ORIGINAL ARTICLE



Spatio-temporal patterns of the European wildcat in a Mediterranean coastal area

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Received: 21 January 2022 / Accepted: 26 September 2022 © The Author(s) 2022

Abstract

Like most small felids, the European wildcat *Felis silvestris* is a rather elusive species, poorly detectable in the wild, due to several aspects of its biology. Camera trapping can represent a suitable tool to understand temporal activity patterns and habitat preferences of such elusive species. We used intensive camera trapping over two full years to investigate spatio-temporal patterns of the wildcat in a Mediterranean coastal protected area (Maremma Regional Park, central Italy). At the seasonal scale, the wildcat showed a marked twilight activity in summer and winter (mating period), and nocturnal activity in autumn. Conversely, a peak of activity during the day, i.e., in broad daylight, was reported in spring. Reproductive females may limit their nocturnal movements in spring to increase protection from predators to their kittens at the den, although further data are required to support this conclusion. At seasonal, semestral, and yearly temporal scales, the frequency of wildcat detections increased along with availability of shrubwood. These results emphasise the importance for this small felid of areas with dense vegetation cover (Mediterranean maquis and shrubwood, in our study area). Areas densely covered with shrubby vegetation are expected to provide benefits to this elusive small cat in terms of reduced human disturbance (included tourists), availability of prey (e.g., small mammals), as well as shelter, essential to ensure protection towards potential larger predators.

Keywords Felis silvestris · Mesocarnivores · Temporal activity patterns · Felids

Introduction

Understanding temporal activity patterns and habitat preferences of wild living species are crucial steps in identifying their ecological requirements (Linck et al. 2021), offering important implications for the conservation of elusive and rare species (Gese 2001; Nichols et al. 2011). Assessing basic aspects of behaviour and ecology of these species is a challenging task, and camera trapping is an increasingly adopted tool to meet this goal (Caravaggi et al. 2017).

Handling editor: Rebecca Ray.

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However, the management of camera trapping data over long periods can be time-consuming. Most studies are based on short term surveys (i.e., month or season), especially suitable to meet assumptions of population closure for occupancy/ abundance estimates within monitoring programmes (Rovero and Zimmermann 2016). However, animal behaviour can vary seasonally along with environmental (e.g., seasonality of climate and food resources) and endogenous (e.g., reproduction and relevant constraints) factors (e.g., Theuerkauf et al. 2003; Morellet et al. 2013; Pagon et al. 2013), leading to activity and habitat use. Thus, an assessment of spatiotemporal patterns covering the entire annual cycle would provide a wider information, representative of variations in behaviour throughout the year.

Like most small felids, the European wildcat *Felis silvestris* is a rather elusive species, poorly detectable in the wild due to several aspects of its biology, such as low population densities, preference for habitats providing dense cover, and its mainly crepuscular or nocturnal activity (Sunquist and Sunquist 2002; Kilshaw et al. 2015; Anile et al. 2021; Migli et al. 2021). Given the wide range of altitudinal, climatic and environmental conditions of the areas supporting different wildcat populations in Europe (Yamaguchi et al. 2015), local differences in the way the European wildcat interacts with the environment are likely to occur. Acquiring knowledge on basic aspects of its ecology and behaviour in specific contexts is hence of paramount importance to identify possible local threats and to set up proper conservation measures.

The European wildcat is a species of conservation interest, classified as a "particularly protected" in Italy and included in Appendix II of CITES, in Appendix II of the Berne Convention and in Annex IV of Directive 92/43/EEC "Habitats" Directive. Despite its currently wide distribution, ranging from Scotland in the North (although with extensive genetic admixture with domestic cat; Senn et al. 2018) to South-Eastern Europe, including some Mediterranean islands, it was once much widespread throughout Europe. Several populations underwent a drastic decline during the nineteenth century, mainly caused by direct persecution and habitat loss (Schauenberg 1970; Nowell and Jackson 1996). In Italy, this species has been protected by national law since 1977. In recent times it has slowly recolonised portions of its former distribution range and, more recently, it successfully colonised portions of the central-Northern Apennines that were not part of its known historical range (Ragni et al. 1993). Although recent research has been carried out on wildcat populations living in Mediterranean habitats (Monterroso et al. 2009; Lozano 2010; Migli et al. 2021), little information from studies conducted over more than 1 year is currently available for this biogeographic area. To contribute to fill this gap we used intensive long-term camera trapping in a Mediterranean protected area, to assess: (i) temporal activity patterns and (ii) habitat associations of wildcats in different seasons. Based on information on behaviour and ecology of this small carnivore, we predicted that wildcat showed (i) nocturnal activity patterns all the seasons (Migli et al. 2021; Lazzeri et al. 2022), and (ii) a positive association with wooded habitats (Monterroso et al. 2009; Lozano 2010; Migli et al. 2021).

Methods

Study area

Our study was conducted in the Maremma Regional Park, (central Italy, *c*. 90 km²; 42.626371°N, 11.099303°E). The local climate is Mediterranean, with hot-dry summers, mean daily temperature ranging from 9 °C (January) to 24 °C (August), and monthly rainfall ranging from 9.3 mm (July) to 81.8 mm (November). Mediterranean sclerophyllic scrubwood dominates the area (58% of extent), of three main wood types: oakwood (mainly holm oak *Quercus ilex* trees with a height > 7 m); shrubwood (holm oak and other trees, mainly strawberry tree *Arbutus unedo*, with a

height <7 m); garrigue (a shrubwood with bushes including holm oak, rosemary *Rosmarinus officinalis*, juniper *Juniperus* spp., rockrose *Cistus* spp., Mencagli and Stefanini 2008; Sforzi et al. 2013; Melini et al. 2019). Other habitats include the pinewood (10%, with *Pinus pinea* and *P. pinaster*), abandoned olive groves, meadows and pastures (15%), set-aside grassland (4%) and crops (12%, mainly cereals and sunflower).

The wolf Canis lupus is the apex predator in the area (Ferretti et al. 2019). Three species of ungulates are present, i.e., the fallow deer Dama dama, the wild boar Sus scrofa, and the roe deer Capreolus capreolus, as well as many medium-sized mammals (i.e., the crested porcupine Hystrix cristata, the coypu Myocastor coypus, the European brown hare Lepus europaeus, the red fox Vulpes vulpes, the European badger Meles meles, the wildcat, the stone marten Martes foina, the pine marten Martes martes), and various species of smaller mammals. Livestock is also present, including mainly cattle, sheep and horses. Population control of wild boar (through trapping and culling) and fallow deer (culling) is implemented by the Maremma Regional Park Agency to limit the negative impacts of these ungulates on habitats, species with conservation relevance and agriculture (Fattorini and Ferretti 2020; Ferretti and Fattorini 2020).

Data collection

Data were collected through camera trapping (Ferretti et al. 2021; Rossa et al. 2021, for our study area), in two study periods. The study was primarily designed to evaluate activity patterns and spatial relationships among species of medium-sized and large mammals (Ferretti et al. 2021; Rossa et al. 2021). During a first study period (October 2017–September 2018), a study area of c. 30 km² was defined including the northern part of the Uccellina hills, the pinewood and part of meadows and marshland (Fig. 1). Twenty-one locations were identified through a sampling grid (cell size: 1.3×1.3 km; 1 location per grid cell: Rossa et al. 2021) that was superimposed to the study area through a Geographic Information System (GIS) (Li et al. 2012; Bu et al. 2016). On October 2017, 7 cameras were put along animal trails or forest roads. Cameras were subsequently rotated to other 7 locations monthly, to monitor all 21 locations for at least c. 1 month/season ("autumn": October–December; "winter": January-March; "spring": April-June; "summer": July-September), i.e., each location was monitored c. 4 months throughout the study (Rossa et al. 2021). About 52% locations occurred in oakwood/shrubwood (n = 11) and 24% locations occurred in the pinewood and in ecotonal/ open habitats (i.e., 5 locations in each habitat), reflecting habitat proportion in the study area. During a second study period (April 2019-March 2020), a larger study area was defined, encompassing Uccellina hills, Pinewood and plain



Fig. 1 Camera trapping locations monitored in April 2019–March 2020 (Period 2, red stars) and borders of the study area monitored also in October 2017–September 2018 (Period 1, see text). The red line indicates the borders of the Maremma Regional Park

pastures and marshland of the Trappola area (c. 60 km^2 ; Fig. 1). Fifty-seven locations were identified in a grid (cell size: 1 × 1 km: 1 location per cell); 19 cameras were rotated on a monthly basis to monitor each location c. 1 month per season and c. 4 months per year, as in the first study period. About 61% locations occurred in oakwood/shrubwood (n=35), 23% locations occurred in ecotonal/open habitats (n=13), and 16% locations (n=9) occurred in the pinewood, generally reflecting habitat proportion in the study area. We used cameras triggered by an infrared motion sensor (first period: IR-Plus HD-2; second period: IR-Plus HD-2, up to n = 13; Scout Guard, up to n = 8). The cameras were supplied with 16 GB SD cards and external batteries and set to operate continuously (i.e., 24 h per day) to record videos of 30 s; trigger time was ≤ 1 s. The cameras were inspected every c. 2 weeks to replace batteries and memory cards and relocated every 4 weeks.

The reliability of European wildcat identification made on pelage characteristics should be carefully evaluated (Sforzi 2021). The similarity of the coat colour and pattern of the wild phenotype to those of some domestic (tabby) cats or their hybrids is in fact a matter of concern, affecting the process of data verification. Seasonal variation also occurs, especially in Mediterranean habitats, where the summer coat tends to be much shorter, sometimes affecting the (slenderer) body shape. Extension and disposition of black and grey stripes on the coat have a specific diagnostic value, showing a clear ontogeny and age-evolution. In the early stages of life, the fur of kittens shows a marked spotted pattern that then evolves into the final one. Some parts of the drawings (evanescent) tend to disappear almost completely, while others (permanent) characterize the coat-color pattern typical of the adult individuals. The objectively complex identification of the species imposes the adoption of selective criteria to identify wildcats in the field. All videos were hence carefully evaluated and verified considering several aspects, described below. Data (date, time of day-solar time-, location, individual classification, minimum number of individuals, notes) were recorded in Excel sheets. Wildcat identification was performed on a morphological basis, according to the typical phenotypic characteristics that define the subspecies (Ragni and Possenti 1996). Since identifications were made on videos recorded in different field conditions, several aspects were considered to potentially infer the verification procedure: camera trap placement (height, orientation, field of view), distance of the subject from the camera, movement of the subject in relation to the camera, light conditions, season, behaviour. Videos where diagnostic characters of individuals were impossible or very difficult to detect were filtered out. Verification through visual analyses of morphological features were hence carried out only on videos, where individuals showed a clearly detectable coat marking system. For recordings filmed in daylight, colour provided additional clues useful to refine the identification.

Data analyses—temporal patterns

Temporal activity patterns were estimated through Kernel density estimation (Ridout and Linkie 2009), i.e., through density functions related to time as continuous and circular. Graphically, the area under the function corresponds to the probability of observing individuals throughout the 24 h (Foster et al. 2013; Bu et al. 2016). The homogeneity of activity patterns was assessed through the Watson's test of homogeneity (Lund et al. 2017). To limit pseudoreplication, when the same camera trap took more than 1 wildcat video in less than 30 min, we counted them as 1 event (hereafter "detection"; Tobler et al. 2008; Lucherini et al. 2009; Torretta et al. 2016; de Satgé et al. 2017). For all estimates of temporal activity, we also estimated 0.95 confidence intervals through a simple random sampling with replacement based on 1000 bootstraps (Mori et al. 2020; Ferretti et al. 2021; Rossa et al. 2021). All the analyses were conducted at three temporal scales, i.e., considering the full data set, at the 6 months ("warm" period: spring-summer; "cold" period: autumn-winter) and at the seasonal temporal scales. All the statistical analyses were performed through the R software (RStudio Team 2020), version 3.6.2, using the "circular" and "overlap" packages (Lund et al. 2017; Meredith and Ridout 2017).

Data analyses—spatial patterns

We evaluated habitat features influencing the frequency of wildcat detections. We considered three temporal (i.e., season; 6 months; year) scales and the percentage of habitat in a circular buffer around the camera. As radius of the buffer, we considered the half of the minimum distance between neighbour cameras, to avoid overlap between contiguous buffers, thus avoiding that habitat information be replicated between observations conducted in different locations (first period: 307 m radius; second period: 219 m radius). For each location, the percentage of different habitats in the buffer was assessed through QGIS software, version 3.10.13, using geoprocessing tools to the land use map of our study area (Mencagli and Stefanini 2008) based on buffers previously obtained. We considered 4 habitat types: oakwood; shrubwood (including also garrigue); pinewood; ecotone and open meadows. Other habitats are present in the area (e.g., cultivated fields, marshland), but they occurred with negligible extent in the buffers (mean percentage cover: 2.8% for cultivated fields; 3.6% for marshland).

Generalized linear mixed models with negative binomial errors were used to model the number of wildcat detections in each location, in each considered temporal scale. Models fitted using a negative binomial distribution performed better than models using a Poisson one (negative binomial: AICc = 338.17, seasonal; AICc = 266.59, semester; AICc = 194.27, yearly; Poisson: AICc = 348.75, seasonal; AICc = 275.65, semester; AICc = 220.08, yearly). Thus, for each location we defined the sampling effort as the number of days with the camera operating. When batteries ran flat before they had been replaced, the time of the last exposure was determined from the downloaded videos and considered as the last operational date (Rowcliffe et al. 2008; Rossa et al. 2021). Sampling effort was included as offset(log(effort)) to standardise the number of wildcat detections for the actual number of days with cameras operating. As predictors we considered: (i) the percentage of each habitat in the buffer; (ii) camera type (Ir-plus; ScoutGuard); (iii) height of the camera from the ground; (iv) study period (first: October 2017 to September 2018; second: April 2019–March 2020); (v) the rate of detections of people (either on foot or by bike/ car), as number of detections divided by sampling effort, to evaluate whether people influenced spatial patterns of wildcat. In the case of people, since we could distinguish individuals/groups, we considered for analyses all consecutive detections of different individuals/groups collected at temporal intervals greater than 3 min, to limit the risk of underestimating human presence in our sampling locations. As for the habitat, we did not consider the percentage of cultivated fields and marshland, because they covered only a negligible area in the buffers (c. 3-4%, on average, see above). The ID code of each camera trapping location was included as random effect in models at seasonal and 6-month temporal scales.

For each model set, we initially calculated global models including all predictors. Then, we carried out a model selection by fitting all the possible models including different combinations of predictors (including the null model), because each of them could represent a different a priori hypothesis (Burnham and Anderson 2002). Model selection used Akaike's Information Criterion corrected for small sample sizes (AICc) and models were selected if they had AICc ≤ 2 , and if their AICc value was lower than that of any simpler alternative (Burnham and Anderson 2002). Thus, more complex versions of models with lower AICc were excluded from the list, as the extra parameters do not improve model fit, and can thus be considered uninformative (Burnham and Anderson 2002; Arnold 2010). Standardised model weight was calculated among selected models. Model selection was conducted through the R package 'MuMIn' (MuMIn 2020). We estimated parameters (B coefficients and 95% confidence intervals) of the best models using the R packages 'glmmTMB' (Brooks et al. 2017). Best models were validated through visual inspection of residuals through the 'DHARMa' package (Hartig 2021).

Results

General results

Overall, 76 detections were collected over a total of 6681 trapping days (first period: n = 28 detections in 1943 trapping days; second period: n = 48 detections in 4738 trapping days). Detection rate was 1.11 detections per 100 trapping days (first period: 1.44 detections/100 days; second period: 1.01 detections/100 days). In the first period, the wildcat was detected in 11 out of 21 locations (52%); in the second period it was detected in 16 out of 57 locations (28%).

Temporal activity patterns

At all scales, temporal activity of wildcat showed a distribution different from a uniform pattern (Watson Test, W=1.09-5.84, p < 0.01). At the 6-month scale, activity peaks at twilight and at night emerged, although during the warm period this pattern was less pronounced, showing some diurnal activity (Fig. 2). However, temporal activity patterns did not differ significantly between periods (W=0.16, p > 0.05).

At the seasonal scale, the wildcat showed a marked twilight activity in summer and winter (the latter season corresponding broadly to the mating period), and nocturnal activity in autumn (Fig. 3). Conversely, a peak of activity during the day was reported in spring (Fig. 3). Significant differences occurred between temporal activity patterns in spring and those observed in the other seasons (W=0.33-0.43, p<0.01), but not between all the other seasons (W=0.05-0.13, p>0.05).



Fig. 2 Temporal activity patterns of wildcat considering the full data set (**a** 2 years, n=76 detections) and at a 6-month temporal scale (**b** "Warm" period: April–September, n=29; **c** "Cold" period: October–March, n=47). Red solid lines indicate estimated activity patterns. Coloured lines represent bootstrapped estimates of activity patterns (n=1000 replicates); dashed red lines represent relevant 0.95

Spatial patterns

Selected models included the effects of the percentage of shrubwood in the buffer, study period, semester, and camera type, depending on the temporal scale (Tables 1, 2). At all temporal scales, the frequency of wildcat detections increased with the percentage of shrubwood in the buffer (Tables 1, 2; Fig. 4). At the 6-month scale, there was slight support for the frequency of wildcat detections being greater in the cold than in the warm period, although 0.95 confidence intervals of the model coefficient included '0' (Tables 1, 2).

confidence intervals. Grey rectangles indicate times of day included between the minimum and the maximum sunrise and sunset times, derived through the R package 'suncalc' for each considered temporal scale. Black rectangles indicate times of day preceding the dawn and following the dusk

Discussion

Results suggest some delineated trends in spatio-temporal patterns of the wildcat. This small carnivore showed a general peak of activity at night and dawn/dusk, although patterns differed at a finer temporal scale. In fact, substantial activity was reported during broad daylight, in spring. Furthermore, wildcat detection rates were the greatest in sites, where habitats with dense vegetation cover were available, at all considered temporal scales. Our results also provide a significant update of the local status of this small carnivore. In the half-Seventies of last century, the wildcat was considered critically endangered in Southern Tuscany (Renzoni 1974). In 1988, a study confirmed the historical presence of this felid in the Maremma Regional Park but failed to collect evidence of its recent presence, bringing to the conclusion that it was possibly extinct or present at very low population density. To enhance the reconstitution of a



Fig. 3 Temporal activity patterns of wildcat at a 3-month temporal scale (a Spring, i.e., April–June, n=13 detections; b Summer, i.e., July–September, n=16; c Autumn, i.e., October–December, n=18; **d** Winter, i.e., January–March, n=29). Red solid lines indicate estimated activity patterns. Coloured lines represent bootstrapped estimates of activity patterns through n = 1000 replicates; dashed red

lines represent relevant 0.95 confidence intervals. Grey rectangles indicate times of day included between the minimum and the maximum sunrise and sunset times, derived through the R package 'suncalc' for each considered temporal scale. Black rectangles indicate times of day preceding the dawn and following the dusk

Table 1Model selection formodels including the effects ofhabitat features on probabilityof detection and detection rateof wildcat, estimated throughgeneralized linear mixed models	Temporal scale	Model	Variables	df	logLik	AICc	ΔAICc	W _i
	Season	Best	Shrub + Period	5	- 158.239	326.7	0.00	0.614
		Second	Shrub	4	- 159.741	327.6	0.93	0.386
	Semester	Best	Shrub + Semester + Camera type	6	- 121.999	256.6	0.00	0.531
		Second	Shrub+Camera type	5	- 123.211	256.8	0.26	0.469
	Year	Best	Shrub + Camera type	4	- 87.393	183.3	0.00	1.000

viable population, in 1990 a translocation project was started (Sforzi et al. 2008). Regular monitoring surveys carried out over time attested the establishment of a viable population of European wildcat in the area (Sforzi et al. 2008).

Wildcats showed a generally prevalent activity at night and dawn/dusk, especially during the cold period, in line with the eco-ethology of the species (Sunquist and Sunquist 2002; Kilshaw et al. 2015; Anile et al. 2021; Migli et al. 2021; Lazzeri et al. 2022). However, at a finer temporal scale some differences occurred between periods. At the 6-month temporal scale, a more even distribution of the activity pattern was reported in the warm period, as
> witnessed by the increase of diurnal detections, especially in late morning—early afternoon. At the seasonal scale, a peak of diurnal activity was observed in spring, whereas nocturnal and dawn/dusk activity was sensibly reduced during this season. Our results are in line with a preliminary study carried out in the area through VHF (Very High Frequency) telemetry (Bizzarri 1997). Birth, nursing and rearing of kittens occur in spring (Schauenberg 1970) and reproductive females would be expected to increase their activity to meet energy requirements determined by reproduction costs. Suggestively, a recent study based on satellite telemetry and carried out in Northern Greece found that reproductive

Table 2Factors influencingthe frequency of detectionsof wildcat, estimated throughgeneralized linear mixedmodels. Effects of predictorsincluded in best models areshown: model coefficients (B),their standard error (SE) and0.95 confidence intervals (CIs)

Temporal scale	Model	Variables	В	SE	0.95 CIs		
					Lower	Upper	
Season	Best	Intercept	- 4.683	0.403	- 5.474	- 3.892	
		Period [Second]	- 0.704	0.414	- 1.516	0.108	
		Shrub	0.667	0.203	0.269	1.066	
	Second	Intercept	- 5.131	0.327	- 5.772	- 4.490	
		Shrub	0.607	0.194	0.226	0.987	
Semester	Best	Intercept	- 4.500	0.366	- 5.216	- 3.383	
		Shrub	0.697	0.186	0.333	1.062	
		Semester [Warm]	- 0.542	0.356	- 1.241	0.156	
		Camera type [Scout]	- 1.279	0.587	- 2.429	- 0.128	
	Second	Intercept	- 4.755	0.326	- 5.393	- 4.117	
		Shrub	0.660	0.185	0.297	1.024	
		Camera type [Scout]	- 1.254	0.588	- 2.405	- 0.102	
Year	Best	Intercept	- 4.507	0.232	- 4.961	- 4.053	
		Shrub	0.647	0.212	0.231	1.062	
		Camera type [Scout]	- 1.507	0.648	- 2.778	- 0.237	



Fig. 4 Detection rate (N detections per location per camera trapping site day) of wildcat in relation to percentage of shrub in the buffer around the camera trapping site, at the yearly temporal scale. Fitted relationship and relevant 0.95 confidence intervals are shown

European wildcat females tended to become more diurnal and less nocturnal during the denning period, shifting from a generalised dawn/dusk pattern to a more evenly distributed one (Migli et al. 2021). These results might be interpreted as a behavioural response to the increase in energy demand because of breastfeeding, weaning and growth of the kittens. However, this interpretation would only be valid for reproductive females, since adult males are solitary and parental care is the responsibility of the female only. Nevertheless, the reduction of nocturnal activity detected in spring is difficult to interpret and should be considered with caution, due to the low number of observations for this season. Wolves and other smaller carnivores show predominantly nocturnal activity in our study area (Ferretti et al. 2021; Rossa et al. 2021). During night (and, to a lesser extent, twilight) these carnivores may pose a threat to wildcat offspring, especially if they are left unattended at the den. In turn, reproductive females might be constrained to limit their movements during these riskier time slots to assure protection to their kittens at the den. If so, their limited mobility would explain the small number of detections in spring, although a greater sample size is needed to support this conclusion.

Wildcat detection rates were the highest in sites characterised by dense vegetation cover (Mediterranean maquis and shrubwood). Although these results would require confirmation through a study based on telemetry, which would be unaffected by the specific location of camera trapping sites, they are consistent with findings obtained in other Mediterranean areas (Portugal: Monterroso et al. 2009; Spain: Lozano 2010; Greece: Migli et al. 2021; Italy: Lazzeri et al. 2022) and support the importance of habitat rich in wood cover for this small carnivore. Mature and structured woods-locally present in our study area-are usually described as elective to European wildcats (Stahl and Leger 1992; Ragni 1993; Sarmento et al. 2006; Jerosch et al. 2010) even if a significant variability in habitat use (Stahl 1986) was found in relation to different environmental conditions and prey availability. However, most studies have been conducted in continental areas with abundance of mature deciduous forests. In our study area, availability of sectors with abundant shrubby vegetation is expected to provide wildcats with suitable shelter, enhancing protection toward potential larger predators. Moreover, areas with dense cover with shrubby vegetation are also poorly

frequented by humans, since they are located in sectors with limited or restricted access to tourists and other visitors.

In conclusion, our study emphasises the importance of habitats with dense vegetation cover to the wildcat and confirms the full recovery of this small carnivore in our protected study area, compared to three decades ago. Our findings support the use of camera trapping as an efficient tool to study the basic spatio-temporal ecology of rare and elusive species, including temporal and spatial patterns. Nevertheless, significant differences in temporal activity patterns across seasons indicate that all year-round data collection is able to provide evidences of behavioural variations throughout the year.

Acknowledgements We are indebted to L. Venturi and E. Giunta for their support to our research. The Park wardens-in particular L. Tonini, G. Anselmi and G. Martini-provided fundamental and continuous assistance in fieldwork. We thank the Maremma Regional Park Agency for logistic support, and Ente Terre Regionali Toscane in addition to many landowners, who allowed us to conduct fieldwork. We thank students who helped in data collection/entry (M. Rossa, F. Bazzoni, B. ten Cate, B. Malik, R. Oliveira, G. Pacini and C. Riggio), and L. Chelazzi for help and discussions. Author contributions were as follows: conceptualization and data collection: FF; species validation: AS; data analyses: FF, LL, AS; writing the first draft: FF, LL, AS; writing and approval of the final manuscript: all authors. Our study has been supported financially by the Maremma Regional Park Agency and by the German Society for Mammalian Biology (DGS Project Funding 2018). We thank three anonymous reviewers for comments to a previous draft.

Funding Open access funding provided by Università degli Studi di Siena within the CRUI-CARE Agreement.

Declarations

Conflict of interest Authors declare no competing interests. Our study has been supported financially by the Maremma Regional Park Agency and by the German Society for Mammalian Biology (DGS Project Funding 2018).

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