



Original investigation

An analysis of intrinsic and extrinsic factors affecting the activity of a nocturnal species: The wild boar

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ABSTRACT

Over the last century, the wild boar (*Sus scrofa*) has become an important wildlife species in both economic and ecological terms. Considered a pest by some and a resource by others, its rapid increase in population and distribution has raised management concerns. Studies on activity rhythms may provide useful insights into its overall ecology and help develop effective management strategies. By examining highly detailed activity data collected by means of accelerometers fitted on GPS-collars, we studied wild boar daily activity rhythms and the effect of environmental conditions on their diurnal and nocturnal activity. We thus provided evidence of the predominantly nocturnal and monophasic activity of wild boars. All year round, we reported low activity levels during the day, which opportunistically increased under the most favourable environmental conditions. Activity was found to be significantly affected by such weather conditions as temperature, precipitation and air relative humidity. Moreover, we found that nocturnal activity slightly increased as moonlight increased. Part of our analysis was focused on the hunting period in order to investigate whether wild boars modify their activity levels in response to hunting disturbance. Our results suggested that wild boar nocturnal habits are not directly influenced by the current hunting disturbance, though we hypothesised that they may have evolved over several decades of hunting harassment. Alternatively, but not exclusively, nocturnal habits may have evolved as a low-cost strategy to achieve an optimum thermal balance (i.e., behavioural thermoregulation).

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Introduction

Currently, the wild boar (*Sus scrofa*) represents one of the ungulate species of major and growing management concern in Europe. On the one hand, it is considered a pest causing severe economic problems (e.g., Bruinderink and Hazebroek, 1996; Gortázar et al., 2007; Labudzki and Wlazełko, 1991) and damage to human activities (Amici et al., 2011; Ballari and Barrios-García, 2014; Lagos et al., 2012). On the other hand, it is one of the most attractive and valued game species (Apollonio et al., 2010). For these reasons, in the last decades, a strong public and governmental interest in identifying practical approaches that may help reduce wild boar negative effects and improve management strategies has arisen.

An increasing consensus is emerging among ecologists that, in order to develop an effective and biologically based management of wildlife, it is essential to gain a detailed knowledge about population structure, reproduction and behaviour (Caro, 1998). In recent

years, a surge of research has been directed at improving knowledge on wild boar populations in Europe, in the context of the recent EUROBOAR network initiatives (<http://euroboar.org>). These studies agree that the wild boar is characterised by a great phenotypic and behavioural plasticity (e.g., Ballari and Barrios-García, 2014; Podgórski et al., 2013), which explains its particularly high adaptability. At the same time, this characteristic makes the study of this species more complex and underscores the need to conduct new research on a variety of ecological and behavioural topics in different geographical ranges.

Studies on activity patterns provide useful insights into the overall ecology of a species. Activity rhythms are important in controlling the energy balance of animals (Aschoff, 1979), resulting from a simultaneous adjustment of the multiple behavioural traits aimed to meet the energy requirements for maintenance, growth and reproduction (Daan and Aschoff, 1982). It is now well established that such activity rhythms are endogenously generated by biological clocks (Refinetti, 2016), endowed with special mechanisms adapting them to the periodic challenges posed by the environment. Activity patterns rely on endogenously fixed rhythms which have been called “circadian” or “circannual”. Circadian and

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circannual rhythms are entrained to the 24-h day and the calendar year by periodically changing environmental stimuli, the so-called “Zeitgebers”, such as the daily cycle of light and darkness, food availability, weather conditions, moonlight, predation and human-related disturbance (Brivio et al., 2016; Daan and Aschoff, 1982; Ohashi et al., 2013; Paul et al., 2008).

Many authors described wild boar activity patterns (e.g., Cahill et al., 2003; Caley, 1997; Cousse et al., 1995; Keuling et al., 2008; Massei et al., 1997; Ohashi et al., 2013; Podgórski et al., 2013; Russo et al., 1997; Stolle et al., 2015), reporting considerable variations in its activity rhythms and high adaptability to external factors. Activity rhythms were reported to be monophasic, biphasic or polyphasic (Caley, 1997; Cousse et al., 1995; Keuling et al., 2008; Russo et al., 1997) and it was suggested that wild boars may switch from predominantly diurnal to predominantly nocturnal activity in response to anthropic disturbance (Keuling et al., 2008; Kurz and Marchinton, 1972; Ohashi et al., 2013; Podgórski et al., 2013).

Many studies found that seasonality is a main factor affecting wild boar activity (Cahill et al., 2012, 2003; Caley, 1997; Keuling et al., 2008; Massei et al., 1997; Podgórski et al., 2013), thus suggesting that weather conditions strongly influence their activity rhythms. Weather conditions can influence animals' activity patterns either directly, i.e., through day-to-day weather changes, or indirectly, i.e., through the seasonal effects of the climate on environmental conditions, particularly on food availability (Olson and Wallander, 2002; Owen-Smith, 1998; Roberts and Dunbar, 1991; Shi et al., 2006). Thurfjell et al. (2014) used the speed of movement as a proxy of the animals' activity and showed that wild boars reduce their activity in response to suboptimal weather conditions. However, wild boars often showed on-site activity, which resulted in a non-significant relationship between activity and speed of movement (Podgórski et al., 2013). This raises the need to conduct direct studies on the effect of weather conditions on wild boar activity levels.

By taking advantage of highly detailed information on wild animals' activity levels obtained by means of GPS-collars equipped with accelerometers, we studied wild boar circadian and circannual activity rhythms with a chronobiological approach. We investigated the effect of environmental conditions on their year-round total activity levels and focused on diurnal and nocturnal activity, separately. Following previous studies on other ungulates as well as on wild boar biology, we supposed that wild boar activity rhythms vary throughout the year, also in relation to human disturbance, which may induce a reduction or a shift in their activity patterns. We also expected an increase in activity levels under humid conditions (e.g., rainy days), because wild boars may benefit from the increased efficiency of their olfactory organ and their rooting behaviour may be facilitated. Finally, we assumed that changes in activity rhythms may help to control their thermal balance and, therefore, we expected a reduced activity on the days with extreme temperatures. As regards the nocturnal activity, we also took into account the influence of moonlight. Indeed, it has been shown that light changes during the lunar cycle can affect rhythms in organisms. Moonlight can represent a time cue, acting as a synchroniser for reproduction; it can change the animals' ability to use visual cues, affecting their sensorial experience (e.g., use of senses for communication, navigation, prey and predator location); moreover, it can indirectly change the biotic environment by affecting activity levels of predators, competitors and prey (reviewed in Kronfeld-Schor et al., 2013). We expected wild boars to decrease their activity levels during brighter nights, as a consequence of the increased predation risk by the wolf, which typically improves its hunting success during moonlit nights (Theuerkauf et al., 2003).

Hunting pressure was shown to influence wild boar activity patterns to a significant extent (Keuling et al., 2008; Russo et al., 1997), thus suggesting that nocturnal activity should increase when they

are exposed to hunting pressure. In the light of this finding, we analysed the effect of hunting disturbance on two different time scales. On a broad scale, we analysed both diurnal and nocturnal activity, expecting a modification of the rhythms during the hunting season. Additionally, we conducted an analysis on a finer scale, i.e., by considering only the hunting season, and observed whether wild boars showed different diurnal and nocturnal activity levels during hunting and non-hunting days. We expected wild boars to reduce their activity levels during daylight hours so as to avoid hunters and their hounds (i.e., direct response) and to increase their nocturnal activity so as to compensate for the foraging opportunities lost during the day (i.e., delayed compensatory response).

Material and methods

Study area

The study was conducted in the Apennine mountains in the province of Arezzo (North-East of Tuscany, Italy, 43°48'N, 11°49'E). The study area covers a surface of about 120 km², including an unfenced protected area of 27 km² (Oasi Alpe di Catenaia). Altitude within this site ranges from 300 to 1414 m above the sea level. Vegetation cover is mainly composed of mixed deciduous woods (76% of the total area, dominated by oaks, *Quercus* spp., chestnut, *Castanea sativa*, and beech, *Fagus sylvatica*). Conifer woods are also present (7% of the total area) and composed of black pine (*Pinus nigra*) and Douglas fir (*Pseudotsuga menziesii*), while open areas and bushes cover the rest of the area (about 17%). Climate is temperate-continental, with hot and dry summers, and cold and rainy winters. Monthly mean temperature ranges from 4.7 °C in January to 21.9 °C in July, while monthly precipitation levels average between 34.2 mm in June and 214.3 mm in November. Snowfalls are occasional and usually start in October and may continue through April. Wild boar and roe deer (*Capreolus capreolus*) are the most abundant ungulate species, but also red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) were observed. Wild boar predators are red fox (*Vulpes vulpes*, only on piglets) and wolf (*Canis lupus*), in whose diet wild boar resulted to be the main component (Bassi et al., 2012). Outside the protected area, wild boar hunting is performed with drive hunts usually involving tens of dogs and 25–50 hunters who harvest an average of 9.6 boars/100 ha. Hunting is permitted on Wednesdays, Saturdays and Sundays from mid-September to mid-January, with a relatively constant intensity (see also Grignolio et al., 2011 for more details).

Data collection

Activity data

In the period 2013–2015, we captured a total of nine adult wild boars (five females and four males) by using vertical drop nets and traps baited with maize. To avoid sampling individuals from the same social group, we marked only one adult wild boar for each capture session. Once captured and immobilised, wild boars were sedated with a dose of 0.5 ml/10 kg of Zoletil®. Each individual was weighed, measured and aged on the basis of teeth eruption and wear (Heck and Raschke, 1980). Finally, they were fitted with GPS-collars (GPS PRO Light collar, Vectronic Aerospace GmbH), equipped with a dual-axis accelerometer, which measured the animals' activity based on the actual acceleration experienced by the collars. The accelerometer had a dynamic range from –2G to +2G (G = gravitational constant) and measured activity as the change of static acceleration (gravity) and dynamic acceleration (collar) 4 times/second. On the X-axis the accelerometer was sensitive to acceleration events with forward/backward direction, while on the Y-axis it recorded acceleration events with a sideward and

rotary direction. On each axis, activity was calculated as the difference between consecutive acceleration values, averaged over a time interval of four minutes and given within a relative range between 0 (no activity) and 255 ($-2G/+2G$: maximum activity). Activity data were then associated with the date and time recorded by the collar memory. The activity data recorded were downloaded by means of Vectronic Handheld Terminal and Yagi antenna. A total of 763,920 activity records was acquired during 2122 monitoring days (see Supplementary material A, Table A1 for more details on the sampling period of each individual marked). As activity values measured on X and Y axes resulted to be highly correlated, we only analysed X activity data.

As the wild boar is a highly social species, individuals of the same social group may have very similar activity patterns and thus represent replicates rather than independent sample points. In order to exclude wild boars marked from the same sounder, we visually checked the GPS localisations recorded by the collars and ascertained that individuals did not belong to the same social unit.

Weather and astronomical data

Weather data were recorded hourly in the weather station of Poppi (Province of Arezzo, 43°44'09"N, 11°45'42"E) by the Tuscan Hydrological Service. Data included values of minimum, mean and maximum temperature (°C), maximum and mean solar radiation (W/m^2), minimum, mean and maximum relative humidity (%), rain (mm) and rain intensity (mm/min). Cloud cover estimates were downloaded from the NCEP/NCAR data set (Kalnay et al., 1996) by using the RNCEP-package for the R software. Cloud cover data were expressed as the percentage of sky covered by clouds and had spatial and temporal gridded resolution of 2.5° and 6 h, respectively. In our analyses, only cloud cover data recorded at 00.00 A.M. were used. To estimate cloud cover in our study area, we used the interpolation method "Inverse Distance Weighting" (Shepard, 1968), by means of the NCEP.interp R function. Moon phase data were obtained from the Astronomical Applications Department of the U.S. Naval Observatory web site (<http://aa.usno.navy.mil>), expressed as the proportion of moon disk illuminated at 00.00 A.M. The value 0 corresponded to new moon conditions and the value 1 to full moon conditions. From the same web site, we acquired the times of sunrise and sunset (civil twilight) for each day of the study period.

Data analyses

Actograms were drawn by using the Activity Pattern software (ver. 1.3.1, Vectronic Aerospace GmbH, Berlin, Deutschland). The presence of circadian periodicity in the activity rhythms was determined by means of χ^2 periodogram analysis, by using the ActogramJ software for circadian analysis (version 1.0, Schmid et al., 2011). Periodogram analyses were performed with intervals of 10 days during equinoxes and solstices. Phase angle differences (ψ) between activity onset and the beginning of civil twilight at dusk were calculated for each season (ActogramJ 1.0). Positive ψ indicated that the activity onset anticipated the onset of civil twilight.

Since the visual analysis of the actograms showed that wild boars switched from a nocturnal to a diurnal temporal activity niche, we implemented a specific analysis to calculate the daily acrophase (ActogramJ 1.0). In addition we determined the average acrophase for each period by using vector addition. We then performed a Rayleigh test to determine whether the acrophases deviated from uniform dispersion around the clock and whether they were concentrated at a given time of the day ($p < 0.05$). Mardia-Watson-Wheeler test was performed to test for differences among average acrophases of different periods ($p < 0.05$).

For each wild boar, the raw activity data recorded by the collar were scaled dividing them by the maximum value recorded by

the accelerometer (255). Thus, we obtained activity rate (AR) values on a relative scale from 0 to 1, where 0 meant no activity and 1 maximum activity. Then, for each wild boar, all AR values were classified as diurnal and nocturnal by considering the recording date and time, and the relative sunrise and sunset times: the AR values recorded between sunrise and sunset of day i fell into the diurnal activity subset of day i , while those recorded between sunset of day i and sunrise of day $i+1$ fell into the nocturnal activity subset of day i . After splitting activity data into the two subsets, Diurnal Mean Activity (DMA) and Nocturnal Mean Activity (NMA) values were calculated as the average of all the AR values recorded during each day and each night, respectively. Likewise, we calculated the diurnal and nocturnal mean values for each meteorological parameter (i.e., minimum, mean and maximum temperature; minimum, mean and maximum relative humidity and rain intensity; maximum and mean solar radiation, only for daylight hours): we assigned each hourly value to either a day or a night according to the recording time and then calculated the mean values for each day and each night of the data collection period. For each date of data collection, diurnal and nocturnal precipitation values were calculated by summing the values recorded throughout the corresponding day and night. Finally, for each night we calculated moonlight illuminance (hereafter moonlight) according to the formula: moon phase of day i – (moon phase of day i × cloud cover at midnight of day i), with the values closer to 0 representing darker nights and the values closer to 1 representing brighter nights.

To assess the effect of intrinsic and extrinsic factors on wild boar diurnal and nocturnal activity patterns, we modelled DMA and NMA, separately, by using Generalised Additive Models (GAMs) with Binomial distribution. GAMs were implemented within the mgcv package (version 1.8–10) in R (version 3.0.2; R Core Team, 2014). The following predictor variables were considered: wild boar sex and weight (at capture), diurnal and nocturnal weather parameters for DMA and NMA, respectively, and moonlight (for NMA only). Moreover, in order to better define the pattern of both DMA and NMA variations throughout the year, we included the Julian date as a continuous variable in the models. Finally, to evaluate the effect of hunting on a broad temporal scale, we included a dummy variable, scored 1 for the days of the hunting season and 0 for the other days. Wild boar identity was used as a random factor to control for repeated measurements of the same individual, by fitting it in the GAMs by using "re" terms and smoother linkage (Wood, 2013). Possible correlations between the predictor variables were checked by means of a correlation matrix (Pearson correlation coefficient, r_p) to avoid collinearity (Sokal and Rohlf, 1995). Besides the obvious correlation between the mean, minimum and maximum values of each meteorological parameter, we found high correlation ($r_p > 0.7$) between temperature and radiation, and between the Julian date and the hunting season. For both DMA and NMA, we chose the best predictor out of the collinear variables by carrying out a pre-selection through a random forest calculation (randomForest-package of R) which ranks the importance of the parameters based on a certain number ($n=500$) of randomly generated decision trees (Supplementary material B). Based on the results of this random forest calculation, we chose weight, sex, Julian date, maximum relative humidity, minimum air temperature and precipitation as DMA predictor variables and weight, sex, Julian date, maximum relative humidity, minimum air temperature and moonlight as NMA predictor variables.

The selected predictor variables were used to build a GAM (full model) in which the effects of all continuous variables, except for the Julian date, were modelled as natural cubic spline functions. The effect of the Julian date was modelled as a cyclic cubic regression spline in order to take into account the circularity of this variable: thus, we ensured that the value of the smoother at the far left point (1 January) was the same as the one at the far right point

(31 December). As precipitation may increase the effect of cold weather (Parker, 1988) and decrease the effect of warm temperature, we also included an interaction term between temperature and precipitation. Subsequently, for both DMA and NMA, we fitted a set of models with all the possible combinations of the variables of the full model by testing for the relative importance of the variables by using the dredge function of the R package MuMIn (Barton, 2013). Model selection was carried out by comparing the corrected values of Akaike's information criterion (AICc, Richards et al., 2011). The goodness of fit of the full and selected models (homoscedasticity, normality of errors and independence) was checked by visual inspection of residuals (Zuur et al., 2009).

Finally, in order to test whether wild boars modify their diurnal and nocturnal activity in response to hunting disturbance on a finer temporal scale, we analysed DMA and NMA, separately, from the beginning to the end of the hunting season (from mid-September to mid-January) for each year of data collection. For both DMA and NMA, we fitted the best model selected for the full-year analyses and added a dummy variable scored 1 for hunting days (Wednesday, Saturday and Sunday) and 0 for non-hunting days. The effect of the Julian date was evaluated by using a continuous variable, namely the hunting date, scored from 1 (first hunting day of September of year x) to 135 (last hunting day of January of year $x + 1$), in order to account for both the discontinuity between January and September of the same year and the continuity between 31 December and 1 January of the following year.

Results

Both male and female wild boars investigated showed a marked daily rhythmicity in activity throughout the year (Fig. 1 and Supplementary material A, Figs. A1–A6). The activity pattern was unimodal and mainly nocturnal. A crepuscular activity was reported to occur in all seasons but, interestingly, the time interval between activity onset and the onset of civil dusk significantly changed during the year ($K_4 = 116$, $p < 0.0001$; Kruskal-Wallis One-way ANOVA), with the highest values recorded in summer (3.57 ± 2.14 h, mean \pm sd, Dunn's Multiple Comparison Test, $p < 0.001$; Supplementary material C, Fig. C2). Wild boars showed a significant anticipation of activity onset with respect to the civil dusk in summer only. Furthermore, a twilight activity at sunrise was reported in spring and summer (Fig. 1; Supplementary material C, Fig. C1).

Two of the five females showed an inversion of activity pattern and switched from nocturnal to diurnal in late spring (Supplementary material C, Fig. C1 A) and in late summer (Fig. 1H). In order to ascertain the statistical significance of this phenomenon, for these two females we calculated the daily acrophases prior to, during and after the inversion (Supplementary material C, Figs. C3 and C4). Subsequently, by using a circular statistic approach, we showed that the distribution of acrophases of both females deviated from uniform in all periods (Supplementary material C, Figs. C3 B–D and F–H; C4 B–E; Rayleigh test, $p < 0.0001$). The mean acrophases fell between 21:36 and 23:18 during nocturnal activities and between 12:36 and 17:24 during diurnal activities. The distribution of acrophases differed significantly among periods in both females (Mardia-Watson-Wheeler Test; #12292: $W_3 = 50.12$, $p < 0.00001$; $W_3 = 26.9$, $p < 0.0001$; #12286: $W_4 = 83.9$, $p < 0.00001$).

A total of 1110 days/wild boar for females and a total of 1019 days/wild boar for males were obtained during the data collection period. Wild boar NMA (0.311 ± 0.120) was higher than DMA (0.063 ± 0.067).

Full-year models

According to the minimum AIC criterion, the best global model for DMA included the Julian date, maximum humidity and the interaction term between minimum temperature and precipitation as predictor variables ($R\text{-sq.} = 0.328$). Throughout the year, a single peak of DMA was recorded around 19th June, while minimum values were recorded around 11th March and 6th December (Fig. 2A). Wild boar DMA had a positive relation with air maximum humidity (Fig. 2B). The maximum activity values were reported in conditions of low temperature and intermediate precipitation levels (about 27–43 mm/day), while the minimum values were reported in conditions of high temperature and low precipitation levels (Fig. 2C).

The best model for NMA included Julian date, maximum humidity, maximum temperature and moonlight as predictor variables ($R\text{-sq.} = 0.292$). Weight and sex were also included in the best model, though results showed no significant difference among individuals of different weight and sex. Analyses showed a non-linear relationship between wild boar NMA and the Julian date, with the lowest activity values recorded around 9th February and 16th November and maximum values around 29th July and 27th September. An irregular pattern between the maximum and the minimum peak was observed (Fig. 3A). The relation between NMA and maximum humidity followed a non-linear pattern characterised by a wide confidence interval, thus making this result hardly understandable (Fig. 3B). During the night, wild boar activity was positively related to maximum temperature (Fig. 3C). Finally, a weak influence of moonlight was observed, with wild boars being slightly more active when the available moonlight was more intense (Fig. 3D).

Hunting period models

By restricting the analyses to the hunting period, we observed no significant influence of hunting disturbance on wild boar DMA and NMA. The effect of the other predictor variables remained similar or was less noticeable than in the full-year models. Model predictions showed a decrease in DMA from the beginning to the end of the hunting period (Supplementary materials D, Fig. D1 A), which corresponded to the general decrease in DMA occurring from summer to winter (Fig. 2A). We found no significant effect of maximum humidity. The interaction term between mean temperature and precipitation produced a pattern similar to that observed in the full-year model, with wild boars reported to be more active with low minimum temperature and intermediate precipitation levels (Supplementary materials D, Fig. D1 B). A general decrease in wild boar NMA was observed from the beginning to the end of the hunting period, with the exception of a temporary gain around 19th December (Supplementary materials D, Fig. D2). No clear influence was detected of moonlight, maximum humidity and maximum temperature on NMA during the hunting period.

Discussion

Our study on wild boar activity rhythms showed that, in our study area, these animals are nocturnal, with a marked daily rhythmicity in their total activity throughout the year. Unlike other ungulate species (e.g., Aschoff, 1966; Brivio et al., 2016; Pagon et al., 2013), the activity pattern that we found was not bimodal. It appeared to be continuous during the whole night, with an acrophase during the first hours of the night (between 21:36 and 23:18). A crepuscular activity was reported throughout the year, but the onset of activity significantly anticipated the civil dusk only in summer. Anticipation of changes in the environment allows for appropriate changes in the physiological state of animals. Con-

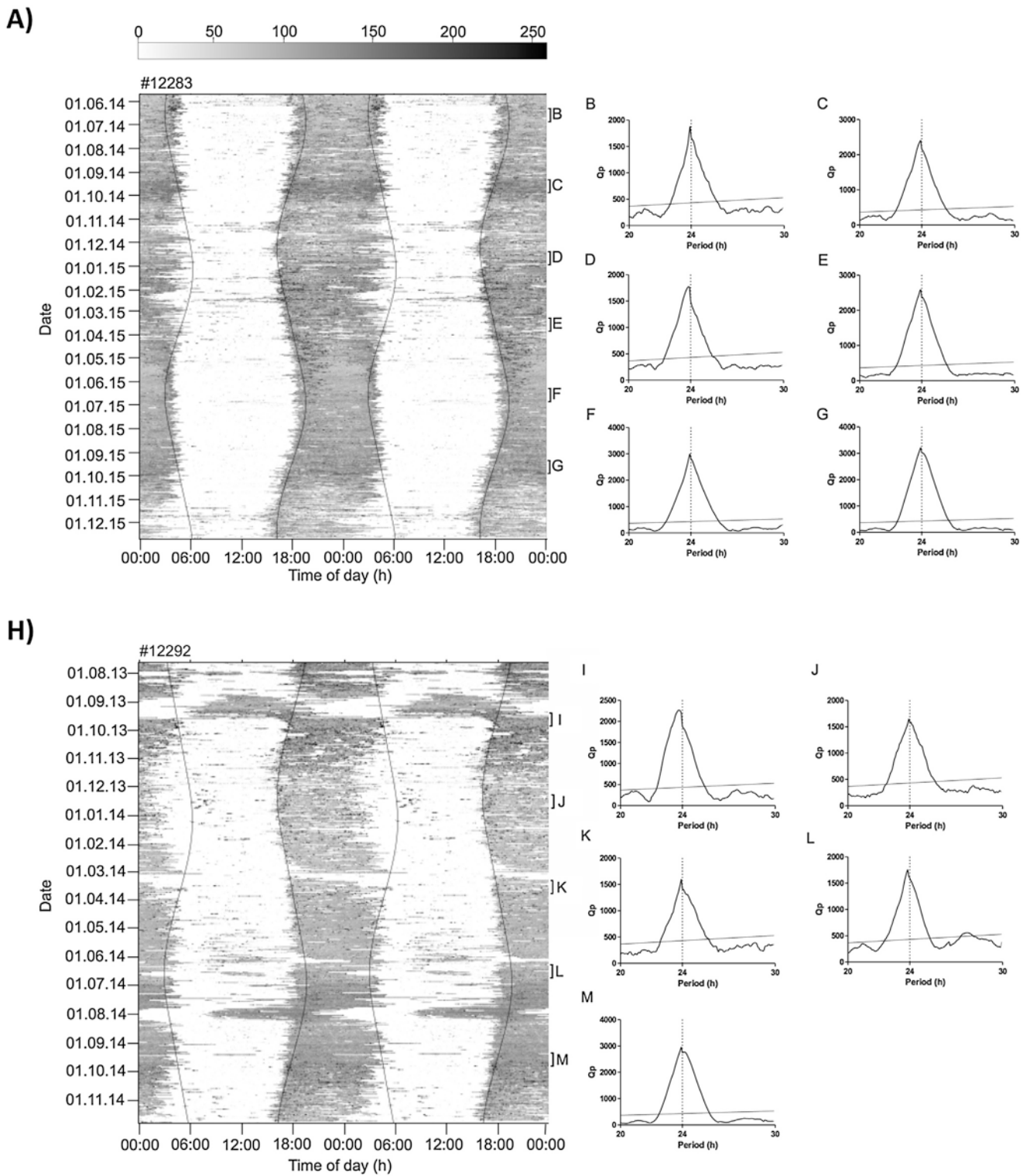


Fig. 1. Representative actograms of daily activity of A) one radio-collared male wild boar (#12283) and H) one radio-collared female wild boar (#12292) in the province of Arezzo (Italy). Vertical bars represent their activity levels (over intervals of five minutes), the colour of the bar being a function of activity level: from white (=0) to black for maximum values (i.e., 255). Black vertical lines indicate dawn and dusk according to civil twilight. Records are double plotted on a 48-h time scale to help the interpretation. B–G and I–M delimit 10-day intervals of activity during different periods of the year that were separately subjected to χ^2 periodogram analysis (plots in the right-hand panels) to test for the presence of circadian periodicity. In each periodogram, an index of rhythmicity [$Q(p)$] is plotted with respect to the periods tested (from 20 to 30 h). The sloped dotted lines represent the threshold of significance, set at $p=0.05$.

sequently, the anticipation of activity onsets may result in an adaptive advantage for the wild boar population in our study area and it is likely driven by an internal circadian timing mechanism (Pittendrigh, 1993; Sharma, 2003). Conversely, seasonal changes in

the length of the time interval between the activity onset and the onset of civil dusk may be a response to the seasonal change in light intensity at dawn (Ensing et al., 2014; Hut et al., 2012). Throughout the year, wild boar diurnal activity was low and reached the

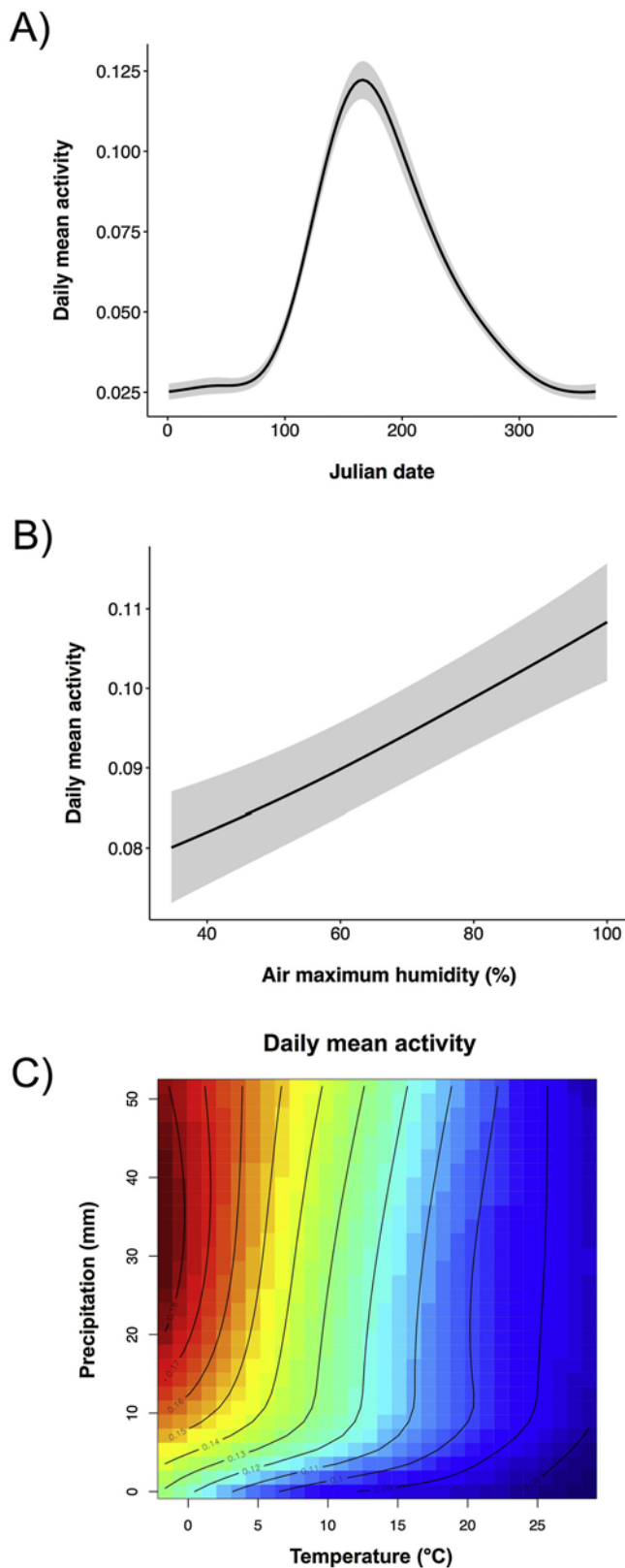


Fig. 2. Values predicted by the best Generalised Additive Model (see the text for more details) of wild boar daily mean activity in the province of Arezzo (Italy). The figure shows the effects exerted by Julian date (A), air relative humidity (B), and the interaction term between temperature and precipitation (C). The predictions are given according to the mean of all other covariates in the model. In the graphs A) and B) the colour-shaded areas are the estimated standard errors. In the graph C) the contour plot shows the variation of daily mean activity under the effect of the interaction term between temperature and precipitation; red colour indicates the higher values and blue colour the lower ones.

maximum levels around the summer solstice, when nights were possibly too short for the achievement of all their energy requirements. A similar behavioural pattern was described for the crested porcupines (*Hystrix cristata*), a nocturnal species which increased its diurnal activity as nights gradually grew shorter, possibly to compensate for the too little nocturnal foraging time (Corsini et al., 1995).

NMA resulted to be about five times higher than DMA, thus confirming the predominantly nocturnal habits of the wild boars monitored. This result is consistent with most of the available evidence in literature (Cahill et al., 2003; Caley, 1997; Keuling et al., 2008; Russo et al., 1997; Saunders and Kay, 1991), even though previous studies were based on data recorded with indirect methods or on a much lower sampling rate. In popular belief as well as in old literature, wild boars are thought to be diurnal (Kurz and Marchinton, 1972; Wood and Brenneman, 1977), with a tendency to switch to a nocturnal behavioural pattern when suffering from intense hunting pressure (Briedermann, 1971; Hennig, 1998). Our dataset was collected in an area where wild boar culling was intensive throughout the hunting season. Nevertheless, our results suggested that, in our study area, the overall impact of hunting on wild boar activity is non-significant, on both a broad and a finer temporal scale. In the same study area, roe deer were also found to reduce their activity levels during the hunting season (Pagon et al., 2013), but this was not the case of the wild boars monitored. Contrary to our predictions and in contrast to the findings of Ohashi et al. (2013) for a Japanese wild boar population, we did not find any increase in their nocturnal activity during the hunting season. On a finer temporal scale, we expected a shift in the activity from daytime to nighttime, as predicted by the risk-disturbance hypothesis (Frid and Dill, 2002) and as described for the Mediterranean mouflon (*Ovis gmelini musimon*) in response to hunting disturbance (Marchand et al., 2014). On the contrary, we did not find any immediate response by the animals monitored in terms of a decrease in their daytime activity, nor in terms of an increase in their nighttime activity levels possibly expected to occur as a delayed compensatory response. Although in our study area hunting was concentrated in four months only (from mid September to mid January) and wild boar activity showed a considerable variation during the annual cycle (Figs. 2A and 3A), nocturnal activity was evident and predominant throughout the year. We may suppose that the nocturnal habits of the population studied are not caused by the current hunting disturbance, but rather amount to the legacy of the hunting harassment which this population suffered from for decades after its reintroduction during the 1970s. The same behavioural adaptation was also suggested for other ungulate species (i.e., *Alces alces*: Ericsson and Wallin, 1996; *Ovis orientalis musimon*: Pipia et al., 2008; *Rupicapra rupicapra*: Carnevali et al., 2016).

The pronounced wild boar nocturnal activity makes this species an important case study to evaluate the effect of moonlight on activity patterns. Contrary to our expectations, wild boars slightly increased their activity levels during the brightest nights. In our study area, the wild boar is the main item in the wolf diet (Bassi et al., 2012) and this finding was recently confirmed by a study conducted in the Italian Apennine (Mori et al., 2017). The higher activity levels reported during the brightest nights contradict the expected response to wolf predation risk, which typically increases during moonlit nights (Theuerkauf et al., 2003). Prugh and Golden (2014) suggested that the net effect of moonlight on prey species activity levels should be determined by the relative importance of its costs (increased vulnerability to predation) and benefits (improved detection of food and predators). As a consequence, we should expect the moonlight effect to be positive for prey species relying primarily on vision to forage and to detect predators. For instance, this is the case of some primate species (*Aotus azarai*: Fernandez-Duque, 2003; *Tarsius spectrum*: Gursky, 2003) and of the Alpine

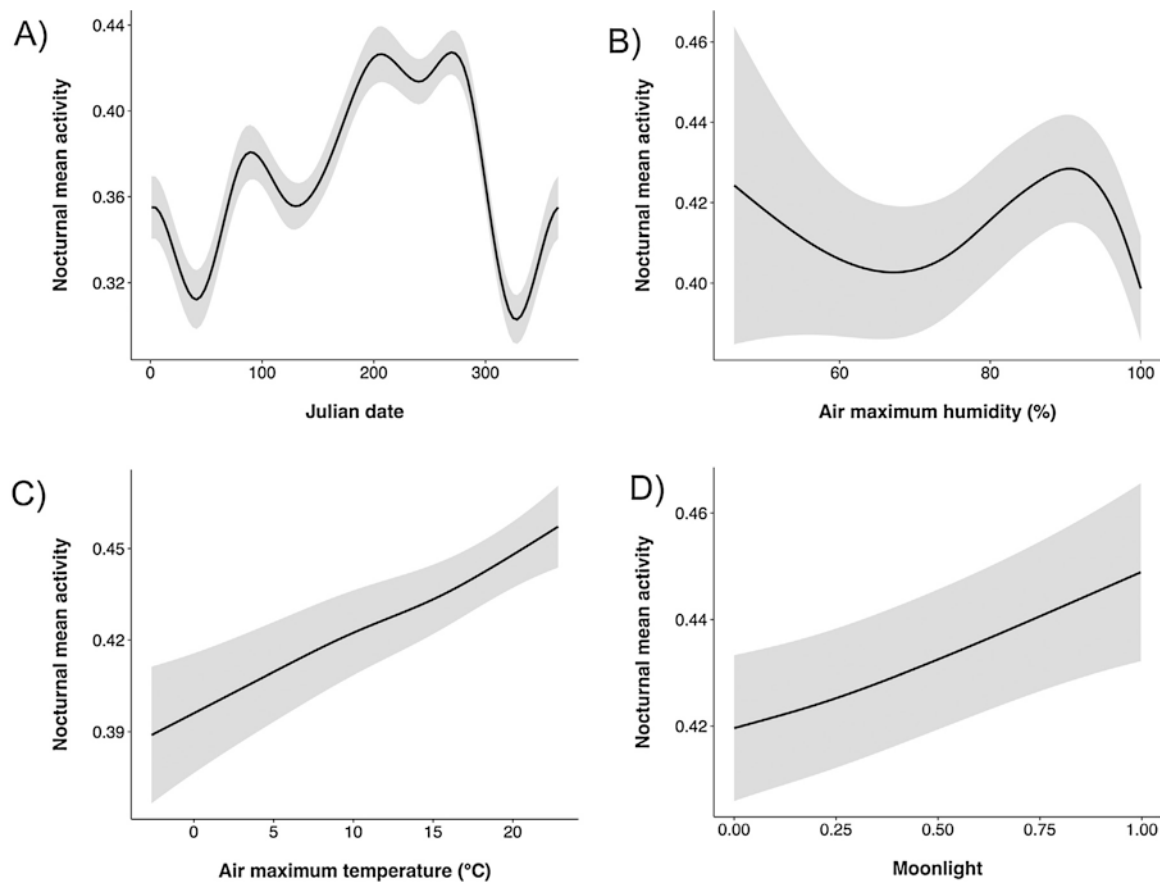


Fig. 3. Values predicted by the best Generalised Additive Model (see the text for more details) of wild boar nocturnal mean activity in the province of Arezzo (Italy). The figure shows the effects exerted by Julian date (A), air relative humidity (B), air maximum temperature (C) and moonlight (D). The predictions are given according to the mean of all other covariates in the model. In the graphs the colour-shaded areas are the estimated standard errors.

chamois (*Rupicapra rupicapra*, Carnevali et al., 2016), which can gain foraging benefits during bright nights by improving visual acuity. In the wild boar, olfaction is the most developed sense, while eyesight is generally thought to be very poor (Morelle et al., 2015). However, our findings, together with studies on the sensory capacities of pigs (Croney et al., 2003), suggested that visual capacity might support wild boar olfaction to some extent. Even so, unlike the majority of nocturnal mammals, the wild boar lacks the *tapetum lucidum*, i.e., a reflective structure enhancing retinal sensitivity under conditions of low luminosity (Acevedo et al., 2007; Ollivier et al., 2004). Such lack supports the hypothesis, already developed for other species (e.g., *Tarsius spectrum*: Gursky, 2003; *Rupicapra rupicapra*: Carnevali et al., 2016), that the wild boar may have originally been a diurnal species which shifted to nocturnal activity only at a later stage, though with no special eyesight adaptation to darkness. For a proper interpretation of our findings, it is important to note that we did not measure the actual illumination on the ground, but rather estimated moonlight luminosity by means of indirect measures (moon phase and cloud cover).

We provided evidence that brief, significant and unambiguous phase inversions from nocturnal to diurnal activity occurred for two females outside the hunting period (i.e., spring and summer). As they occurred in females only and considering that in the Southern part of the wild boar distribution range the birth period is not limited to few weeks (Canu et al., 2015), we conjectured that such inversions of activity were related to reproduction. Nevertheless, we detected this behaviour in two sows only. Interestingly, this dual behaviour was observed in different taxa such as fish and mammals (Hut et al., 2012; Reeb, 2002). Recent investigations showed

a temporal niche switching in nocturnal mice that became diurnal to reduce energy expenditure (Venne et al., 2014). Further studies on larger samples are needed to improve our knowledge of this phenotypic plasticity under natural conditions in such a large-size homeothermic ungulate as the wild boar, as well as to understand which proximate and ultimate factors may determine this phenomenon.

Our analysis showed that wild boars might adjust their diurnal and nocturnal activity in response to variations of such climatic factors as temperature, precipitation and air relative humidity. To the best of our knowledge, this is the first detailed study on the direct effect of weather conditions on wild boar activity levels. Our results suggested that the adjustment of activity levels may be an important behavioural means for wild boars to control their thermal balance. During daylight hours, when air temperature typically reaches the highest values, wild boars reduced their activity levels while temperature increased. However, the negative effect of temperature appeared to be thwarted by precipitation, since wild boars increased their diurnal activity on rainy days. Indeed, they were arguably able to reduce their body temperature by taking advantage of precipitation, as rain can enhance heat dissipation. Moreover, as rain makes the ground softer, rooting activity is strongly facilitated and this may be another factor accounting for the increase in their activity on the rainiest days. The reduction of activity levels in response to increasing air temperature is a strategy commonly used by animals to buffer themselves against overheating. This behavioural pattern was observed in several ungulates (e.g., Belovsky and Slade, 1986; Brivio et al., 2016; Shi et al., 2006), likely because behavioural thermoregulation might be less energetically

ically expensive than autonomic thermoregulation (Terrien et al., 2011). Our findings are consistent with previous studies on wild boar spatial behaviour which reported this species' search for shade, water and cool, moist forest areas under hot and dry climatic conditions (Howe et al., 1981; Dexter 1998). Our results and the abovementioned findings would corroborate the hypothesis that, being physiologically constrained by their lack of any thermoregulation system (i.e., lack of sweat glands, Allwin et al., 2016), wild boars may be particularly reliant on behavioural thermoregulation in their response to high temperature. In this framework, we may suppose that their nocturnal habits are a strategy to concentrate activities during the most favourable (i.e., cooler) hours of the day. In fact, we found that temperature had a different influence on wild boar activity at night, i.e., when the risk of overheating was reduced. Wild boars were more active as night temperature increased. This is likely due to the fact that in our study area air temperature never exceeded 20 °C at night.

Finally, our results also showed that diurnal activity increased with rising air relative humidity. Under humid conditions, wild boars may benefit from the increased efficiency of their olfactory organ (Lemel et al., 2003), which they use to find food as well as for orientation, social interactions and detection of predators (Morelle et al., 2015). Humidity facilitates the rooting behaviour typical of wild boars, which turn over the soil to search for bulbs, invertebrates and even small mammals while foraging (Bueno et al., 2009). The effect of air relative humidity was not evident on nocturnal activity, likely because air relative humidity was generally high at night during the data collection period (mean \pm std err = 91.92 \pm 0.23%).

Conclusions

In conclusion, by focusing on highly detailed data on activity levels we provided evidence of the predominantly nocturnal and monophasic activity of wild boars in a forest area with a temperate-continental climate. During daylight hours, the wild boars monitored had a reduced activity all year round, while diurnal activity opportunistically increased under the most favourable environmental conditions (i.e., low temperature and high humidity). In this respect, our findings confirmed the broad plasticity of this species, one which manages to adopt miscellaneous strategies to best exploit all the available resources. Hunting did not seem to directly influence the nocturnal habits of the population studied, though we hypothesised that wild boars may have evolved it over several decades of hunting harassment. Another hypothesis, one which does not exclude the previous one, is that nocturnal activity in the Southern regions may have evolved as a strategy to achieve an optimum thermal balance with low energy expenditures (i.e., behavioural thermoregulation). Studies on wild boar populations in different regions, where levels of human disturbance and climatic conditions are different, may be a helpful contribution to disentangle these hypotheses and fully understand the drivers associated with the evolution of wild boar activity rhythms.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2017.01.007>.

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