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Abstract: Over the last century, 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, their rapid increase in population and distribution has raised management concerns. Studies on activity rhythms may provide useful insights into the overall ecology of this species and may be helpful in developing effective management strategies. By taking advantage of highly detailed activity data collected by means of accelerometers fitted on GPS-collars, we studied wild boar daily activity rhythms and analysed the effect of environmental conditions on diurnal and nocturnal activity by fitting Generalised Additive Models. We provided evidence for the strictly nocturnal and monophasic activity of wild boars. All year round we also assessed a reduced diurnal activity, which opportunistically increased under the most favourable environmental conditions. Activity was 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 the nocturnal habits of this species are not directly influenced by the current hunting disturbance, though we hypothesised that wild boars may have evolved it 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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The Editor, Mammalian Biology

Dear Sir/Madam,

We submit herewith our new research article, entitled *"An analysis of intrinsic and extrinsic factors affecting the activity of a nocturnal species: the wild boar"*.

In this study we investigated the effects of ecological factors on wild boar (*Sus scrofa*) in the Apennine Mountains in the Central of Italy. This is the first detailed field study on chronobiology of wild boar which analysed high-resolution long-term activity data. The studies on chronobiology generally analyse the effect of the light or of endogenous variables and they are mainly conducted with manipulated animals in laboratories. Instead, thanks to the new technologies (i.e., collars with accelerometers), we studied the activity rhythms of wild animals in relation to environmental conditions and to hunting disturbance. Studies on activity rhythms may provide useful insights into the overall ecology of this species and may be helpful in developing effective management strategies.

We believe that our novel findings, which provide important advances in the knowledge on wild boar behavioural ecology, make this article a worthy *Mammalian Biology* paper. We look forward to hearing from you.

On behalf of the authors, yours faithfully,

Stefano Grignolio

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, 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, their rapid increase in population and distribution has raised management concerns. Studies on activity rhythms may provide useful insights into the overall ecology of this species and may be helpful in developing effective management strategies. By taking advantage of highly detailed activity data collected by means of accelerometers fitted on GPS-collars, we studied wild boar daily activity rhythms and analysed the effect of environmental conditions on diurnal and nocturnal activity by fitting Generalised Additive Models. We provided evidence for the strictly nocturnal and monophasic activity of wild boars. All year round we also assessed a reduced diurnal activity, which opportunistically increased under the most favourable environmental conditions. Activity was 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 the nocturnal habits of this species are not directly influenced by the current hunting disturbance, though we hypothesised that wild boars may have evolved it 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).

Key words: Activity rhythms, hunting disturbance, nocturnal activity, moonlight, *Sus scrofa*

Introduction

Nowadays, 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. On the other hand, it is one of the most attractive and valued game species (Apollonio et al., 2010).

In the last decades, considerable human and economic resources have been directed at understanding how to improve wild boar management strategies. The rapid increase in its population and distribution is thought to be responsible for economic problems in many parts of Europe (e.g., Bruinderink and Hazebroek, 1996; Gortázar et al., 2007; Labudzki and Wlazełko, 1991). Wild boar can cause enormous damage to human activities, such as agriculture, and it can be responsible for numerous road traffic accidents (Amici et al., 2011; Ballari and Barrios-García, 2014; Lagos et al., 2012). Furthermore, it can act as a vector for disease transmission and zoonosis (Costard et al., 2009; Gortázar et al., 2007). This species is also expected to have a significantly negative impact on natural ecosystems because of its ground rooting habit, which affects plant species richness and, consequently, biodiversity (Bruinderink and Hazebroek, 1996; Bueno et al., 2009; Hone, 2002). For these reasons, a strong public and governmental interest in identifying practical approaches that may help reduce wild boar negative effects or ameliorate 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 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 initiative of setting a EUROBOAR network (http://euroboar.org). These studies agree that wild boar is characterised by a great phenotypic and behavioural plasticity (e.g., Ballari and Barrios-García, 2014; Podgórski et al., 2013), which leads to the particularly high adaptability of this species. 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 multiple behaviours 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 their environment. Activity patterns rely on endogenously fixed rhythms which have been called "circadian" or "circannual". Circadian and 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).

Several studies have demonstrated that weather conditions can influence animals' activity patterns and such influence can be either direct, i.e., through day-to-day changes in weather, or indirect, i.e., through the seasonal effects of climate on environmental conditions, particularly on food availability (Olson and Wallander, 2002; Owen-Smith, 1998; Roberts and Dunbar, 1991; Shi et al., 2006). Direct effects are visible on a small time scale (daily or weekly), while indirect ones can be observed on a monthly or seasonal scale (Brivio et al., 2016; Rivrud et al., 2010).

Although wild boar activity patterns were described by many authors (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), a clear consensus among them is still lacking. Most studies agree that wild boar is nocturnal (Cahill et al., 2003; Caley, 1997; Keuling et al., 2008; Russo et al., 1997; Saunders and Kay, 1991), but it was also suggested that diurnal activity should increase when animals are exposed to minor, short-term anthropic disturbance (Keuling et al., 2008; Kurz and Marchinton, 1972; Ohashi et al., 2013; Podgórski et al., 2013). Moreover, activity rhythm was reported to be monophasic, biphasic or polyphasic with high intraspecific variability (Caley, 1997; Cousse et al., 1995; Keuling et al., 2008; Russo et al., 1997).

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), suggesting the strong influence of weather conditions on their activity rhythms. Thurfjell et al. (2014) used speed of movement as a proxy of activity and showed that wild boars reduce their activity in response to suboptimal weather conditions. However, wild boar often showed on-site activity, resulting in a nonsignificant 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 the activity levels of wild boar.

By taking advantage of highly detailed information on activity levels of wild animals obtained by means of GPS-collars equipped with accelerometers, we studied wild boar circadian and circannual activity rhythms with a chronobiological approach. Moreover, we investigated the effect of environmental conditions on their year-round total activity levels, focusing our attention on the influence of weather conditions and, for nocturnal activity, of moonlight. Indeed, it has been shown that light changes during the lunar cycle can affect rhythms in organisms. Thus, moonlight can represent a time cue, acting as a synchroniser for reproduction; it can change the ability of animals to use visual cues, affecting the use of senses (e.g. 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).

Hunting pressure has been shown to influence significantly wild boar activity patterns (Keuling et al., 2008; Russo et al., 1997), thus suggesting that diurnal activity should increase when they are exposed to minor hunting pressure. In the light of this finding, part of our analyses focused on the hunting period thus investigating whether wild boars modify their total activity levels during the day and the night in response to hunting disturbance.

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 km^2, including an unfenced protected area of 27 km^2 (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 4.74 °C in January to 21.95 °C in July, while precipitation levels have a monthly average varying from 34.2 mm in June to 214.3 mm in November. Snowfalls are occasional and usually start in October and may continue through April. Wild boar and roe deer (*Capreoulus capreolus*) are the most abundant ungulate species, but red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) have been observed as well. 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 (Mattioli et al., 2011). Outside the protected area, wild boar hunting is performed with drive hunts involving tens of dogs and 25-50 hunters and allowed to harvest an average of 9.6 boars/100 ha. Hunting is permitted on Wednesdays, Saturdays and Sundays from about mid-September to early January.

Data collection

Activity data - In the period 2013 - 2015, a total of 9 adult wild boars (5 females and 4 males) was captured by using vertical drop nets and traps baited with maize. Once captured and immobilised, wild boars were sedated by using Zoletil®, with a dose of 0,5 ml/10Kg. 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 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. The accelerometer on the X-axis was sensitive to acceleration with forward/backward direction, while the Y-axis had a sideward and rotary direction. On each axis, activity was calculated as the difference between consecutive acceleration values, averaged over a time interval of 4 minutes and given within a relative range between 0 (no activity) and 255 (-2G/+2G: maximum activity). Activity data were then recorded with the date and time associated in the collar memory. The activity data recorded were downloaded by means of a Vectronic Handheld Terminal and a Yagi antenna. A total of 763,920 activity records were acquired during a total of 2,122 monitoring days. As activity values measured on X and Y axes resulted to be highly correlated, we only analysed X activity data.

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 over the entire atmosphere 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 AM 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 AM. 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. Positive ψ indicated that the activity onset anticipated the onset civil twilight. The daily acrophase of the activity rhythm for each wild boar was also calculated by using ActogramJ and the average acrophase for each period was determined by vector addition. Rayleigh test was performed to test whether the acrophases deviated from uniform ($p<0.05$). 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 values of activity rate (AR) on a relative scale from 0 to 1, where 0 means no activity and 1 maximum activity. Then, for each wild boar, all AR values were split into diurnal and nocturnal subset by comparing the date and time recorded with the sunrise and sunset times: the AR recorded in the range between the sunrise of the day_i and the sunset of the day_i were assigned to the subset of diurnal activity of the day_i, while those recorded after sunset of the day_i and prior to sunrise of the day_{i+1} were assigned to the subset of nocturnal activity of the day_i. After splitting activity data into the two subsets, we defined the Diurnal Mean Activity (DMA) and the Nocturnal Mean Activity (NMA), calculated as the average of the AR values recorded during each day and each night, respectively. Likewise, we calculated the diurnal and nocturnal mean for each meteorological parameter (i.e., minimum, mean and maximum temperature; maximum and mean solar radiation; minimum, mean and maximum relative humidity and rain intensity): we assigned each hourly value to a day or a night according to the time recorded 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 the day_i – (moon phase of the day_i * cloud cover at midnight of the day_i).

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 identify the pattern of variation of both DMA and NMA throughout the year, we included the Julian date as a continuous variable in the models. Finally, to evaluate the effect of hunting, we included a dummy variable, scored 1 for the days of the hunting season and 0 for the days outside the hunting season. 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. For both DMA and NMA, we chose the best predictor out of the collinear variables by carrying out a pre-selection by means of 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.

All the predictor variables chosen were used to build a GAM (full model) in which the effects of all continuous variables, except 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: in so doing, 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 corrected values of Akaike's information criterion (AICc, Richards et al., 2011). A value of DAICc= 4 was chosen as a threshold for the selection of the best models (Burnham et al., 2011). To avoid retention of overly complex models (i.e., models having additional parameters that result in a minimal increase of fit), we excluded models that simply constituted more complex versions of those with a lower AIC value (Richards et al., 2011). The goodness of fit of the best model (homoscedasticity, normality of errors and independence) was checked by visual inspection of residuals (Zuur et al., 2009).

Finally, in order to test whether wild boar modify their diurnal and nocturnal activity in response to hunting disturbance, we analysed DMA and NMA separately, from the beginning to the end of the hunting season (September - early January; see Grignolio et al., 2011 for more details) 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 (1 September, year x) to 137 (15 January, year x + 1), in order to account for both the discontinuity between 15 January and 1 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 (representative examples in Fig. 1 and Supplementary material A Fig. A1). The activity pattern was unimodal and mainly nocturnal. A crepuscular activity was reported at sunset in all seasons and onsets of activities were reported ahead of civil dusk. Interestingly, the anticipation of the onsets significantly changed during the year (K_4=116, $p<0.0001$; Kruskall-Wallis One-way ANOVA), with the highest values recorded in summer (3,57±2,14 h, mean±sd, Dunn's Multiple Comparison Test, $p<0.001$; Supplementary material A Fig. A2). Furthermore, the twilight activity at sunset was showed only in spring and summer (Fig. 1; Supplementary material A Fig. A1).

Two of the 5 females showed an inversion of activity pattern and switched from nocturnal to diurnal in late spring (Supplementary material A Fig. A1 F) and in late summer (Fig. 1H). To ascertain the statistical significance of this phenomenon we calculated the daily acrophases prior to, during and after the inversion (Fig. 2; Supplementary material A Fig. A3). Subsequently, by using a circular statistic approach, we showed that the distribution of acrophases deviated from uniform in all periods (Fig 2B-D and F-H; Supplementary material A Fig. A3 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 wild boars (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 1,110 days/wild boar for females and a total of 1,019 days/wild boar for males were obtained during the period of data collection. Wild boar NMA (0.311 ± 0.120) was higher than their 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 mean temperature and precipitation as predictor variables (R-sq. = 0.327). Throughout the year, a single peak of DMA was recorded around the 170th day of the year (19th June), while minimum values were recorded around the 70th and the 340th day of the year (11th March and 6th December, respectively, Fig. 3A). Wild boar DMA had a positive relation with air maximum humidity (Fig. 3B). The effect of the interaction between mean temperature and precipitation on DMA is shown in Fig. 3C. The maximum activity values were reported in conditions of high temperature and precipitation, while minimum values in conditions of high temperature and low precipitation. On the other hand, on cold days wild boars resulted to be more active with intermediate precipitation levels (about 20 mm/day) and less active with higher precipitation levels.

The best model for NMA included Julian date, maximum humidity, maximum temperature and moonlight (R-sq. = 0.292) as predictor variables. Analyses showed a non-linear relationship between wild boar NMA and the Julian date, with the lowest activity values recorded around the 40th and the 320th day of the year (9th February and 16th November, respectively) and maximum values around the 210th and the 270th day of the year (29th July and 27th September, respectively). Moreover, an irregular pattern between the maximum and the minimum peaks was observed (Fig. 4A). The relation between NMA and maximum humidity followed a non-linear pattern characterized by a wide confidence interval, thus making this result hard to be understood (Fig. 4B). During the night, wild boar activity was positively related to maximum temperature (Fig. 4C). Finally, a weak influence of moonlight was observed, with wild boars being slightly more active when the available moonlight was more intense (Fig. 4D).

Hunting period models – By restricting analyses to the hunting period, we obtained 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 compared to the full-year models (see Supplementary material B for more details).

Discussion

Our study on wild boar activity rhythms showed that these animals are nocturnal, with a marked daily rhythmicity in the total activity throughout the year. Unlike other ungulate species (e.g., Aschoff, 1966; Brivio et al., 2016; Pagon et al., 2013), the pattern of activity that we found was not bimodal. It appeared to be continuous during the whole night, with an acrophase during the first hours (between 21:36 and 23:18). A crepuscular activity was present throughout the year and the onset of activity always anticipated the civil dusk. These anticipations significantly changed during the year and reached the highest values in summer (3.57 ± 2.14 h). Unlike those found in other ungulates (Ensing et al., 2014), our results strongly suggested that the beginning of daily activity prior to dawn is driven by an internal circadian timing mechanism. Conversely, the changes in the length of anticipation during the year may reflect a response to the seasonal change in light intensity at dawn. Throughout the year wild boar diurnal activity was low and reached the maximum levels around the summer solstice, when nights are possibly too short for the achievement of all their energy requirements.

NMA resulted to be about 5 times higher than DMA, confirming the strictly nocturnal habits of this species. 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 subjected to intense hunting pressure (Briedermann, 1971; Hennig, 1998). Our dataset was collected in an area where wild boar culling is intensive. Nevertheless, our results suggested that the nocturnal habits of the population monitored were not driven by hunting disturbance. Indeed, we found no influence of hunting on activity either during night or daylight hours. Although in our study area hunting was concentrated in only 4 months (from September to early January) and the activity showed a large variation during the annual cycle (Fig. 3A, 4A), nocturnal activity was evident and predominant throughout the year. We may suppose that wild boar nocturnal habits are not caused by the current hunting disturbance, but rather amount to the legacy of the hunting harassment that this population suffered for decades after its reintroduction during the 1970s.

The pronounced wild boar nocturnal activity makes this species a good case study to evaluate the effect of moonlight on activity patterns. It has been shown that moonlight provides diverse animal species (from invertebrates to large mammals) with information which they can turn into cues for the regulation of their activity patterns (Kronfeld-Schor et al., 2013). One of the most studied effects of moonlight on animal activity is that on foraging and predation (reviewed in Kronfeld-Schor et al., 2013). By modifying the environmental light conditions, moonlight may affect the visual detection of food items, including preys. As a consequence, it may even influence the level of predation risk. Our analyses showed that moonlight had an effect on wild boars, with slightly increased activity levels during the brightest nights. The higher activity levels during the brightest nights contradict the expected response to predation risk from wolf, which typically improves its hunting success during moonlit nights (Theuerkauf et al., 2003). On the one hand, the effect of moonlight on the increased activity of wild boars may result from their improved ability to visually detect predators, as suggested for other nocturnal mammals (Prugh and Golden, 2014). On the other hand, it may result from a better visual detection of food and the increase in their prey activity. Indeed, in balancing conflicting demands of food and safety, animals must also take into consideration possible changes in food detection and availability (Kronfeld-Schor et al., 2013). However, it is important to note that in our analyses night illumination was not reported to influence nocturnal activity substantially. This finding suggested that wild boars might be sensitive to other cues associated with predation risk and food search. For instance, olfaction may play an important role by strongly supporting the visual detection of predators and food items. Indeed, wild boar was shown to be highly sensitive to olfactory stimuli and olfactory receptors are used in navigation, foraging, social interactions and vigilance (Morelle et al., 2015).

We found only few exceptions to the nocturnal habits of the animals studied: in particular, brief reversals of activity from night to daylight were reported for two females outside the hunting period (i.e., spring and summer), likely linked to some intrinsic factors that we were not able to determine. We provided evidence that these inversions of activity rhythms were statistically significant and unambiguous. As they occurred only in females 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. Consequently, new studies on larger samples are needed to figure out the reasons of this behavioural pattern.

Our analysis showed that wild boars adjusted 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 suggest that the adjustment of activity levels may be an important behavioural means for these animals to control their thermal balance. In accordance with previous knowledge on the reduction of movement rate associated with cold weather (Thurfjell et al. 2014), we found that wild boars reduced their activity with low temperature during both daylight and nocturnal hours. During daylight hours such effect of temperature was exacerbated by precipitation, as the minimum activity values were found with low temperatures and high precipitation levels. This result may be due to the mixed effect of rain precipitation and cold weather, which enhances the decline of animal body temperature (Parker, 1988). As suggested by Thurfjell et al. (2014) for wild boar and by Brivio et al. (2016) for Alpine chamois (*Rupicapra rupicapra*), the reduced activity under cold weather conditions may be an attempt to preserve energy and lower the costs of thermoregulation by preventing heat loss. On the other hand, a reduction of activity may be observed also when temperature overtakes the species' thermoneutral zone, as a strategy used by animals to buffer themselves against overheating. This behavioural pattern has been observed in several ungulate species (e.g., Belovsky and Slade, 1986) and our analyses detected it in wild boars as well. During daylight hours, when the maximum air temperatures were reached, wild boars reduced their activity with increasing temperature. However, the negative effect of temperature appeared thwarted by precipitation: wild boars increased their diurnal activity during warmer but rainy days. They were likely 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 help explain the increase in activity during the rainiest days. 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, together with the above mentioned findings, corroborate the hypothesis that, being physiologically constrained by their lack of a thermoregulation system (i.e., absence 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 can 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 showed that wild boars increased their diurnal activity 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 not only to find food, but also for orientation, social interactions and detection of predators (Morelle et al. 2014). Moreover, humidity may facilitate 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 throughout the period of data collection (mean ± std err= 91.92±0.23 %).

Conclusions

In conclusion, by focusing on highly detailed data on activity levels we provided evidence for the strictly nocturnal and monophasic activity of wild boars. During daylight hours, wild boars had a reduced activity all year round, but diurnal activity opportunistically increased under the most favourable environmental conditions (i.e., perceived temperature and 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. Our results suggested that hunting does not directly influence the nocturnal habits of this species, 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 populations at different latitudes, where levels of human disturbance and temperature are different, may be a helpful contribution to disentangle these hypotheses.

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Figure captions

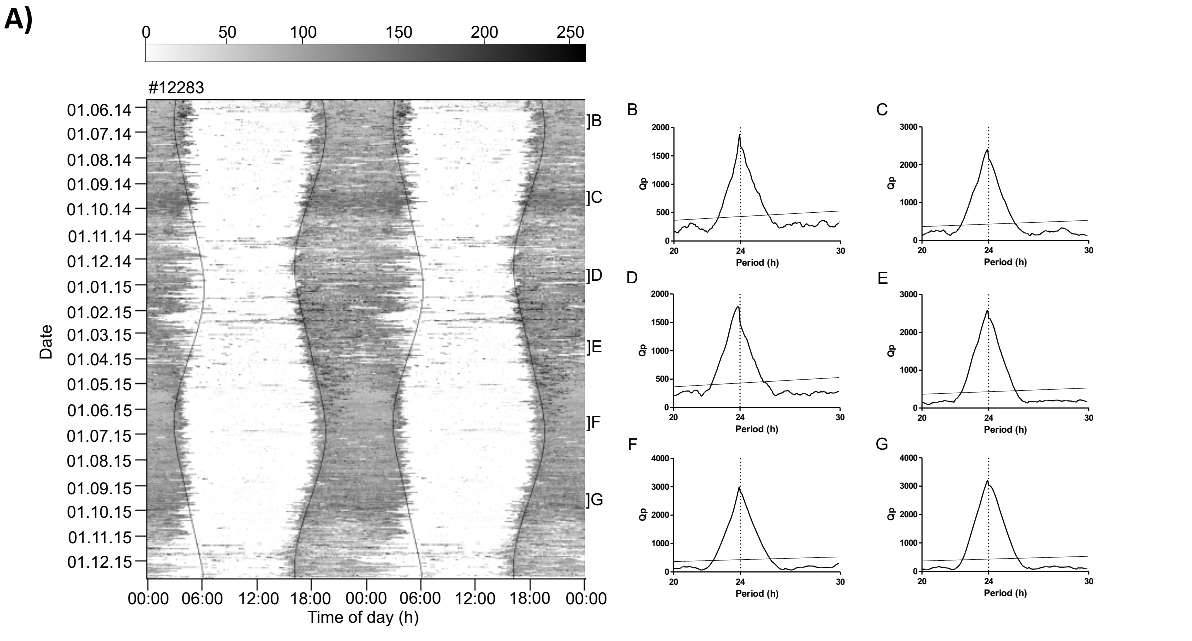
Fig. 1 Representative actograms of daily activity of A) one radio-collared male wild boar (#12283) and H) one radio-collared female wild boar (#12292) in the province of Arezzo (Italy). Vertical bars represent their activity levels (over intervals of 5 minutes), the colour of the bar being a function 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-hour time scale to help the interpretation. B-G and I-M delimit 10 day intervals of activity in 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 over the period tested within a range of 20–30 hours. The sloped dotted lines represent the threshold of significance, set at $p = 0.05$.

Fig. 2. A, E. Extracts of a representative actogram of daily activity of one radio-collared female wild boar (#12292; see Fig. 1H) in the province of Arezzo (Italy), showing the switch from noctunal to diurnal patterns and *viceversa* during the summers of 2013 and 2014. Records are double plotted on a 48-hours time scale to help the interpretation. Red dots on the actograms mark daily acrophases. B-D, F-H. Circular representations of daily acrophases of wild boar activities. Dots represent daily acrophases and arrows indicate the average acrophases represented as vector. The circle inside each panel represents critical values of Rayleigh test ($p<0.05$).

Fig. 3 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 of 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.

Fig. 4 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 of 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.

Figure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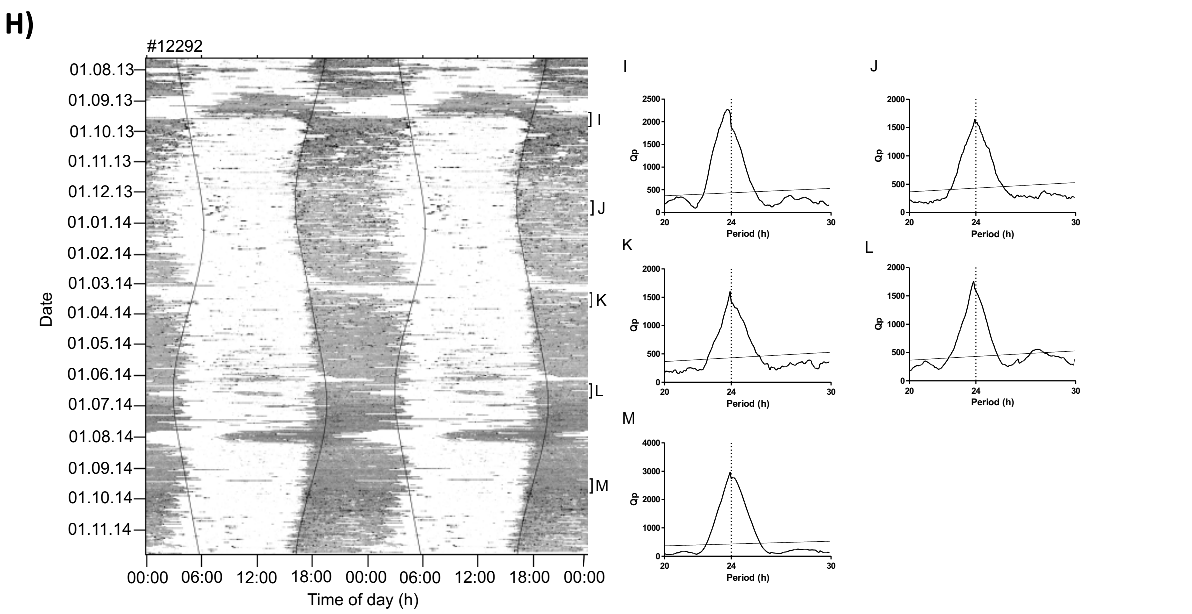
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Figure

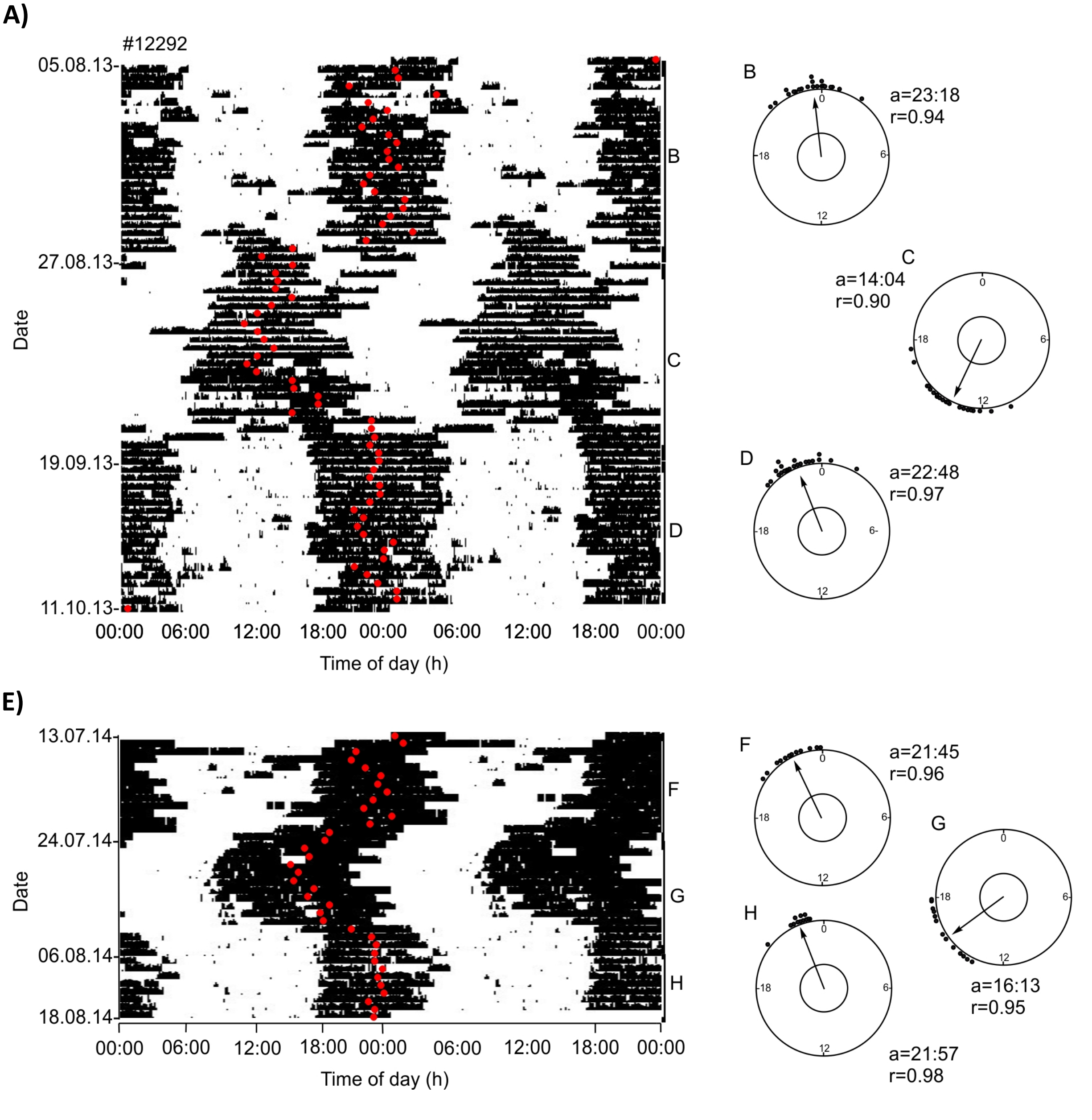
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Figure
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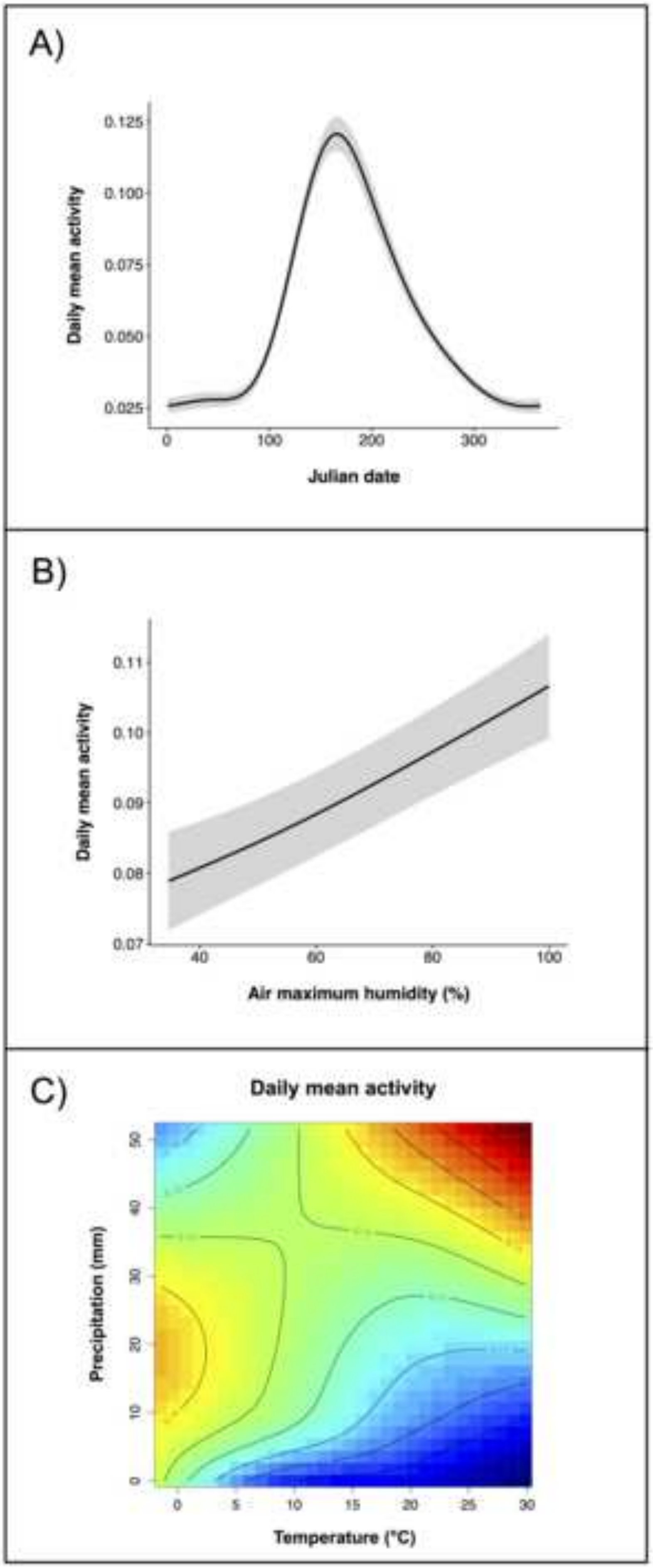

Figure
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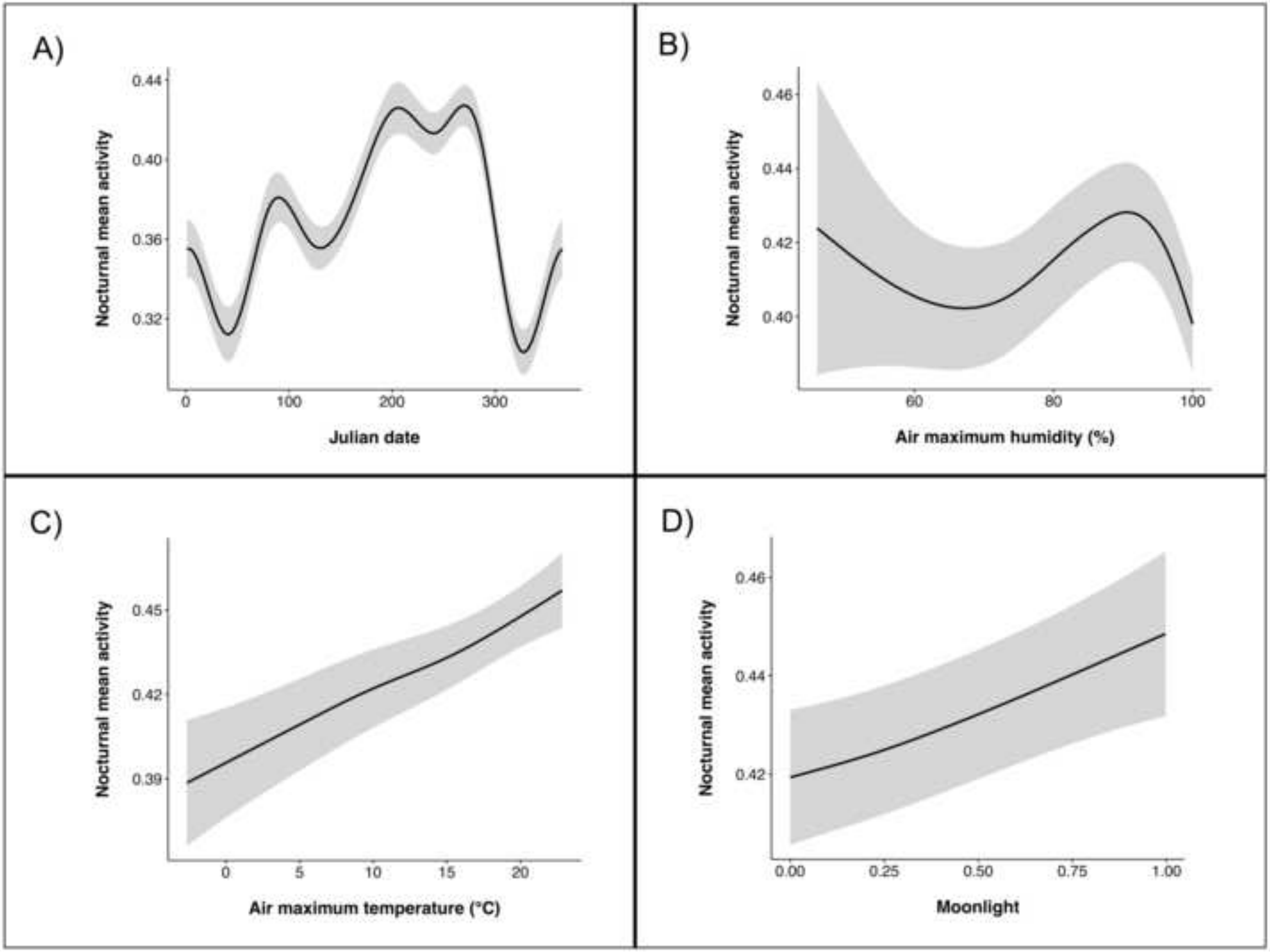

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