

The value of indigenous range data for an invasive species, the crested porcupine (*Hystrix cristata*)

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Abstract:

The crested porcupine is an invasive species in Italy with a growing population and an expanding range. Whilst the species is mainly nocturnal, it has been observed diurnally throughout the year in Italian habitats. Research has attributed these observations to foraging requirements in daylight hours especially in periods when nights are shorter and primary production is more limited. This implied that crested porcupines are under trophic and physiological stress in Italy, which contradicts with their observed demographic and spatial expansion. Here we use data collected over 30,765 camera days by camera-trap grids within the species' indigenous range in two Tunisian semi-arid national parks where primary productivity is limited. We postulated that if the foraging hypothesis was accurate, we would record diurnal activity of crested porcupines in our resource-scarce study sites as the species increases active foraging hours to fulfil its trophic requirements. Analyses however revealed exclusively nocturnal activity patterns in the studied sites in Tunisia, thus contrasting with the foraging hypothesis. Our results indicate that the species is not under stress in Italian ecosystems and diurnal mobility is likely limited to basking, grooming, etc. in the near vicinity of burrow entrances.

Keywords: Biological invasion, Invasion success, Tunisia, Italy, Invader behavior, Activity patterns.

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Short title

Crested porcupine activity patterns

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The crested porcupine (*Hystrix cristata*), endemic to Africa, is an invasive species in Italy (Trucchi and Sbordoni 2009). Tunisian porcupines were transported to Italy by the Romans as a game species, circus animal, or pet (Masseti et al. 2010; Trucchi and Sbordoni 2009). The Italian porcupine population is expanding to cover most of the country's mainland and Sicily, Sardinia and Elba islands (Milana et al. 2022; Vecchio et al. 2018; Mori et al. 2013; Trucchi and Sbordoni 2009).

The species' activity has been consistently revealed as nocturnal, yet investigations in Italy using radio-collaring and camera-trap monitoring of burrow entrances found daytime activity occurred throughout the year (Coppola et al. 2019; Corsini et al. 1995). These detections were mainly made between 13:00 and 15:30 during the hottest hours of the day. Coppola et al. (2019) concluded that the diurnal activity was attributable to the species' foraging strategy, hereafter referred to as the foraging hypothesis, and argued that diurnal detections increased in number between March and June due to decreasing darkness hours and trophic resources leading the crested porcupines to increase their active daytime foraging hours.

Conversely, the species' trophic preferences were diverse with individuals observed consuming carrion (Coppola et al. 2020a), effectively defending themselves from Italian predators (Mori et al. 2014), and breeding pairs producing up to three litters per year (Coppola and Felicioli 2021). All of these traits emphasise the invasive potential of the species and help understand its expansion even into urban areas of Rome in central Italy (Mori et al. 2022). The mutual avoidance between crested porcupines and red foxes (*Vulpes vulpes*) demonstrates its adaptability (Coppola et al. 2020b; Mori et al. 2015). At the same time, Italian ecosystems lack predators capable of killing adult crested porcupines (Coppola et al. 2020b; Monetti et al. 2005) and they have been observed simultaneously using burrows with the native badgers (*Meles Meles*, Coppola et al. 2020b).

The foraging hypothesis (Coppola et al. 2019), traditionally employed to explain the diurnal detections of the crested porcupine, implies a trophic stress resulting from the lack of preferred food sources and concurrent physiological costs stemming from the obligatory activity in unfavourable hot periods of the day (Levy et al. 2018). However, a comprehensive examination of the literature discussed above, indicates the presence of highly favourable conditions within Italian ecosystems for the species, aligning more closely with the observed spatial and demographic expansion (Milana et al. 2022; Vecchio et al. 2018; Mori et al. 2013; Trucchi and Sbordoni 2009). Consequently, a notable incongruity emerges within the existing understanding of the species' activity patterns, not only within Italy but likely extending across its native distribution in Africa as well.

Whilst it is usual for invasive species to be subject to greater scientific interest in their colonised habitats (Pysek et al. 2008), no behavioural data are available on crested porcupines in North Africa, and only one study has been published from the species' wider range in Benin (Viviano et al. 2020). Invasion ecologists argue for increased scientific attention in understudied regions to synthesise contrasting behaviours across a species' indigenous and colonised range, and the identification of general principles in invader behaviour (Bellard et al. 2016; Sax 2001). To test the foraging hypothesis postulated on the crested porcupine's diurnal activity in Italy, we used camera-trapping data from two national parks in Tunisia's southern aridland steppe habitat, Dghoumes and Sidi Toui National Parks (NPs) to evaluate the species' activity patterns in its indigenous range. We postulated that if the foraging hypothesis was accurate, we would record diurnal activity of crested porcupines in our resource-scarce study sites as they increase active foraging hours to fulfil their trophic requirements. We aim to highlight the importance of

indigenous-range information to enhance the comprehension of invasive species ecology in an increasingly connected world.

Dghoumes NP is located 11 km from the closest settlement, Dghoumes village, in the governorate of Tozeur (34.04N; 8.54E) and covers 8,000 ha with an upper arid climate. Its northern area is characterized by a low mountain range and is bordered from the south by the largest salt lake of the Maghreb, the Chott Djerid. A stony plain covers the area separating the salt lake and the mountains and is interspersed by ephemeral wadis. Plants were mainly low shrubs such as *Hammada schmittiana*, *Traganum nudatum*, *Salsola vermiculata*, *Anabasis articulata*, *Suaeda mollis* and *limoniastrum guyonianum*. Sidi Toui NP is located east of the Dhahar mountain chain in the governorate of Medenine 60 km south of the town of Benguerdene (32.74N; 11.24E) and covers 6,315 ha. The soil is covered by a thin sandy upper layer and the vegetation cover mainly comprised low shrub species including *Anthyllis henoniana*, *Gymnocarpus decander*, *Rhanterium suaveolens*, *Hammada schmittiana* and *Hammada scoparia*. The terrain is mostly plain with rare shallow ephemeral wadis and easy clay hills. Both study sites were characterised by an arid climate with mean annual temperatures of 21.8°C in Dghoumes NP and 20.3°C in Sidi Toui NP and precipitations of 96mm/year in Dghoumes NP and 131mm/year in Sidi Toui NP.

We deployed 29 Bushnell and 1 Moultrie cameras at 41 systematically selected locations in Dghoumes NP c. 1km apart between April 2018 and February 2021, and 26 Bushnell Aggressors at c. 1.5km spacing in Sidi Toui NP from October 2020 to March 2022 (figure 1). We attached cameras to rocks and aimed them at visible animal passage trails. We ensured the continuous functioning of the grid over the study period through monthly to bi-monthly verifications. We used detection data to calculate Kernel densities of the species' activity patterns using R package "Activity" and the 95% confidence intervals through 1000 bootstrap samples (Rowcliffe et al. 2014).

We recorded a total of 10,546 animal detections in Dghoumes NP and 7,100 in Sidi Toui NP over a sampling effort of 20,382 camera days and 10,383 camera days, respectively. We observed crested porcupines on 39 (0.37%) and 160 (4.03%) detections respectively in Dghoumes and Sidi Toui NP. Solitary individuals were the most frequently detected social structure in Dghoumes NP forming 79.49% (n = 31) of detections while pairs formed 20.51% (n = 8). Comparable social structures were observed in Sidi Toui NP with solitary individuals observed on 72% (n = 116) of detections, pairs on 26.8% (n = 43), one group of three adults (0.6%) and one adult with one young (0.6%). Our results indicated that the activity of the crested porcupine was strictly nocturnal across the year, with all detections recorded during the night. Throughout the year, and therefore regardless of night-length, crested porcupine activity began after sunset at both study sites and followed a unimodal pattern across the nocturnal phase with a peak at its middle (figure 2).

Detection of diurnal activity in Italy was achieved by placing camera-traps at burrow entrances (Coppola et al. 2019) and through GPS collaring (Corsini et al. 1995). Both monitoring methods are therefore designed to detect diurnal mobility even if the animals only move close to their burrows. The study in Benin used fixed distances between camera-traps, i.e. with a lower probability of detecting limited movements of crested porcupines near their burrows, and reported very rare afternoon observations but comparatively very common nocturnal occurrences (Viviano et al. 2020). Our results did not show evidence of diurnal activity for the crested porcupine in Tunisia, therefore indicating that the animals did not exhibit extended foraging movements during the day. If diurnal activity in the Italian population was a consequence of increased active foraging time to fulfil energetic requirements, similar or even more

pronounced diurnal foraging behaviour with extended movements far from burrows should have been detected in our Tunisian study sites due to limited and widely dispersed resources. Additionally, the foraging hypothesis implies strict dietary requirements for crested porcupines, that in times of limited availability of their preferred food items, roots, bulbs, tubers and rhizomes (Santini, 1980), would be pushed to diurnal foraging at a very high, usually deadly, physiological cost for the nocturnal species (Weyer et al. 2020). This presumed high trophic selectivity is however highly unlikely (Coppola et al. 2020a). Our results show the absence of diurnal foraging for the crested porcupine, yet limited diurnal movements near burrow entrances as observed in Italy remain plausible for porcupines in Tunisia. These movements could serve other functions such as thermoregulation, basking, grooming, etc. Taking these new data into account, we suggest that these functions most likely explain the diurnal mobility of crested porcupines in Italy and that this understanding of diurnal activity for the species aligns more accurately with its demographic and spatial expansion in the country (Milana et al. 2022; Vecchio et al. 2018).

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Data availability statement: The data that support the findings of this study are available from the corresponding author, upon reasonable request.

Conflict of interest: None to declare.

References:

- Bellard, C., Jeschke, J. M., 2016. A spatial mismatch between invader impacts and research publications. *Conserv. Biol.* 30(1), 230-232.
- Coppola, F., Dari, C., Vecchio, G., Scarselli, D., Felicioli, A., 2020b. Cohabitation of settlements among crested porcupine (*Hystrix cristata*), red fox (*Vulpes vulpes*) and European badger (*Meles meles*). *Curr. Sci.* 119(5), 817.
- Coppola, F., Felicioli, A., 2021. Reproductive behaviour in free-ranging crested porcupine *Hystrix cristata* L., 1758. *Sci. Rep.* 11(1), 1-9.
- Coppola, F., Guerrieri, D., Simoncini, A., Varuzza, P., Vecchio, G., Felicioli, A., 2020a. Evidence of scavenging behaviour in crested porcupine. *Sci. Rep.* 10(1), 1-6.
- Coppola, F., Vecchio, G., Felicioli, A., 2019. Diurnal motor activity and “sunbathing” behaviour in crested porcupine (*Hystrix cristata* L., 1758). *Sci. Rep.* 9(1), 1-8.
- Corsini, M. T., Lovari, S., Sonnino, S., 1995. Temporal activity patterns of crested porcupines *Hystrix cristata*. *J. Zool.* 236(1), 43-54.

- Levy, O., Dayan, T., Porter, W. P., and Kronfeld-Schor, N., 2018. Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? *Ecol. Monogr.* 89(1):e01334.
- Masetti, M., Albarella, U., Mazzorin, J. D. G., 2010. The crested porcupine, *Hystrix cristata* L., 1758, in Italy. *Anthropozoologica* 45(2), 27-42.
- Milana, G., Viviano, A., & Mori, E., 2022. Porcupines in Italian islands: update on the distribution of *Hystrix cristata* in Sardinia. *Mammalia*, 87(2), 162-165.
- Monetti, L., Massolo, A., Sforzi, A., Lovari, S., 2005. Site selection and fidelity by crested porcupines for denning. *Ethol Ecol Evol.* 17(2), 149-159.
- Mori, E., Maggini, I., Menchetti, M., 2014. When quills kill: the defense strategy of the crested porcupine *Hystrix cristata* L., 1758. *Mammalia* 78(2), 229-234.
- Mori, E., Menchetti, M., Balestrieri, A., 2015. Interspecific den sharing: a study on European badger setts using camera traps. *Acta Ethol.* 18(2), 121-126.
- Mori, E., Molteni, R., Ancillotto, L., Ficetola, G. F., Falaschi, M., 2022. Spatial ecology of crested porcupine in a metropolitan landscape. *Urban Ecosyst.* 1-7.
- Mori, E., Sforzi, A., Di Febbraro, M., 2013. From the Apennines to the Alps: recent range expansion of the crested porcupine *Hystrix cristata* L., 1758 (Mammalia: Rodentia: Hystricidae) in Italy. *Ital. J. Zool.* 80(4), 469-480.
- Pyšek, P., Richardson, D. M., Pergl, J., Jarošík, V., Sixtová, Z., Weber, E., 2008. Geographical and taxonomic biases in invasion ecology. *Trends Ecol. Evol.* 23(5), 237-244.
- Rowcliffe, J. M., Kays, R., Kranstauber, B., Carbone, C., amp; Jansen, P. A., 2014. Quantifying levels of animal activity using camera trap data. *Methods Ecol. Evol.* 5(11), 1170-1179.
- Santini, L., 1980. The habits and influence on the environment of the old world porcupine *Hystrix cristata* L. in the northernmost part of its range. In *Proceedings of the Vertebrate Pest Conference.* 9(9).
- Sax, D.F., 2001. Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *J. Biogeogr.* 28, 139–150.
- Trucchi, E., Sbordoni, V., 2009. Unveiling an ancient biological invasion: molecular analysis of an old European alien, the crested porcupine (*Hystrix cristata*). *BMC Evol. Biol.* 9(1), 1-10.
- Vecchio, G., Coppola, F., Scarselli, D., Giannini, F., Felicioli, A., 2018. Crested porcupine in the Island of Elba, Italy: native or alien?. *Curr. Sci.* 114(2), 246.
- Viviano, A., Amori, G., Luiselli, L., Oebel, H., Bahleman, F., Mori, E., 2020. 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. *Trop. Zool.* 33(4).
- Weyer, N.M., Fuller, A., Haw, A.J., Meyer, L.C.R., Mitchell, D., Picker, M., Rey, B. and Hetem, R.S., 2020. Increased diurnal activity is indicative of energy deficit in a nocturnal mammal, the aardvark. *Front. Physiol.* 11:637.

Figure legends:

Figure 1: Map of the North Africa and southern Europe separated by the Mediterranean Sea (Top left), of Dghoumes National Park (right), Sidi Toui National Park (bottom left) and camera-trap locations.

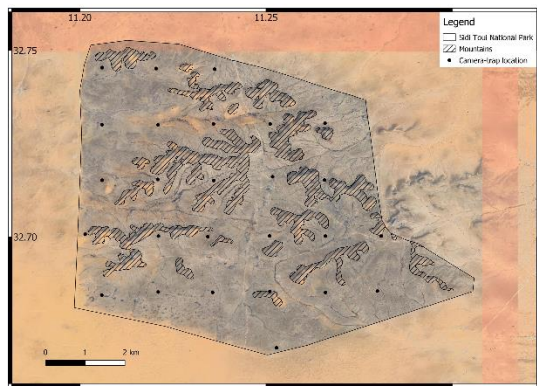
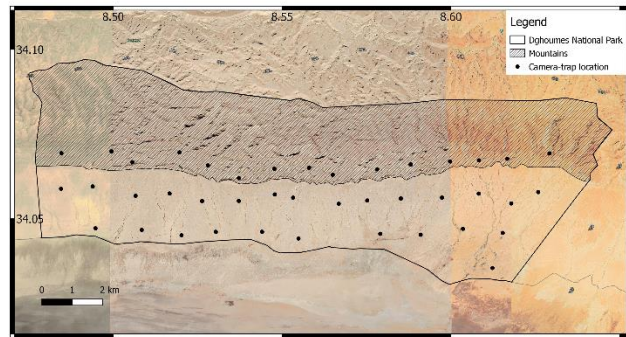
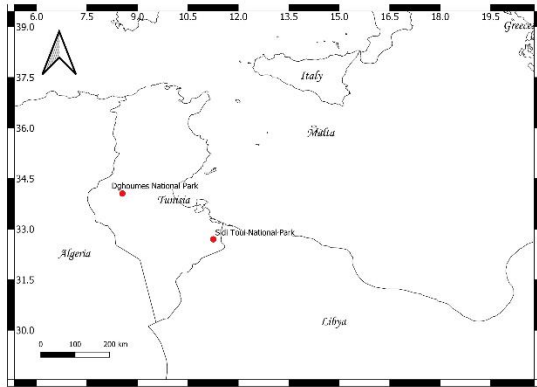


Figure 2: Annual daily activity patterns of the crested porcupine in Dghoumes and Sidi Toui National Parks. Kernel density activity estimates on y-axis with 95% confidence intervals in dotted grey lines. Tick marks on the x-axis show times of independent observations used to estimate the activity pattern. Mean sunrise and sunset times for each season is indicated by the black dashed vertical lines.

