Feeding habits of the crested porcupine *Hystrix cristata* L. 1758 (Mammalia, Rodentia) in a Mediterranean area of Central Italy

E MORI1*, R. BOZZI1, & A. LAURENZI2

1Dipartimento di Scienze della Vita, Università di Siena, Siena, Italy, and 2Dipartimento di Scienze Biologiche, Geologiche ed Ambientali, Università di Bologna, Bologna, Italy

(Received 28 September 2016; accepted 4 May 2017)

Abstract
Old World porcupines are widely recorded as being agricultural pests throughout their distribution range. Despite being legally protected in Italy, the crested porcupine *Hystrix cristata* is extensively poached for its meat as well as for complained crop damages. In this work, we analysed the diet of crested porcupines in a Mediterranean coastal area surrounded by agricultural patches. Feeding habits of this species were assessed throughout the year through faecal analysis. Underground vegetal organs were the staple of the diet of this large rodent in both cold and warm months. Fruits were consumed mainly in cold months (hard epicarp species, e.g. acorns and pine nuts). In warm months, agricultural products, e.g. sunflowers, cereals and watermelons, were mostly consumed. Patterns of food consumption are consistent with a study on habitat selection by crested porcupine within the same study area. According to this previous study, the Mediterranean “macchia” represents a poor habitat in terms of food resources and it is selected only in cold months, when porcupines mainly feed on underground storage organs of woodland plants. During the summer, porcupines are forced to travel long distances to search for other food categories, e.g. cultivated species.

Keywords: *Hystrix cristata*, crop damage, agricultural patches, underground vegetal organs, diet

Introduction
Despite being listed among the protected species by Italian national law and European Conventions (Mori et al. 2013), the crested porcupine *Hystrix cristata* L. 1758 (Mammalia, Rodentia), introduced to Italy probably in early Mediaeval times (Bertolino et al. 2015; Trucchi et al. 2016), is also recorded as an agricultural pest (Laurenzi et al. 2016). Although it has been observed that crop damage by this species usually occurs only in small, private vegetable gardens, this finding is only based on farmers’ complaints and not on information about the actual diet of this large rodent (Laurenzi et al. 2016). Data on the diet of crested porcupines rely mainly on two studies carried out in a deciduous woodland area, where agricultural patches were absent (Bruno & Riccardi 1995), and in a suburban area (Lovari et al. 2017). According to these papers, crested porcupines in Italy adopt a generalist strategy, consuming a variety of food resources according to their seasonal availability (Bruno & Riccardi 1995; Lovari et al. 2017). Fruits growing on the lowest branches of trees and bushes, as well as those fallen on the ground, represented an important component of the diet of this rodent (Lovari et al. 2017). Ranging movements of porcupines are significantly determined by habitat richness (Lovari et al. 2013). Accordingly, the distribution of food resources represents the main determinant of habitat selection of this rodent (Mori et al. 2014a). Where food resources are scarce, seasonal variation in food availability forces crested porcupines to display a spatial behaviour called “seasonal contraction”, i.e. increased home range size when trophic resources are far from the den, and decreased home range size when resources are concentrated in the surroundings of the burrows (Lovari et al. 2013). During the warm period in Central Italy, the Mediterranean “macchia” is a...
relatively poor habitat in terms of food availability (Lucherini & Lovari 1996; Massei et al. 1997; Lovari et al. 2013); therefore, porcupines avoid this habitat and travel long distances to reach agricultural patches (Pigozzi & Patterson 1990; Morie et al. 2014a). Pigozzi and Patterson (1990) analysed the feeding habits of porcupines in a Mediterranean “macchia” area in July, with no reference to the rest of the year. They observed that sunflower and cereals were the main food resources used, although dens were located 2–3 km far from agricultural patches. In this work, we studied the yearly diet of the crested porcupine in a Mediterranean “macchia” habitat. We predicted that (i) variation in the feeding habits throughout the year would occur and that (ii) the seasonal differences in porcupine diet are related to the described variation of the species space-use pattern between monthly periods (i.e. use of agricultural products only when porcupines used agricultural patches; Morie et al. 2014a).

Materials and methods
The study area is located in the northern part of the Maremma Regional Park (Province of Grosseto: 42°39′N, 11°05′E) and it included a 1073-ha evergreen woodland along the Tyrrhenian coast. Monthly average rainfall is about 58 mm. Two periods were recognised according to the average environmental temperature of our study area (Lovari et al. 2013; Morie et al. 2014a): a warm one (April–September) and a cold one (October–March; Figure 1).

The study area was mainly covered by pinewood (Pinus pinea L., 1753: 25.9%) and Mediterranean “macchia” (mainly Quercus ilex L., 1753, Phyllirea sp., Erica multiflora L., 1753 and Pistacia lentiscus L., 1753; 25.6%). Cultivated areas were mainly represented by sunflower, cereals and lucerne (24.0%); fallows and abandoned olive groves covered 15.0% of the area. Shrubs (Juniperus communis L., 1753, Smilax aspera L., 1753, Spartium junceum L., 1753 and Calycotome spinosa (L., 1753)) covered 3.0% of the site, and the remaining 6.3% was constituted by wetlands and coastal dunes (Figure 1; Morie et al. 2014a).

Eight transects of about 2.1 km each (total: 14.8 km; Figure 1) were identified using a stratified sampling design, throughout all the identified habitat types (Lovari et al. 2017). All the transects were located within the routes used by radio-tagged porcupines (Figure 1), placed about 200 m from each other, and visited once a month throughout the year. Droppings were chiefly detected along main routes crossed by animals. All the transects were located in the surroundings of porcupine den setts (Figure 1) and relevant entrances, to maximise scat detection. Most den setts were located within deciduous woodlands, as well as in their surrounding shrub belts (Figure 1), with a few others occasionally used in unsuitable areas (pinewoods, fallows; Monetti et al. 2005). Samples were classified by date and stored in a freezer in plastic bags. Droppings of porcupines are easily distinguishable from those of other species, as they take the form of a series of stacked pellets (Barthelmess 2006). A total of 10 droppings per month (one per transect and two more randomly selected) were analysed, following the protocols reported by Bruno and Riccardi (1995) and by Lovari et al. (2017). This number was considered to be sufficient to determine the proportion of plant parts included in the diet of the crested porcupine, by plotting the cumulative number of prey items against the number of faecal samples analysed (Bruno & Riccardi 1995; Lovari et al. 2017). Droppings were analysed following standard protocols (Bruno & Riccardi 1995; Lovari et al. 2017): first of all, the mucous film covering the droppings was dissolved with a solution of NaOH 0.059 M (10–20 min at 40°C). Then, the sample was washed through a 1-mm square mesh sieve, and fragments separated by hand according to the food categories they belonged to. Identification of fragments was

![Figure 1](image_url)

Figure 1. On the left, habitat composition of the study area; asterisks represent porcupine den setts, dotted lines the transects traveled to collect droppings. On the right, mean ambient temperatures during the study period.
made through a stereomicroscope (WILD M3C, Heerbrugg: 128–320×). Food remains found in faecal samples were grouped into four main categories: (i) underground storage organs and barks of wild plants; (ii) stems and leaves of wild plants; (iii) wild fruits; and (iv) agricultural products (i.e. fruits, cereals and sunflowers; see Table I). Although no data about food availability were available, underground storage organs and wild fruits were mainly present in deciduous woodlands and shrubwoods, whereas agricultural products were only present in the northern part of the study site (Figure 1). Fragments were identified through the use of local reference collection, including those used by Bruno and Riccardi (1995) and Lovari et al. (2017).

Volumes of each food category were measured by water displacement (Bruno & Riccardi 1995). The relative frequency of occurrence was computed as \(RF_{ij} = \frac{n_{ij}}{N_j} \times 100\), where \(n_{ij}\) is the number of times the \(i\) food category was observed in the diet of the porcupine during the season \(j\), and \(N_j\) is the total number of food categories in the same season. Relative volume was calculated as \(V_{ij} = \frac{\sum v_{ij}}{\sum V_j} \times 100\), where \(v_{ij}\) is the volume (in cc) of the \(i\) food category observed in the diet of the porcupine during the season \(j\), and \(V_j\) is the total volume of food categories in the same season (Corsini 1998).

Results

Underground storage organs of wild plants made up the staple of the diet of the porcupine throughout the year, followed by wild fruits in the cold period and by agricultural products (cf. Table I) in the warm months (Figure 2). Accordingly, consumption of both wild and cultivated fruits significantly changed between the warm and the cold period (\(\chi^2 = 21.73, df = 1, P \ll 0.01\)).

Table I. Percentage (relative frequencies) of each fruit species in the diet of the crested porcupine.

| Fruit    | Wild/cultivated | Cold months (%) | Warm months (%) | G-test |
|----------|-----------------|-----------------|-----------------|--------|
| Acorn    | Wild            | 34.92           | 5.28            | 27.78**|
| Pear     | Wild            | 15.93           | 3.02            | 10.57**|
| Pine nut | Wild            | 30.85           | 0.00            | NA     |
| Sunflower| Cultivated      | 0.00            | 37.36           | NA     |
| Lucerne  | Cultivated      | 1.36            | 6.42            | 3.70** |
| Cereals  | Cultivated      | 0.00            | 17.36           | NA     |
| Watermelon| Cultivated  | 0.00            | 10.19           | NA     |
| Fig      | Cultivated      | 1.36            | 8.30            | 5.79** |
| Other    | Wild/cultivated | 15.59           | 12.08           | 0.45   |

**Highly significant P-values (< 0.01); NA, not applicable (i.e., number of records = 0 in one period).

Discussion

Our study area afforded an interesting opportunity to study how the diet of crested porcupine responds to food availability throughout the year, as it included both cultivated and natural habitats. Underground storage organs and barks of wild plants, stems and leaves of wild plants, wild fruits, and agricultural products (i.e., sunflowers) were all present in the diet. The category “Others” (Table I) potentially included both wild and cultivated fruits which were not identified through microscopy analyses.
storage organs (i.e. Cyclamen spp., Rumex spp. and Ruscus aculeatus L., 1753) made up the staple of the diet of the crested porcupine throughout the year. Wild fruits were observed in the diet during cold months and were substituted with agricultural products (oats, figs, watermelons, sunflowers and apples) in warm ones. Alkon and Saltz (1985) defined as “crop foragers” Indian crested porcupines feeding mainly on cultivated species, whereas those feeding mainly on wild food resources were called “natural foragers”. Usually, crop foragers have small home ranges and are more specialised in terms of feeding ecology, with den sets close to cultivated fields, whereas natural foragers show larger home ranges and are generalist feeders (Sever & Mendelssohn 1991; Lovari et al. 2013). Habitat productivity and home range size are inversely proportional for porcupines (Sever & Mendelssohn 1991; Lovari et al. 2013). In deciduous woodlands, fruits and epigal parts of plants were largely consumed throughout the year (Bruno & Riccardi 1995). In arid/semiarid environments (e.g. our study site), wild fruits are not available throughout the year and porcupines have to travel long distances (up to 3.5 km from the dens) to search for food (Alkon & Saltz 1985; Sever & Mendelssohn 1991; Lovari et al. 2013; Mori et al. 2014a). In our study area, the diet of porcupines seems to be determined by fruit phenology. In other words, porcupines behaved as generalist, natural foragers, choosing food items according to their seasonal availability. Furthermore, although digging geophytes may require a relevant amount of energy and expose porcupines to predators, underground storage organs of geophytes and hemicryptophytes represent the only food category consumed that is available throughout the year (Sever & Mendelssohn 1991). Underground storage organs and agricultural products free porcupines from the need to drink water, an important adaptation in a semiarid environment (Alkon & Saltz 1985). This feeding habit provides porcupine with an adaptive advantage where predation risk is the lowest, e.g. in Italy (Mori et al. 2014b). Seasonal changes in ranging movements (showed by Mori et al. 2014a) are due to a sensitive response in forage availability; “natural” forage, i.e. roots and wild fruits, mostly feed porcupines between October and March. During the warm months, when fruit production in Mediterranean macchia reaches its yearly minimum (Lucherini & Lovari 1996; Massee et al. 1997; Lovari et al. 2013), crested porcupines range towards other areas, i.e. farmlands (Mori et al. 2014a), determining an increase in the usage of agricultural products.

Acknowledgements

Financial support for this project was provided to Professor Sandro Lovari (University of Siena) by the Provincial Councils of Grosseto. Two anonymous reviewers and the Assistant Editor significantly improved our first draft with their comments.

Funding

This work was supported by the University of Siena.

References

Alkon PU, Saltz D. 1985. Potatoes and the nutritional ecology of crested porcupines in a desert biome. The Journal of Applied Ecology 22:727–737. DOI: 10.2307/2403225.
Barthelmess E. 2006. Hystrix afer. Mammalian Species, American Society of Mammalogy 788:1–7. DOI: 10.1644/788.1.
Bertolino S, Colangelo P, Mori E, Capizzi D. 2015. Good for management, not for conservation: An overview of research, conservation and management of Italian small mammals. Hystrix, the Italian Journal of Mammalogy 26:25–35.
Bruno E, Riccardi C. 1995. The diet of the crested porcupine Hystrix cristata L., 1758 in a Mediterranean area. Mammalian Biology 60:226–236.
Corsini MT. 1998. Selezione trofica nell’istristo Hystrix cristata in un’area rurale. Tesi di Dottorato di Ricerca in Biologia Animale (Zoologia). Università degli Studi di Siena, Siena, Italy.
Kruuk H. 1989. The social badger: ecology and behaviour of group-living carnivore (Meles meles). Oxford: Oxford University Press.
Laurenzi A, Bodino N, Mori E. 2016. Much ado about nothing: Assessing the impact of a problematic rodent on agriculture and native trees. Mammal Research 61:65–72. DOI: 10.1007/s13364-015-0248-7.
Loveri S, Corsini MT, Guazzini B, Romeo G, Mori E. 2017. Suburban ecology of the crested porcupine in a heavily poached area: A global approach. European Journal of Wildlife Research 63:10. DOI: 10.1007/s10344-016-1075-0.
Loveri S, Sforzi A, Mori E. 2013. Habitat richness affects home range size in a monogamous large rodent. Behavioural Processes 99:42–46. DOI: 10.1016/j.beproc.2013.06.005.
Lucherini M, Loveri S. 1996. Habitat richness affects home range size in the red fox Vulpes vulpes. Behavioural Processes 36:103–105. DOI: 10.1016/0376-6357(95)00018-6.
Massei G, Genov PV, Staines BW, Gorman ML. 1997. Factors influencing home range and activity of wild boar (Sus scrofa) in a Mediterranean coastal area. Journal of Zoology, London 242:411–423. DOI: 10.1111/j.1469-7998.1997.tb03845.x.
Monetti L, Massolo A, Sforzi A, Loveri S. 2005. Site selection and fidelity by crested porcupines for denning. Ethology Ecology & Evolution 17:149–159. DOI: 10.1080/08927014.2005.9522604.
Mori E, Loveri S, Sforzi A, Romeo G, Pisani C, Massolo A, Fattorini L. 2014a. Patterns of spatial overlap in a monogamous large rodent, the crested porcupine. Behavioural Processes 107:112–118. DOI: 10.1016/j.beproc.2014.08.012.
Mori E, Maggini I, Mennetetti M. 2014b. When quills kill: The defense strategy of the crested porcupine Hystrix cristata L.,
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. Italian Journal of Zoology 80:469–480. DOI: 10.1080/11250003.2013.857729.

Panzeri M, Menchetti M, Mori E. 2014. Habitat use and diet of the Eurasian scops owl *Otus scops* in the breeding and wintering periods in Central Italy. Ardeola 61:393–399. DOI: 10.13157/arla.61.2.2014.393.

Pigozzi G, Patterson IJ. 1990. Movements and diet of crested porcupines in the Maremma Natural Park, central Italy. Acta Theriologica 35:173–180. DOI: 10.4098/0001-7051.

Sever Z, Mendelssohn H. 1991. Spatial movement patterns of porcupines (*Hystrix indica*). Mammalia 55:187–205. DOI: 10.1515/mamm.1991.55.2.187.

Trucchi E, Facon B, Gratton P, Mori E, Stenseth NC, Jentoft S. 2016. Long live the alien: Is high genetic diversity a pivotal aspect of crested porcupine (*Hystrix cristata*) long-lasting and successful invasion? Molecular Ecology 25:3527–3539. DOI: 10.1111/mec.2016.25.issue-15.