



Habitat richness affects home range size in a monogamous large rodent



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ABSTRACT

In monogamous species, after pair formation, the main reason for ranging movements is not searching for a mate, but for other important resources e.g. food. We monitored a total of 20 radio-tagged adult, paired crested porcupines in four areas of different habitat richness. No sexual size dimorphism was assessed. Body mass and habitat richness showed collinearity. For both sexes, home range size was correlated to habitat richness, with a significant inverse exponential regression. Opposite to natural foragers, living in poor habitats, crop foragers had smaller home ranges, with their dens significantly closer to cultivations. Both availability of food resources and den sites are key variables to determine home range size.

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1. Introduction

Ranging movements vary between species (e.g. Harestad and Bunnell, 1979) and between individuals of the same population (e.g. Hewison et al., 1998; Smith and Schaefer, 2002). Intraspecific variation of movements is inversely related to distribution and availability of food resources (e.g. Macdonald, 1983; McLoughlin and Ferguson, 2000; Herfindal et al., 2005). While large species are forced by their metabolic requirements to occupy wide areas, small species, e.g. rodents, may show a greater variety of home range sizes (Schmidt-Nielsen, 1984), e.g. depending on availability of key-resources (Gaston and Blackburn, 1996). As to large rodents, so far, no study has been carried out to compare variations of home range size between different populations of the same species in areas with different habitat characteristics.

The crested porcupine *Hystrix cristata* L., 1758, is a sedentary (Amori et al., 2009), monogamous (Kleiman, 1977) large rodent. Apparently, porcupines show a sexual size dimorphism privileging females, who are c. 11% larger than males (Pigozzi, 1987). Crested porcupines are generalist rodents who can live in a variety of habitats, from deciduous moist forest to arid environments and to suburban areas (Amori et al., 2009). Vegetation types influence crested porcupine ranging behaviour, by providing cover against predation (Corsini et al., 1995). Underground storage organs

(e.g. roots, bulbs, tubers), vegetables and fruits, depending on their availability, build up the staple of diet (Bruno and Riccardi, 1995). Two feeding strategies were described for the closely related species *H. indica* and *H. africae australis*: Saltz and Alkon (1989) termed as “crop foragers” Indian porcupines from populations feeding only in cultivated fields, whereas those feeding mainly on wild food resources were called as “natural foragers”. Usually, the former had small home ranges, with burrows close to cultivated fields, whereas the latter showed larger home ranges (e.g. Saltz and Alkon, 1989; Corbet, 1991; Sever and Mendelsohn, 1991).

Crested porcupines are active during the night (Corsini et al., 1995) and spend most of the daylight hours in their dens (Monetti et al., 2005). Knowledge on the spatial ecology of *H. cristata* is limited to two studies, with a very small number of radio-tagged individuals (1 individual: Pigozzi and Patterson, 1990; 4 individuals: Sonnino, 1998). Our work has been based on ten years (1990–2000) of radiotracking data, on a sample of 20 adult individuals, 12 “natural foragers”, 8 “crop foragers” (*sensu* Saltz and Alkon, 1989). Not only the amount, quality and availability of food resources determine the habitat value/size to a forager (Brown and Alkon, 1990), but the availability of suitable denning sites seems to be another important variable (Monetti et al., 2005).

We compared range sizes of individuals from localities with different levels of habitat heterogeneity, to test the hypotheses that (i) habitat richness, (ii) sex, (iii) distance between den and feeding sites and (iv) body mass influence home range (hereafter, HR) size.

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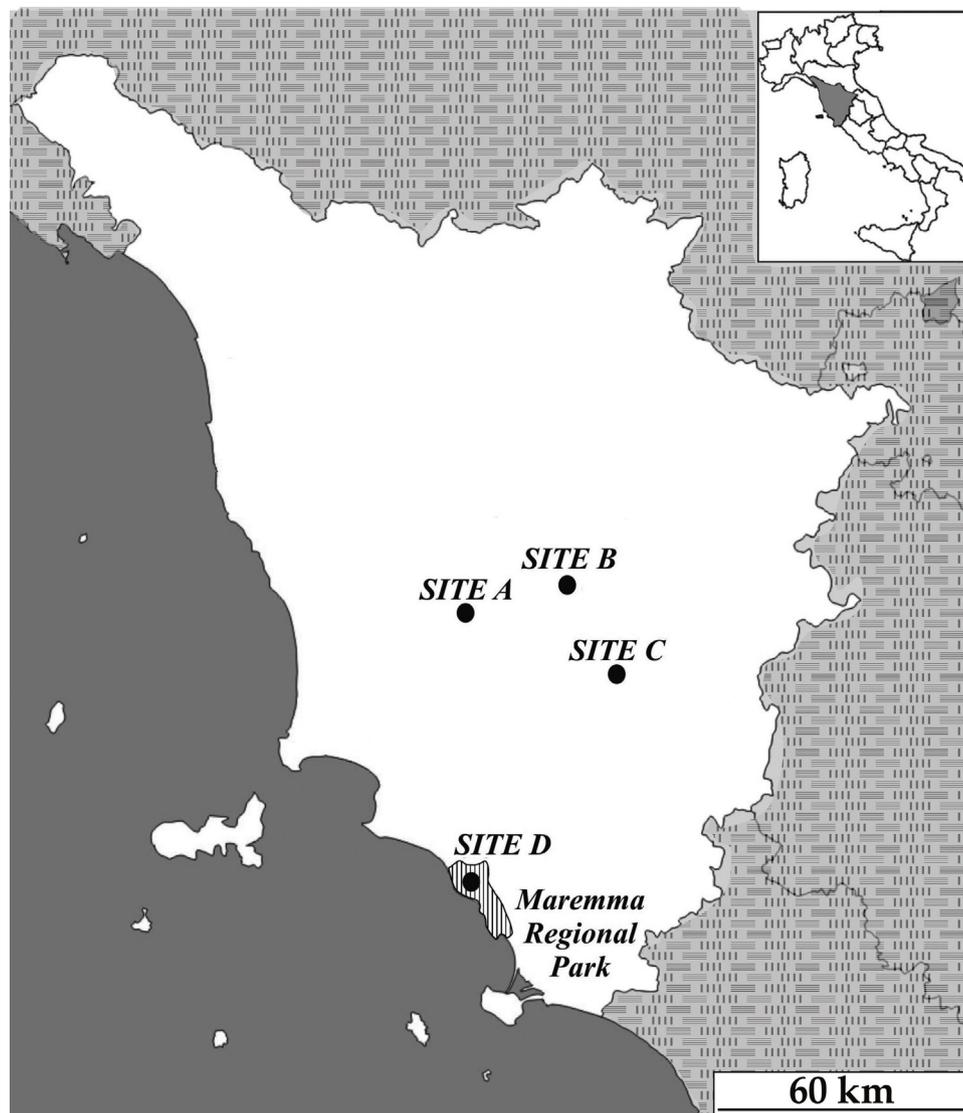


Fig. 1. Location of study sites.

2. Study area

The study area included four sites in Southern Tuscany (Siena and Grosseto districts: Central Italy), characterized by different vegetation features (Fig. 1).

Site A (Calvaiano, Siena: private estate, deciduous wood/fallow: 43°18' N, 11°05' E; altitude: 201–388 m a.s.l.; size: c. 750 ha) was a rural hilly area characterized by a mesophilic mixed oakwood (54%: mainly *Quercus cerris*, *Quercus pubescens*, *Acer campestre*, *Fraxinus oxycarpa* and *Ulmus minor*), fallows (38%) and scrubwoods (6.4%: *Juniperus* sp., *Rubus* sp., *Arbutus unedo* and *Spartium junceum*): just 1.6% was covered with cultivated fields. Monthly average rainfall was about 54 mm.

Site B (San Miniato, Siena: vegetable gardens, sub-urban gardens/cultivations: 43°20' N, 11°20' E; altitude: 270–345 m a.s.l.; size: c. 250 ha) was a suburban area of Siena. About 26% was constituted by cultivated fields (turnip, barley and other cereals) and 16% by vegetable gardens (with a high variety of vegetables) and orchards (apples, peaches, olive groves and vineyards). Just 13% of the area was covered with woods (mainly *Q. pubescens*, *Castanea sativa* and introduced *Robinia pseudoacacia*) and shrubs (*S. junceum* and *Rubus ulmifolius*): about 17.4% of the area was covered with buildings and urban settlements. Other habitat

types (uncultivated fields, hedges and ditches) represented the remaining 27.5%. Monthly average rainfall was about 63.8 mm.

Site C (“Le Malandrine”, Siena: agricultural estate, farmland: 43°10' N, 11°30' E, altitude: 140–250 m a.s.l.; size: 400 ha) was a highly fragmented rural area. About 80% was characterized by cultivated (c. 76%: cereals, sunflowers, legumes) and abandoned fields (c. 4%). The remaining 20% was covered with woods (mainly *Quercus* sp. and *Ostrya carpinifolia*) and shrubs (*S. junceum*, *Prunus spinosa*, *Ligustrum vulgare*, *Crataegus monogina*, *Cornus sanguinea*, *Rosa canina* and *Rubus* sp.). Monthly average rainfall was about 61 mm.

Site D (Maremma Regional Park, Grosseto: scrubwood/pinewood: 42°39' N, 11°05' E, altitude: 0–229 m a.s.l.; size: about 2315 ha) was located in a protected area along the Tyrrhenian coast. It was characterized by a pinewood (*Pinus pinea* and *P. pinaster*), with a dense belt of junipers (*Juniperus oxycedrus*) and shrubs (*S. junceum*, *Cytisus scoparius*, *Calycotome spinosa*) near the shore, and Mediterranean “macchia” (*Quercus* sp., *Phyllirea* sp., *Cistus* sp., *Rosmarinus officinalis*, *Erica multiflora*, *Pistacia lentiscus*, *Limonium etruscum*). Monthly average rainfall was about 58 mm.

The environmental parameters of the four study areas have been summarized in Table 1.

Table 1
Main environmental parameters of study sites. For proportions of ecological parameters, see text. Bottom row, mean \pm SD.

Site	Altitude (m a.s.l.)		Mean annual temperature ($^{\circ}$ C)	Monthly mean rainfall (mm)
	Min.	Max.		
A	201	388	15.2	54
B	270	345	16	63.8
C	140	250	14.4	61
D	0	229	15.3	58
	152.75 \pm 114.85	303 \pm 75.88	15.23 \pm 0.66	59.20 \pm 4.20

3. Materials and methods

Home-made metal box traps, baited with fruits and vegetables (potatoes, apples, pears, plums, corn, carrots), were activated for at least seven nights per month and checked at sunset and dawn, during each trapping session.

The analyses of spatial data were carried out on adult (age determined through eruption of permanent premolars: van Aarde, 1985; Pigozzi, 1987) individuals radio-tracked continuously (VHF radio-collars: AVM, USA; Biotrack, UK) for a minimum of 12 months and a maximum of 14 months (10 males and 10 females; site A: $n=4$, site B: $n=4$, site C: $n=4$, site D: $n=8$). All our radio-tagged porcupines were paired, *i.e.* male and female of 8 pairs were radio-tagged, whereas the mates of the remaining individuals had radio-tags on, but they were not included in this study because of premature tag failure. As there were 8 pairs of porcupines in our radio-tracked sample and pair members tend to move together (Sever and Mendelsohn, 1991; Corbet and Van Aarde, 1996), relevant data on HR size could be pair-autocorrelated. Then, we cross-analysed our data by sex, including also the porcupines whose mates wore non-functioning radio-tags.

After sampling evenly throughout the day and the night for one week, fixes were concentrated in dark hours, because of the consistent nocturnal activity of this species (Corsini et al., 1995). We controlled for the biological independence of fixes between successive locations (Swihart and Slade, 1985). The same telemetry procedure was used throughout all the study areas, *i.e.* a mixture of distance locations (*i.e.* median, 1 fix/37.5 min, Q1–Q3 = 30–63.75; median location error = 58 m, Q1–Q3 = 52–64) and homing in (1 fix/15 min; median location error = 17.85 m, Q1–Q3 = 6–31.58), for a median value of 46.54 fixes/month/individual, Q1–Q3 = 36.35–50.31. HR data for

site A have been taken from Corsini (1992) and Sonnino (1998). Since these authors estimated HR sizes of porcupines through the Minimum Convex Polygon (MCP), the same method was used to compare their results with those of the other sites. The shortcomings of MCP (*e.g.* Burgman and Fox, 2003) have been mitigated (*cf.* Saltz and Alkon, 1989; Corbet and Van Aarde, 1996) by discarding the peripheral 5% of fixes, *i.e.* the extreme locations. Home ranges for sites B, C and D were also estimated through 95% fixed kernel. This probabilistic method may provide a more accurate estimation of space use within the home range (Worton, 1989).

MCP and kernel estimates were calculated through the statistical software R 2.13.1, packages *ade4* (Dray and Dufour, 2007) and *adehabitat* (Calenge, 2006).

We used general linear models (Crawley, 2007) to analyse the effects of sex, body mass, maximum linear distance between dens and cultivated fields and habitat richness of HR size. Habitat richness has been estimated as a function of the number of habitat types (*i.e.* main vegetation cover) per ha, within each HR (*cf.* Lucherini and Lovari, 1996). The body mass of each individual was measured in autumn, thus avoiding a seasonal bias. As HR sizes were not normally distributed (Shapiro–Wilk test = 0.834; $P=0.003$), they were log-transformed (Shapiro–Wilk test = 0.907; $P=0.065$). Body mass and habitat richness showed a high value of intercollinearity ($r=0.688$), as well as habitat richness and linear distances between dens and cultivated fields ($r=-0.767$). Only habitat richness was retained for analyses (*e.g.*: Green, 1979; Sergio et al., 2003). All the variables were included in a total model. Non-significant ones were removed one at a time, until the elimination of terms caused a significant increase in the residual deviance (Crawley, 2007). *F*-Like deletion tests were used to assess the significance of changes in residual deviance (Crawley, 2007).

Table 2
Annual HR size for all the individuals, sex, body mass, habitat richness (number of habitat types per ha) and linear distance between dens and cultivated fields.

Site	Sex	Body mass (kg)	HR size		HR habitat richness		Distance den-cultivated fields (m)
			95% MCP	95% kernel	95% MCP	95% kernel	
A	F	13.80	98.00	–	0.02	–	225.00
A	M	12.10	265.90	–	0.13	–	345.0
A	M	13.50	30.10	–	0.15	–	90.00
A	M	11.40	34.20	–	0.04	–	120.00
B	F	14.50	18.00	13.69	0.33	0.44	93.67
B	F	13.60	32.88	13.87	0.18	0.43	120.44
B	M	14.80	10.88	8.85	0.55	0.56	93.67
B	M	13.80	28.38	16.19	0.32	0.47	120.44
C	F	14.50	57.73	46.10	0.09	0.11	162.5
C	F	12.30	21.27	8.58	0.19	0.23	34.20
C	M	11.10	16.65	6.74	0.24	0.29	162.5
C	M	11.40	14.79	5.92	0.27	0.34	34.20
D	F	10.60	308.61	194.76	0.03	0.03	2230.6
D	F	11.30	116.45	91.88	0.07	0.08	685.11
D	F	12.20	181.78	146.62	0.03	0.04	318.60
D	F	10.10	478.15	152.93	0.01	0.03	2125.6
D	F	10.20	372.82	236.28	0.02	0.02	1219.1
D	M	9.80	398.69	179.62	0.02	0.03	2125.6
D	M	11.70	280.74	238.77	0.03	0.03	2230.6
D	M	12.60	189.84	154.39	0.05	0.05	1219.1

Table 3
Factors affecting HR size in *Hystrix cristata*, estimated through a general linear model.

Variable	B	Standard error	P
Site A	0.038	0.143	0.794
Site B	0.251	0.141	0.096
Site C	0.594	0.201	0.015*
Site D	0.716	0.133	<0.001***
HR habitat richness	-2.056	0.520	0.001**
Intercept	1.774	0.132	<0.001***

* Significant $P < 0.05$.

** Significant $P < 0.01$.

*** Significant $P < 0.001$.

4. Results

All porcupines were monitored (median number of fixes per individual, 558.5; Q1–Q3, 436.3–603.8) for 14–20 h/week/individual. HR size was not associated to sample size, *i.e.* number of fixes ($r = 0.482$; $n = 20$, $P = 0.345$). HR sizes of male crested porcupines varied from 10.0 to 398.7 ha (median value, 32.2; Q1–Q3, 19.6–246.9; $n = 10$; Table 2), whereas those of females ranged from 18 to 478.15 ha (median value, 107.225; Q1–Q3, 39.093–276.903; $n = 10$; Table 2). No significant difference was found between the HR sizes of males and those of females (Wilcoxon sum range test: $W = 36$; $P = 0.38$).

No significant difference was also found between the mean body mass of adult male (mean \pm SD: 12.23 ± 1.57 kg) and female (mean \pm SD: 12.14 ± 1.74 kg) porcupines ($t = 0.13$; $P = 0.899$).

In our total model, HR sizes did not differ significantly between sexes ($B = 0.1056$; $P = 0.9417$). In the final model, HR size was significantly influenced by HR habitat richness (Table 3; Fig. 2; $R^2 = 0.965$). The former decreased significantly with the increasing of the latter, and was significantly greater in sites A and D (Table 3).

Since HR size showed no significant difference between sexes, data of all individuals from the four sites were pooled together. An exponential model explained 97.9% of the variance in HR sizes (Fig. 2). Comparable results were obtained when the 95% kernel was used to assess HR sizes for sites B–C–D (Fig. 2).

We analysed our data also by sex and we obtained comparable results (95% MCP: $N = 10$ males, $y = 4.6689x^{-1.104}$, $R^2 = 0.953$; $N = 10$ females, $y = 4.5405x^{-1.095}$, $R^2 = 0.962$; 95% kernel: $N = 7$ males, $y = 3.1399x^{-1.203}$, $R^2 = 0.876$; $N = 9$ females, $y = 4.0962x^{-1.083}$, $R^2 = 0.884$).

We looked for differences in spatial behaviour both overall (*i.e.* study area) and at the local (within each study site) scale. At the study area scale (sites A, B, C, D), crop foragers showed smaller

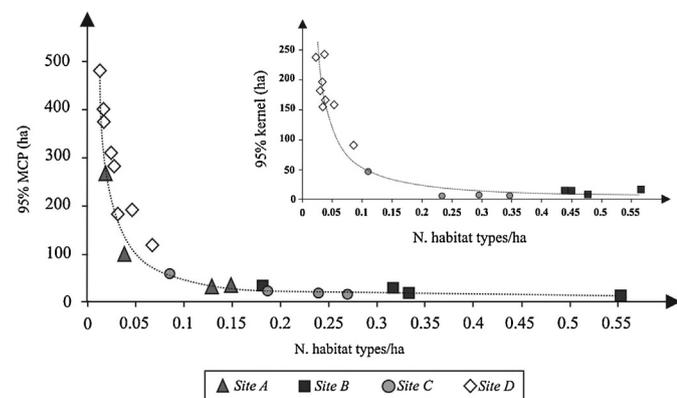


Fig. 2. Relationship between annual HR size of 20 adult individuals (each symbol is one individual) and habitat richness within their own HRs (95% MCP: $y = 4.6523x^{-1.095}$, $R^2 = 0.979$; 95% kernel: $y = 3.5478x^{-1.141}$, $R^2 = 0.882$).

annual HRs than those of natural foragers (Wilcoxon sum range test: $W = 4$; $P = 0.0002$).

In sites A and D, during the summer, porcupines travelled significantly greater distances to reach their feeding grounds (cereal crops), located at the border of the site, with a median straight-line distance of 1219.1 m (Q1–Q3, 331.8–2125.6; Wilcoxon sum range test; $W = 86$; $P = 0.0038$).

5. Discussion

Individuals tend to occupy the smallest area containing the resources they need (Harestad and Bunnell, 1979), adjusting their spatial movements to fulfil metabolic requirements (Armstrong, 1965). Mainly, mate and food resource availability influences movements of animals (*e.g.* Powell, 1979; Kruuk, 1989). According to the Resource Dispersion Hypothesis (RDH; Macdonald, 1981, 1983; Carr and Macdonald, 1986), the distribution and quality of natural resources, *e.g.* partners/sites for reproduction, refuge areas, food resources, determine HR size and group size. While there is a wealth of studies supporting RDH for Carnivores (*e.g.* Macdonald, 1981; Kruuk, 1989; Valenzuela and Macdonald, 2002), the picture is much less clear for herbivores and relevant studies are few (Herrera and Macdonald, 1989; Taber and Macdonald, 1992; Brambilla et al., 2006). The ecological determinants of monogamy in porcupines have not yet been identified. Subadult and adult crested porcupines are well protected by long quills covering their bodies, which makes them rarely preyed upon (Mohr, 1965). In the first few days of life, cubs have relatively soft quills and, thereafter, up to three months old, they have sturdy, but quite short quills (Mohr, 1965), which makes them much more exposed to predation than the adults. Thus, parental defence could be triggered (*cf.* Sever and Mendelsohn, 1989) and obligate monogamy may develop, as both members of the pair are necessary to protect the cubs (*e.g.* Kleiman, 1977; Morris and Van Aarde, 1985; Sever and Mendelsohn, 1988). In fact, male and female alternate in the den with cubs, while the other partner is out foraging (Mohr, 1965), and, when outside the den, the cubs are kept between the parents (*e.g.* Gosling, 1980; Corbet, 1991).

As crested porcupines are monogamous (Kleiman, 1977), one could rule out mate search as the main reason for ranging movements of paired individuals, which supports our finding on the importance of habitat richness to determine their movements.

Our finding that sex does not influence HR size is consistent with the lack of a significant sexual size dimorphism in our sample of crested porcupines (sex ratio, 1:1), whereas the variables “distance den-feeding site” and “body mass” were collinear with habitat richness. Thus, we did not consider them in our analysis, which we centred on habitat features.

Crops are concentrated and predictable food resources, influencing the size of the individual’s HR in both crop and natural foragers (Alkon and Saltz, 1985; Saltz and Alkon, 1989; Sever and Mendelsohn, 1991). In extensive-agricultural landscapes, characterized by a high environmental heterogeneity (sites B and C), porcupines showed small HRs. In areas where environmental heterogeneity was low (sites A and D), *i.e.* with scarce food resources and/or denning sites, the size of HRs was larger. Most likely, HR size reflected the seasonal dispersion of food resources in respect to the den location, which, in turn, may have led to an increase of HR size throughout the year. Seasonal variation in food availability could have forced natural foragers (sites A and D) to display a spatial behaviour known as “seasonal contraction” *i.e.* increased HR size when resources are dispersed/far from the den, and decreased HR size when resources are concentrated/close to the den (Kruuk and Macdonald, 1985; Corbet and Van Aarde, 1996). In other studies (Saltz and Alkon, 1989; Corbet, 1991), crop foragers lived in dens

near cultivations, but in our study area (*sites A and D*), cultivated fields were located in sandy areas, unsuitable for denning (Corsini et al., 1995; Monetti et al., 2005). In *sites B and C*, where dens were located close to cultivated fields, crested porcupines behaved as crop foragers throughout the year, possibly integrating with natural food resources during the winter.

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