Evidence of scavenging behaviour in crested porcupine

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The vegetarian diet of many herbivorous mammals is supplemented with proteins of animal origin, especially in young individuals and in breeding females, to provide key proteins necessary for both growth and breeding. Among porcupine species, only the Cape porcupine (Hystrix africaeaustralis) has been observed to consume carrion flesh. From June to August 2019, a pigeon carcass was placed together with corn in 7 study settlements and near 2 monitored capture-traps, in order to assess the carrion flesh feeding habits of the crested porcupine (Hystrix cristata). Scavenging behaviour was recorded on four occasions. All the recorded individuals were adults and at least one was female. This demonstrates that the crested porcupine occasionally does eat flesh. Such evidence raises important questions concerning the relationship between feeding habits and the physiological needs of this herbivorous rodent.

Within Old world porcupines of the sub-genus Hystrix (H. indica, H. africaeaustralis and H. cristata), only H. africaeaustralis (Cape porcupine) and H. cristata (crested porcupine) show a sympatric distribution overlap in southeast Africa1, while H. indica (Indian porcupine) is widely distributed in semi-arid areas of south-western Asia. The three species have thrived amidst anthropic activities, such as agriculture and manmade riverbanks, which provide rodents with enough food resources and burrowing habitats, respectively. These rodents are infamous as pests for destroying economically important crops and damaging riverbanks by burrowing4–6.

All these species are monogamous, burrowing, mainly nocturnal rodents7–11 and spend most of their night-time hours searching for food12–14. The porcupine diet is mainly based on bulbs, tubers (also truffles), and roots, dug up with strong legs, but also includes flowers, fruits, grass, leaves, berries, barks, twigs, corns, and grains and seeds of wild and cultivated plants15–18. Porcupines usually partially eat their food, chewing it loudly and discarding the rest of the food after just a few mouthfuls19. Season, habitat richness and ecology strongly influence the porcupine diet16,20,21. Feeding habits change according to food availability and show wide ecological tolerance and fitness maximization3. All porcupines of the sub-genus Hystrix show osteophagia (i.e. gnaw the bones)22,23 and have long been known to collect bones inside and outside their burrows24. The reason for osteophagia in porcupines is still not clear. Honing of open-rooted incisors and/or calcium and phosphorous assumption are the two main hypothesis20,22. Porcupines have a simple stomach, a voluminous caecum25 and a peculiar furrow in the large intestine26. These anatomic features are compatible with caecotrophy practise although it has never been observed in porcupines27.

Of the three Hystrix species only the cape porcupine has been observed to eat carrion flesh1,28. Futhermore, Roth28 reported an 8–10 week old cape porcupine reared in captivity, that was fed on boiled ham and fried meat. Animal-based feeding behaviour has been reported also in Hystrix indica29, in Atherurus africanus (African brush-tailed porcupine, genus Atherurus), Atherurus macrourus (Asiatic brush-tailed porcupine, genus Atherurus)29,30 and in Hystrix pumila (Palawan porcupine, genus Hystrix, sub-genus Thecurus)31, although there is no direct observation. No data are available concerning this feeding habit neither in H. cristata nor in any of the new world porcupines.

Animal proteins in a vegetarian diet are a feature of frugivorous and granivorous rodents32. Animal proteins supplement the vegetarian diet of many herbivorous mammals, especially in growing youngsters and breeding females33. Therefore according to White33, otherwise vegetarian mammals actively looking for meat may be a far more common breeding strategy than has previously been presumed. The aim of this investigation was to assess whether animal proteins supplement the vegetarian diet of the crested porcupine as previously observed in the cape porcupine.

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Results

The average size of the family clans inhabiting the study settlements was 4.1 (SD = 1.6) individuals. All the study settlements were located in the woody ecotone strip within a maximum distance of 86.5 (M = 37.3, SD 22.7) meters from food-patch areas (i.e. cultivated or uncultivated zones), in sandy soil with a slope range from 5 to 10%. The average number of ground holes per settlement was 5.7 (SD = 4.5) holes. Five of the 7 monitored settlements were South-east/South-west oriented, while the other 2 were North-east/North-west oriented. Overall a total of four distinct scavenging events of a pigeon carcass by crested porcupines were observed (Fig. 1). The scavenging events were observed on one occasion in each of two settlements (S1 and S7, respectively) and on two occasions near 1 of 2 monitored capture-traps (T2). All the individuals observed to perform scavenging were adults and only one was certainly the adult female of family 1 (Table 1). In the events observed near the capture-traps the marking of the individuals could not be assessed. However, in one case it is plausible that it was the adult female of family 1. In one of the two events recorded near T2, a youngster was present with the adult porcupine without displaying an interest in the carcass. The same lack of interest was observed in the adult male present with the adult female of family 1. On four occasions two identified sub-adults, a male and a female of family 3, sniffed the pigeon but did not proceed to scavenge.

Methods

Study area and design. The study area of 514 ha was located in the Camugliano wildlife hunting reserve (10.64955 N–4359995 E) in Ponsacco-Capannoli, in the Province of Pisa (Tuscany, Central Italy). The area is characterized by low biodiversity and fragmentation, with a woody surface of about 100 ha evenly distributed. The woody cover is characterized by cops of Quercus cerri, Q. pubescens and Q. ilex while the undergrowth is mainly composed of Ruscus aculeatus. Wheat, sunflower, alfalfa, and vegetable crop areas, as well as vineyards and olive groves, surround the woody area. The cultivated areas are freely and easily accessible to wildlife through a network of pathways. The wildlife hunting reserve “Camugliano” supports pheasant breeding and hunting. Disposable mixed crops (chicory, forage cabbage, and sorghum) are annually sown to provide free food and shelter to pheasants. Corn is also provided daily throughout the year in artificial feeders located within the reserve. The mixed crops and corn are also a ready food source for crested porcupines throughout the year. In the study area 16 porcupine settlements (2.4 settlements/Km²) were known for a population density of 4 porcupines/Km².

Between March and April 2019, a porcupine capture campaign in the vicinity of 7 study settlements, among the 16 known, was performed. Six capture-traps were placed in the porcupines’ most used pathways, being those pathways where signs of porcupine presence (quills and faeces) were detected on a weekly basis. All these pathways connected the inhabited settlements to the food patch-areas showing signs of new digs. All the study settlements and capture-traps were continuously monitored by camera-traps (Num’axes PIE1009) with passive infrared sensor (PIR) during the whole period of investigation. Each camera-trap was set to record 20 s of

Table 1. Scavenging events of a pigeon carcass by crested porcupines recorded during the monitoring period. For each event the date, time, and site of observation and the age class, sex, and family of the focal porcupine are reported.

| Events | Data          | Time  | Site | Age class | Sex    | Family |
|--------|---------------|-------|------|-----------|--------|--------|
| 1      | 13/06/2019    | 20:53 | S1   | Adult     | Female | Family 1 |
| 2      | 05/06/2019    | 22:04 | S7   | Adult     | Unidentified | Family 4 |
| 3      | 24/06/2019    | 01:45 | T2   | Adult     | Unidentified | Unidentified |
| 4      | 14/07/2019    | 23:20 | T2   | Adult     | Unidentified | Unidentified |

Figure 1. An unidentified adult porcupine of family 4 in settlement 7 (left) and the identified adult female porcupine of family 1 in settlement 1 (right) scavenging on a pigeon carcass (in black circle). Both the images are screenshots of videos recorded by camera-traps.
video each time it was triggered, without time-lapse and was active 24/7. The camera-traps' video recordings were checked and filed on a weekly basis. Porcupines were trapped in wire mesh cages with a double entrance (110 × 42 × 42 cm), and baited with corn and potatoes. Porcupines' capture and handling were carried out in accordance with the protocol approved by the Italian Institute for Environmental Protection and Research (ISPRA) and Tuscany Region. Captured porcupines were anesthetized, weighed, and sexed with age attributed according to weight10. Each captured porcupine was individually marked with coloured adhesive tapes applied to the quills, and/or by white or black paint sprayed on the crest and/or on the tail to support recognition in camera-trap videos. In addition, the individual recognition of some unmarked specimens was also possible due to the presence of phenotypic peculiarities such as blindness (Fig. 2), scars, and injuries. During the study, a total of eight porcupine individuals were identified, of which five were captured and marked, and three were identified according to recognizable phenotypic features. The individual recognition of these specimens allowed us to identify four different porcupine families inhabiting the monitored settlements (Table 2).

From June to August 2019 a pigeon carcass and 500 g of corn were placed in each of the 7 monitored settlements (S1–S7) and in the vicinity of two out of six monitored capture-traps (T1–T2) (Fig. 3 and Fig. 4). Pigeon carcasses were obtained from authorized programmed culling performed in the Camugliano wildlife hunting reserve for agricultural crops damage control.

Every 2 days, the pigeon carcasses were replaced and the camera traps’ videos were checked. Scavenging of pigeons by porcupines was assessed when tearing of meat from the carcass could be clearly observed. For each pigeon scavenging event, the date, time and, whenever possible, age class and sex of the individuals were recorded. Unmarked porcupettes and youngsters up to 5–6 months old were identified on the recorded camera-traps’ videos, by their smaller body sizes. Conversely, youngsters over 7 months old, thereby with a body size similar to adults, were identified only when both adults of the family were individually recognisable. Whenever porcupine age class identification was not possible, the animals were attributed as adults.

**Ethical approval.** The capture-marking procedures performed during the study were approved by the Italian Institute for Environmental Protection and Research (ISPRA) [Protocol No.:150071; Dated: 16 March 2018] and by Tuscany Region [Decree n. 4842; Dated: 6 April 2018]. The procedure for pigeon containment was authorized by the Province of Pisa, according to art. 37, L.R.T. 3/94 [Intervention code 113; Dated: 4 February 2019].

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**Table 2.** Age class, sex, and recognisable features of the eight porcupines. For each recognisable porcupine the phenotypic peculiarity observed is reported.

| Family | Age class | Sex   | Recognisable features                        |
|--------|-----------|-------|---------------------------------------------|
| Family 1 | Adult     | Female | Marked                                      |
| Family 1 | Adult     | Male   | Injury in the rump (left) Blindness of the right eye |
| Family 2 | Adult     | Female | Marked                                      |
| Family 3 | Sub-adult | Female | Marked                                      |
| Family 3 | Porcupette | Female | Marked                                      |
| Family 4 | Adult     | Male   | Blindness of the right eye                  |
| Family 4 | Sub-adult | Female | Marked                                      |

**Figure 2.** Porcupine with both eyes reflecting the light (left) and porcupine blind to the left eye (right) with a porcupette.
Discussion

This investigation confirms carrion scavenging behaviour in crested porcupines (*H. cristata*) for the first time. Among the old world porcupines, such scavenging behaviour has been previously observed and described only in Cape porcupines. Feeding on carrions has also been reported, although not directly observed, in *H. indica*, *Atherurus macrourus*, *Atherurus africanus* and in *Hystrix pumila*, the latest reported as the most common Palawan carnivore (Table 3). To the best of our knowledge this scavenging behaviour seems not to be reported in new world porcupines.

The scavenging behaviour of crested porcupine reported here, was recorded in a habitat characterized by high food availability. Moreover, the presence of both pigeon and corn during all the scavenging events recorded, indicates a potential preference for flesh by porcupines, at least on these occasions. Therefore, feeding on carrion flesh by crested porcupine is not related to a lack of food and is more likely due to physiological needs. A primarily vegetarian diet supplemented with animal protein is common in many frugivorous and granivorous rodents, especially in growing young and breeding females. Integration of animal protein into otherwise vegetarian diets seems to be the result of behavioural and physiological adaptations to increase reproductive success. In this investigation, feeding on carrion flesh was clearly observed only in adult specimens, at least one of which was certainly a female. The observation of this feeding behaviour in a porcupine female suggests that eating animal
protein could be a feeding strategy for the assumption of key proteins necessary for breeding as suggested by White. Scavenging behaviour by porcupines could also be a route to infection of zoonotic diseases. The recent detection of *Giardia duodenalis*, several *Leptospira* serogroups and the isolation of *Leptospira* serovar Pomona in crested porcupines supports this possibility. Further investigations are necessary how scavenging behaviour in crested porcupines relates to age, sex, and physiological state.

### Data availability
All data are available on request to the corresponding author.

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Table 3. Comparative table of the available scavenging behaviour data in old world porcupines. For each species the type of data and source are reported.

| Genus  | Type of data | Literature source |
|--------|--------------|-------------------|
| Genus *Hystrix* |          |                   |
| *H. australis* | Observed | Roth                  |
| *H. cristata* | Reported | Kingdon               |
| *H. indica* | Reported | Hutchins et al.          |
| *H. pumila* | Reported | Marler et al.          |
| Genus *Atherurus* |        |                   |
| *A. africanus* | Reported | Jori et al.          |
| *A. macrourus* | Reported | Kleiman et al.        |

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