

Blessing the rains down in Africa: spatiotemporal behaviour of the crested porcupine *Hystrix cristata* (Mammalia: Rodentia) in the rainy and dry seasons, in the African savannah

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Abstract: The assessment of habitat selection and temporal patterns of activity rhythms is paramount for wildlife conservation. Studies on behavioural ecology of wild mammals are particularly challenging in tropical areas, mostly when involving rare or elusive species. Despite being a common species in Italy, the crested porcupine *Hystrix cristata* is threatened of extinction throughout most of its sub-Saharan range. All available information on the ecology of this species has been collected in Italy, whereas no data is present in the scientific literature on spatiotemporal behaviour of this large rodent in Africa. In this work, we attempted to determine habitat selection and temporal patterns of activity rhythms of the crested porcupine in northern Benin and neighbouring countries, through intensive camera-trapping. We collected a total of 146 records of crested porcupine, 91 in the dry season (October-March) and 55 in the rainy season (April-September). Porcupines used most habitats in proportion to their local availability, while selecting rock outcrop formations (possibly used as shelter sites) and avoiding open areas, wetlands and gallery forests. A mostly nocturnal behaviour was confirmed throughout the year, with some diurnal activity at the start and at the end of the rainy season. The importance of rains in determining birth peak has been also showed, with juvenile individuals always observed at the start and at the end of the rainy season. Full moon always inhibited activity of this large rodent, most likely evolved as an antipredatory behaviour to limit encounters with potential predators (common leopard *Panthera pardus*, spotted hyaena *Crocuta crocuta* and honey badger *Mellivora capensis*) and humans. Poaching pressure towards porcupines in West Africa is strong. Porcupines are killed for the traditional medicine, for their meat and because they are widely considered as a crop pest. This assessment should therefore be used as a basic tool to design conservation plans to preserve this rodent species in its native range.

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Key words: Activity patterns; habitat selection; moonlight avoidance; native range; wildlife camera-trapping.

Introduction

The assessment of the spatiotemporal behaviour of wildlife species is important for conservation and management programs, particularly to preserve rare and elusive species, and to manage pest or invasive species (Di Bitetti *et al.* 2006; Valeix *et al.* 2009; Caravaggi *et al.* 2017; Karanth *et al.* 2017; Ossi *et al.* 2020). Wild mammals may show different patterns of habitat use, diet and temporal activity rhythms in the different areas of their range and at different population densities (Bridges and Noss 2011; Soe *et al.* 2017; Bonnot *et al.* 2019; Hinckley *et al.* 2020). This is particularly evident for species showing wide native distribution ranges (e.g., Gehring *et al.* 2003; Díaz-Ruiz *et al.* 2016; Karanth *et al.* 2017), and for those introduced in new environments (Cox 2004; Drygala *et al.* 2008; Blight *et al.* 2017; Luna *et al.* 2017). The estimation of habitat use/selection and patterns of activity rhythms may be challenging, particularly for those species inhabiting jungles, thick scrublands, high mountains or other geographical areas which are hard to be investigated (De Luca and Rovero 2006; Bowkett *et al.* 2008; Botts *et al.* 2020; Lovari *et al.* 2020; Ossi *et al.* 2020). In these contexts, camera-traps have provided important ecological information on the behaviour of a high number of species (Tobler *et al.* 2008; Rovero *et al.* 2008, 2010; Hamel *et al.* 2013; Caravaggi *et al.* 2017), when a remarkable number of records is collected (i.e., at least 30 per species: Lashley *et al.* 2018).

The crested porcupine *Hystrix cristata* Linnaeus, 1758 is a large rodent, and its body mass may reach up to 15–17 kg (Mori and Lovari 2014). The distribution of this species is scattered and encompasses the whole North Africa, from Morocco to Lybia and a savannah belt south to the Sahara Desert ranging from Senegal to Ethiopia and Tanzania (Amori and De Smet 2016; Mori *et al.* 2019). A population of this species also occurs in Italy, as a result of an ancient introduction (Trucchi *et al.* 2016; Mori *et al.* 2018, 2019). Similarly, few individuals of this species are also present in the Sinai Peninsula, Egypt (Trucchi *et al.* 2016). In central and southern Tanzania, the range of *H. cristata* partly overlaps with that of the closely related *H. africae australis* Peters, 1852 (Trucchi and Sbordoni 2009). The ecology of this species, i.e., orientation (Massolo *et al.* 2009), use of den setts (Pigozzi 1986; Monetti *et al.* 2005), habitat use/selection (Pigozzi and Patterson 1991; Mori *et al.* 2014a; Mori 2017), patterns of activity rhythms (Mori *et al.* 2014c; Lovari *et al.* 2017), diet (Bruno and Riccardi 1995), reproductive behaviour (Mori *et al.* 2016) and interspecific interactions (Mori *et al.* 2014b; Lazzeri *et al.* 2020) have been studied mostly in the introduced range, i.e., in Italy. Ecology and behavioural biology of the crested porcupine in its native range are mostly unknown, a part from a study on its diet in Tunisia (Ettiss *et al.* 2020), which reported that this rodent is mostly a consumer of grasses and cultivated species. Mouzoun *et al.* (2018a) attempted to assess habitat selection by the crested porcupine in Western Africa by collecting signs of presence and occasional observations. This method may provide several misinterpretations, as signs of presence (i.e., quills, excrements, footprints) may not be equally detectable in all habitat types (e.g., Romani *et al.* 2018). In Western Africa (e.g., Ghana, Benin, Niger and Burkina Faso), the crested porcupine is threatened with extinction, with apparently declining populations because of habitat loss, poaching, bushmeat overexploitation (Mouzoun *et al.* 2018b), traditional medicine and mystic practices (Ouoba *et al.* 2020). This highlights the need to assess its spatial and temporal behaviour in these areas, so to trigger reliable conservation actions for its preser-

vation (Amori and De Smet 2016). In recent times, camera-trapping has been shown to be effective in assessing spatiotemporal behaviour of crested porcupines, even in areas hard to be directly investigated and even when the porcupine is not the target species of the camera-trap survey (e.g., Fattorini and Pokheral 2012; Mazzamuto et al. 2019). A citizen science project on the iNaturalist platform including data collected through camera-trapping since 2011 has allowed researchers to access to biodiversity data on protected areas of Western Africa (Schmidt et al. 2016). Aims of this work were to describe habitat use and patterns of activity rhythms of the threatened crested porcupine in western Africa. We predicted that (i) the crested porcupine will show a generalist behaviour in terms of habitat selection (Santini 1980; Pigozzi and Patterson 1990), (ii) with mostly nocturnal habits throughout the year. We also expected that (iii) crested porcupines would exhibit moonlight avoidance (Mori et al. 2014c) to limit potential encounters with its main predators, i.e. the common leopard *Panthera pardus* (Linnaeus, 1758), the spotted hyaena *Crocuta crocuta* Erxleben, 1777 and the honey badger *Mellivora capensis* (Schreber, 1776).

Materials and methods

Study area

Our study was conducted in an area of about 850,000 ha, encompassing northern Benin, southwestern Niger and eastern Burkina Faso, including transboundary reserves between these countries. The study area was covered with shrub savannah (33%), arboreal savannah (30%), gallery forests (20%), rock outcrop formations (11%), wetlands (5%) and fallows (1%: Mouzoun et al. 2018a). The study area has a typical tropical climate, with rainy season concentrated between April and September, but with rainfall peaks in August and September.

Monitoring of wildlife through camera-trapping has increased in the W-Arly-Pendjari (hereafter, WAP) complex in the last 10 years, particularly in the Pendjari National Park, before being extended to other Protected Areas of WAP (Arly, West Niger, Burkina-Faso and Benin).

Sampling design

Data collection was conducted between January 2011 and April 2020. Camera -traps (Magainon, Victure, Tec.Bean, SpyPoint™ Force-10, Browning Strike Force HD Pro, PenCam Camera-Traps, N=175) were placed at 175 stations, i.e., fixed georeferenced locations (i.e., to shrubs, sand pits or rocks) where each camera-trap was tied with ropes and chains, at a height of ~40-50 cm from the ground, in all habitat types (Monterroso et al. 2014). Stations were separated one-another by at least 10 km, to limit pseudoreplication bias (O'Connell et al. 2011). We built up a regular grid (side = 10 km) through QGIS (QGIS Development Team 2019). Cameras were placed in the center of each randomly selected 100 km² cell, or in its immediate surroundings (max. distance from cell center = 2 km), opportunistically on wildlife trails or at water points to maximise camera-trapping success. We removed the grass in front of the cameras to prevent vegetation from triggering the cameras which were configured to work continuously (24h a day), to take 1 picture/animal passage. Camera-traps were checked once every 2 weeks to download data and replace dead batteries.

Habitat selection

Habitat types were assessed by camera-trap shots and confirmed through satellite photos on Google Earth. We calculated the Ivlev's electivity index (Ivlev 1961) to assess the habitats selection of crested porcupine, through the statistical software R 3.1.1, package gplots

(Warnes *et al.* 2014). This index compares the availability of each habitat type with its use by the species according to the formula $E = (U_i - A_i) / (U_i + A_i)$, where U_i is the proportion of use of habitat “*i*” and A_i is its local availability. The values of this index ranged from -1 to $+1$, with values between -1 and 0 indicating avoidance, and values from 0 to $+1$ indicating preference for a habitat type. A true selection or avoidance can be declared only at values >0.3 or <-0.3 , respectively (Lazzaro 1987; Laurenzi *et al.* 2016).

Patterns of activity rhythms

Our dataset was divided into two periods (dry season: October–March; rainy season: April–September: Dossou-Yovo *et al.* 2016), to conduct analyses on both total-year and seasonal scales. The “activity” was defined as the cumulate period spent by porcupines outside dens (Lashley *et al.* 2018). Photographs of porcupines were downloaded from iNaturalist; date and the solar hour of capture directly shown on each capture were then reported on a dataset. We identified juvenile (including cubs) and adult individuals according to body size, i.e. with juveniles being about 25–30% smaller than adults (e.g., Mori *et al.* 2016). Records occurring at the same site within less than 30 min were removed from the dataset to limit pseudoreplication (Meredith and Ridout 2014). Seasonal patterns of activity rhythms of the crested porcupine and their 95% confidence intervals (hereafter, CIs) were computed through the R 3.6.1 package “overlap” (Meredith and Ridout 2014). We estimated the coefficient of overlapping (Δ) between temporal activity patterns of the crested porcupine in the dry and rainy seasons. The coefficient of overlapping ranges between 0 (no overlap) and 1 (total overlap: Meredith and Ridout 2014). We calculated the Δ_4 estimator and its 95% Confidence Intervals, CIs, as also the smallest sample of the pairwise comparison was over 75 records (Meredith and Ridout 2014). The Hermans-Rasson test (*r* test) was used to estimate whether a random activity pattern was exhibited by the crested porcupine round-the-clock (Landler *et al.* 2019). The 95% CIs were computed by using 10,000 bootstrap replicates (Mori *et al.* 2020). We tested whether moonlight had an effect on the locomotor activity patterns of the crested porcupine, by classifying moon phases as it follows: phase (1) from new moon to $\frac{1}{4}$; phase (2) from $\frac{1}{4}$ to $\frac{1}{2}$; phase (3) from $\frac{1}{2}$ to $\frac{3}{4}$ and phase (4) over $\frac{3}{4}$ and full moon. Then, we performed a chi-squared test on the numbers of records in each moon phase, to assess if they were uniform throughout the four phases (Mori *et al.* 2020). Similarly, we also analysed the effects of moonlight on camera-trap records of the potential predators of the crested porcupine from the same study area, i.e. the common leopard, the spotted hyaena and the honey badger.

Results

Habitat selection

We collected a total of 146 records of crested porcupine (mean per year: 17.2 ± 15.9 , range = 1–58), 91 in the dry season and 55 in the rainy season (Figure 1). Only rock outcrop formations were selected throughout the year and in the rainy season, whereas gallery forests, wetlands and fallows were avoided. Conversely, arboreal savannah and shrub savannah were used proportionally to their local availability throughout the year (Table 1).

Patterns of activity rhythms

The crested porcupine was mostly nocturnal with few bouts of diurnal activity (Figure 2a), mostly by juveniles (at the very start or at the end of the rainy one). Throughout the

year, activity patterns were significantly different from random according to the Hermans–Rasson test ($r=79.42$, $P<0.001$). Temporal overlap of activity patterns between the rainy and the dry season was very high ($\Delta_4=0.81$, 95% CIs=0.69-0.91: Figure 2b).

Table 1. Ivlev’s Electivity Indices for habitat selection of the crested porcupine in West Africa.

	Available (%)	Used (%)		Year	Ivlev’s Electivity Index (E)		
		Dry season	Rainy season		Dry season	Rainy season	Year
Gallery forest	20.00	5.49	1.82	4.11	-0.57*	-0.83*	-0.66*
Shrub savannah	33.00	48.36	47.27	47.27	0.19	0.18	0.18
Arboreal savannah	30.00	28.57	21.82	27.39	-0.02	-0.16	-0.05
Rock outcrops	11.00	17.58	29.09	21.23	0.23	0.45*	0.32*
Wetlands	5.00	0.00	0.00	0.00	-1.00*	-1.00*	-1.00*
Fallows	1.00	0.00	0.00	0.00	-1.00*	-1.00*	-1.00*

*Significant selection (positive sign) or avoidance (negative sign).



Figure 1. Individuals of crested porcupine camera-trapped in northern Benin.

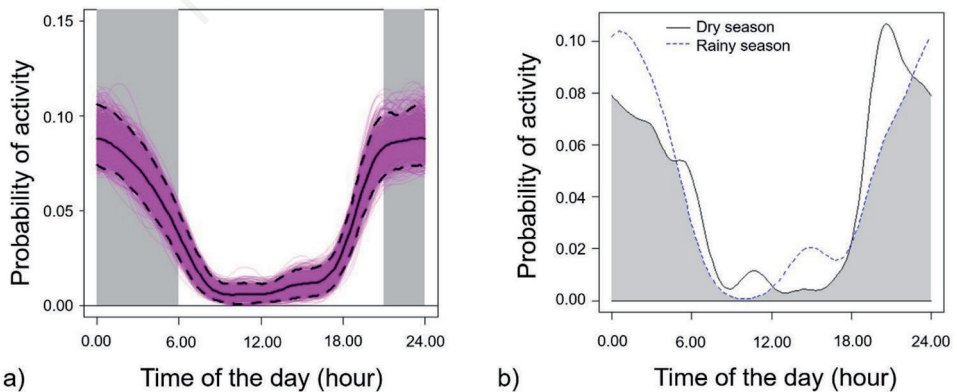


Figure 2. Patterns of activity rhythms of the crested porcupine. a) Kernel density estimate of activity throughout the year. Purple lines represent bootstrap estimates, and dashed black lines represent 95% CIs; b) inter-seasonal overlap of activity patterns (Kernel density estimates) of the crested porcupine in West Africa.

Crested porcupines avoided bright moonlight nights throughout the year and were mostly active in total darkness ($\chi^2=83.85$, $\text{dof}=3$, $P<0.01$). Conversely patterns of activity rhythms of all potential predators were not related to moon phases (common leopard: $N=50$ records, $\chi^2=2.16$, $\text{dof}=3$, $P>0.25$; spotted hyaena: $N=71$ records, $\chi^2=3.53$, $\text{dof}=3$, $P>0.25$; honey badger: $N=31$ records, $\chi^2=3.64$, $\text{dof}=3$, $P>0.25$).

Discussion

To the best of our knowledge, this work provides the first data on the behavioural ecology of the crested porcupine in its native range (West Africa), thus providing important information on this species and bringing new interpretations on ecological data collected where it was possibly introduced, i.e. in Italy (Loy *et al.* 2019). The crested porcupine was shown to be a “habitat-generalist”, avoiding only habitats which do not provide it with food and shelter sites, such as wetlands, gallery forests and fallows, thus fulfilling our prediction (i). This behaviour mirrors habitat selection studies in central Italy, where porcupines may also use suburban areas, if covered by thick vegetation (Santini 1980; Pigozzi and Patterson 1990; Sonnino 1998; Mori *et al.* 2014a; Lovari *et al.* 2017). A similar spatial behaviour has been described in South Africa for the Cape porcupine *Hystrix africaeaus-tralis* in a savannah ecosystem and for the Indian crested porcupine *H. indica* Kerr, 1792 in the forest, where thick vegetation was reported as a pivotal determinant of habitat selection (Fattorini and Pokheral 2012; Ngcobo *et al.* 2019). Conversely, it selected rock outcrop formations, which are often sloping and may host den sites (Tinelli and Tinelli 1980; Filibeck *et al.* 1981; Monetti *et al.* 2005). Rock outcrop formations may provide also porcupines with natural shelter sites, preventing them to directly excavate dens (see Akram and Ilyas 2016; Talukdar *et al.* 2019, for *H. indica*). This may represent a further explanation for the selection of this habitat type also in West Africa. Crested porcupines were mostly active in night hours, spending daylight hours in their underground dens: therefore, also our prediction (ii) has been verified. This fits with data on this species collected in Italy (Corsini *et al.* 1995; Mori *et al.* 2014c; Mori 2017; Coppola *et al.* 2019). At northern latitudes, a reduction in porcupine activity has been observed during the cold months (Alkon and Saltz 1988a, b; Corsini *et al.* 1995). Conversely, in our tropical area, we did not detect any activity reduction in any season, which is consistent with the very constant ambient temperatures characterizing this region of Africa throughout the year. Diurnal behaviour during the afternoon was only detected at the start and at the end of the rainy seasons mostly by juvenile individuals. The peak of activity during the afternoon is a typical cub behaviour also in Italy in April–June, and it may be related to thermoregulation or synthesis of metabolites e.g. Vitamin D, necessary for growth (Coppola *et al.* 2019). Also, in our study area, cubs were mostly observed at the start of the rainy season, in April. This reflects the birth peak in Italy, which occurs in mid-winter with juvenile individuals starting following their parents in late March (Mori *et al.* 2016). The African evolutionary origin of the crested porcupine has brought this rodent to show its peak of births at the end of the African dry season, so that cub may emerge from the den at the start of the rainy season, when food is mostly available (Mori *et al.* 2016). Yellen (1991) and Coppola *et al.* (2019) reported that most of the diurnal activity of porcupines in South Africa and central Italy respectively was exerted in the surroundings of den setts. The mostly nocturnal behaviour is also confirmed by the fact that crested porcupine avoids bright moonlight nights. This dependence of porcupine activity to moon phases has also been recorded in Italy (Mori *et al.* 2014c; Mori 2017) and in Asia (*H. indica*: Alkon and Saltz 1988a; Mukherjee *et al.* 2018), and it

may be related to antipredatory behaviour. Accordingly, Fattorini and Pokheral (2012) showed that Indian crested porcupines tend to range in concealed habitats and darkest nights to avoid visibility to large predators, e.g., common leopards, in Nepal. Similarly, in West Africa, crested porcupines were poorly active in moonlight nights, as we predicted (prediction *iii*). Preliminary information on predators occurring in our study areas suggested that all of them (the common leopard, the spotted hyaena and the honey badger) are active also at night and irrespectively of moon phases. Given the quill armor all around their bodies, porcupines represent most often an ancillary component of the diet of these predators (Henschel and Skinner 1990; Begg et al. 2003; Breuer 2005; Lovari et al. 2013; Mori et al. 2014b), and they are rarely killed. Hayward et al. (2006) reported that in Africa common leopards consume porcupines in proportion to their local availability. However, in some cases, porcupines may become important prey of large felids (Kumar 2016), and cubs can be occasionally killed by honey badgers even within their den (Arbon 2019). Furthermore, poaching pressure is generally high for the traditional medicine, for porcupine meat and because it is widely considered as a crop pest. This may bring porcupines to avoid ranging movements when and where they are visible to humans, e.g. open areas and bright nights (Laurenzi et al. 2016; Lovari et al. 2017; Talukdar et al. 2019).

Conclusions

Despite being a very common species in Italy (Loy et al. 2019), the crested porcupine is threatened with extinction in Africa, particularly in the western countries. In these areas, porcupines are widely poached for meat and for traditional medicine, as a cure for men sexual weakness, migraine, breast pain and coughing (Ouoba et al. 2020). Our work represents the first attempt to clarify the behavioural ecology of this rodent in its native range, which is necessary to address well-designed management plans. Further research is however needed to assess feeding habits and den site selection. Poaching pressure should be also locally estimated (Cerri et al. 2017) as a prerequisite for improving their conservation.

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Conflict of interest

The authors declare no conflict of interest.

Authors' contributions

AV and EM conceived the study, conducted statistical analyses and wrote the first draft. HO and FB conducted field work. LL and GA participated in data interpretation and writing up all drafts.

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