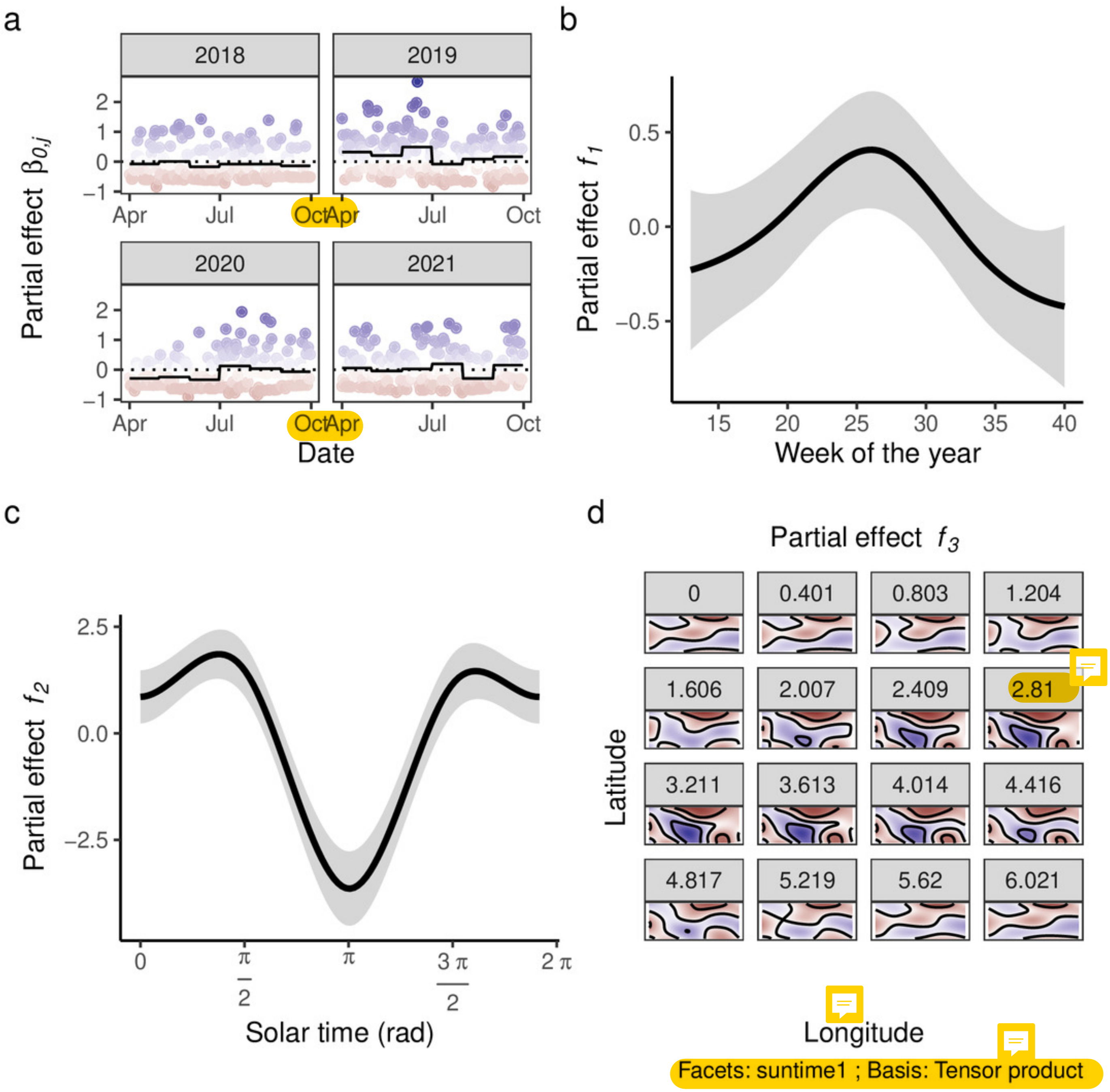
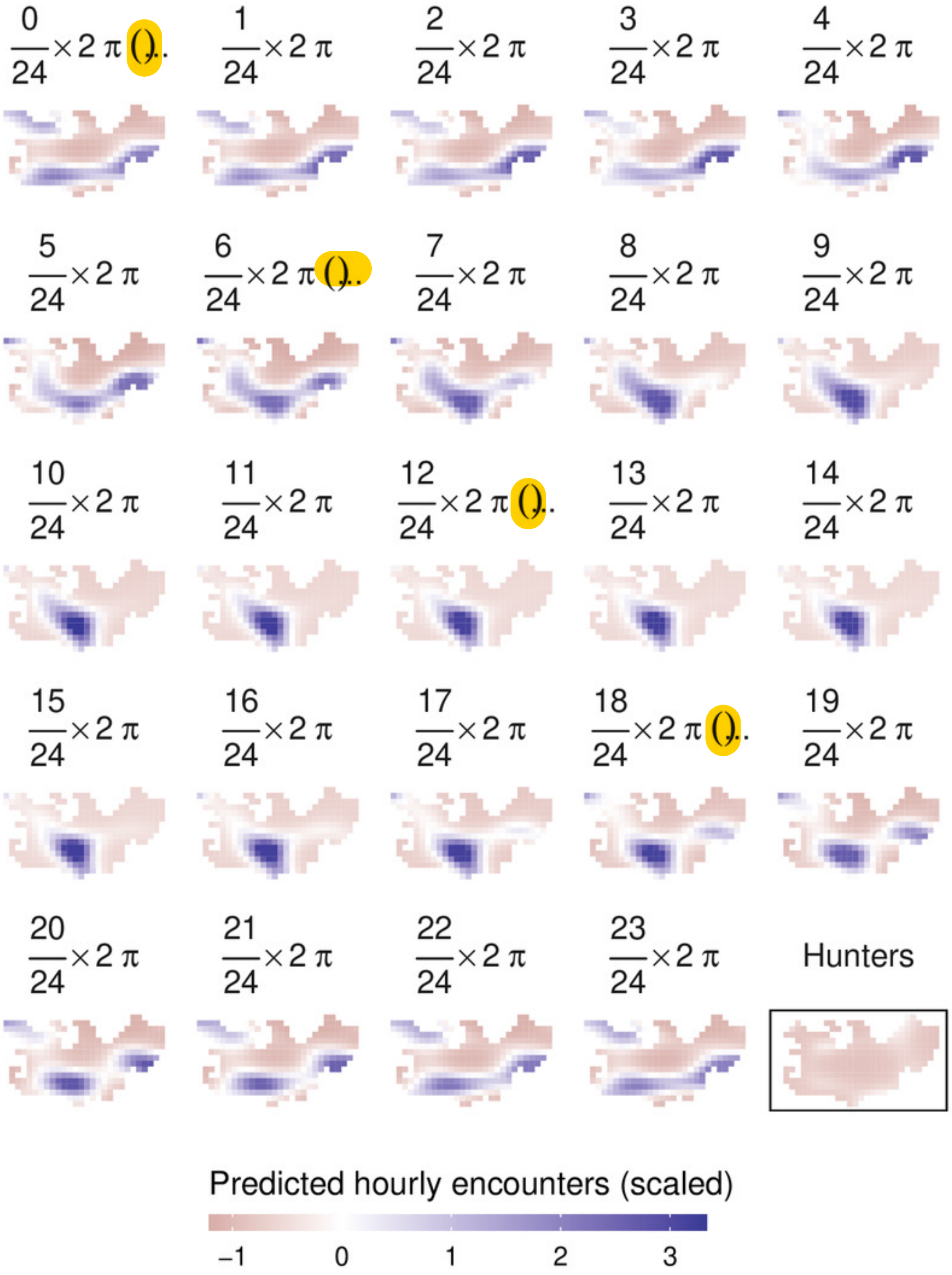

a
2018
2019
2020
2021
Partial effect $\beta_{0,j}$
2
1
0
−1
Apr
Jul
Oct
Date
b
Partial effect f_1
0.5
0.0
−0.5
15
20
25
30
35
40
Week of the year
c
Partial effect f_2
2.5
0.0
−2.5
0
$\frac{\pi}{2}$
π
$\frac{3\pi}{2}$
2π
Solar time (rad)
d
Partial effect f_3
0
0.401
0.803
1.204
1.606
2.007
2.409
2.81
3.211
3.613
4.014
4.416
4.817
5.219
5.62
6.021
Latitude
Longitude
Facets: suntime1 ; Basis: Tensor product

Figure 3

Spatial variation in the encounter rates of wild boar across 24 solar hours and in the encounter rate of hunters.

Encounter rates are z-transformed per panel. For visual clarity scaled encounter rates of hunters are multiplied by factor 10. Nadir (●), sunrise (↑), zenith (○), sunset (↓).


0/24 × 2 π
1/24 × 2 π
2/24 × 2 π
3/24 × 2 π
4/24 × 2 π
5/24 × 2 π
6/24 × 2 π
7/24 × 2 π
8/24 × 2 π
9/24 × 2 π
10/24 × 2 π
11/24 × 2 π
12/24 × 2 π
13/24 × 2 π
14/24 × 2 π
15/24 × 2 π
16/24 × 2 π
17/24 × 2 π
18/24 × 2 π
19/24 × 2 π
20/24 × 2 π
21/24 × 2 π
22/24 × 2 π
23/24 × 2 π
Hunters
Predicted hourly encounters (scaled)
−1
0
1
2
3