

## Site selection and fidelity by crested porcupines for denning

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The crested porcupine is a large rodent living in Central and North Africa, with a European distribution limited to Italy. Its biology and particularly its denning habits are inadequately known. Our study was carried out in a Mediterranean coastal area of central Italy.

We radiotagged 13 adult porcupines, assessing their den site selection and use each month, from February 1998 to September 1999.

Porcupines preferred steep, compact soils covered with dense vegetation, for denning. Each den was always used by the same 2 individuals, possibly forming a reproductive pair. Paired individuals seemed to show a greater site fidelity than single ones. Interpretations of this behaviour are discussed.

KEY WORDS: crested porcupine, *Hystrix cristata*, rodents, burrowing mammals, site fidelity, resource selection.

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### INTRODUCTION

Dens provide refuge against predators and shelter against harsh weather conditions (FERNANDEZ & PALOMARES 2000, ROPER et al. 2001). Den site selection and use in mammals may be determined by the sex and age of individuals, as well as by ecological factors (e.g. availability of suitable sites, ENDRES & SMITH 1993).

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The crested porcupine *Hystrix cristata* L. 1758 is an ecologically generalist, large (8-16 kg) burrowing rodent. Its distribution extends from tropical forests to arid environments (KINGDON 1974, WOODS 1993, ANGELICI & AMORI 1999). In Central Italy, the crested porcupine mainly feeds on roots, bulbs, fruit and cultivated plants (sunflowers *Helianthus annuus*, cereals and others), both on hypogeal and epigeal parts (SANTINI 1980, BRUNO & RICCARDI 1995, BOZZI & LOVARI 1999), whereas no information on its diet is available elsewhere.

In daylight, crested porcupines stay in dens located in dry ground, usually covered with dense vegetation (TINELLI & TINELLI 1988, CORSINI et al. 1995). Den structure is described as a network of chambers connected by tunnels, with one or several entries (TINELLI & TINELLI 1988, FELICIOLI & SANTINI 1994). Each den may be inhabited by one or more pairs and their offspring (SANTINI 1980).

Den site selection and the use of dens by crested porcupines have never been studied. Our purpose was to investigate the characteristics of denning sites and their selection by porcupines, and to draw inferences concerning the spatial aggregation of porcupines in their dens. In particular, as in our study area den sites were not a limited resource, we expected porcupines not to aggregate for denning as reported elsewhere (SANTINI 1980), but rather that den site selection would really be the result of active selection instead of the use of a few available sites.

#### MATERIALS AND METHODS

Our study site (Fig. 1) was located in a Mediterranean coastal area, the Maremma Regional Park (42°39'N, 11°05'E, Grosseto Province, Tuscany, Italy). The vegetation was characterised by dense scrubwood, pinewood, sparse pasture, cultivated and abandoned olive groves *Olea europaea*, maize *Zea mays*, and sunflower *Helianthus* spp. (ARRIGONI 1988). Mean monthly temperature was 15.0 °C, and mean monthly rainfall was 57.6 mm. Altitude ranged from sea level to 417 m a.s.l. The geology of the area is characterised by a calcareous massif, with diffuse karstic formation. Mainly scrubwood (*Quercus ilex*, *Arbutus unedo*, *Fraxinus ornus*, *Pistacia lentiscus* and *Quercus pubescens*) covered most of the study area, alternating to open areas of *Erica multiflora*, *Rosmarinus officinalis*, *Juniperus oxycedrus macrocarpa* and *Pistacia lentiscus* (ARRIGONI 1988). Along the coast, a wide patch of pinewood, *Pinus pinea* and *P. pinaster*, and a retrodune of *Juniperus oxycedrus macrocarpa* (BERTANI & PASQUALI 1988) occurred (Fig. 1).

The area is a typical Mediterranean ecosystem. Its wildlife included wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, fallow deer *Dama dama* and red fox *Vulpes vulpes*, along with Eurasian badger *Meles meles*, wild cat *Felis silvestris*, stone marten *Martes foina*, an introduced population of coypus *Myocastor coypus*, and several species of small mammals.

The study took place between February 1998 and September 1999. The animals were trapped using 14 double entry box traps (150 × 40 × 55 cm), positioned along the main trails used by porcupines. Traps were baited daily and set for at least 7 nights/month (98 trap nights/month, for 20 months) to be checked at dawn. Animals were darted and immobilised as described in MASSOLO et al. (2003).

Handling procedures consisted of sexing, weighing, taking standard body measurements, assessing tooth wear and ear-tagging. Adult porcupines were fitted with VHF radio-collars (125 gr, 150-151 MHz, Televilt® Ltd, Sweden, and Biotrack® Ltd, UK), whose weights were about the 1.24% (± 0.032) of male porcupines, and the 1.14% (± 0.038) of female ones. Following these procedures, porcupines were placed back in the trap covered with vegetation and released about two to three hours later. Re-locations of radio-tagged animals occurred in the first day after release, then twice a week for at least 6 months, using Telonics® (TR2) or Yaesu® (IIMFT-290RII) receivers, and Yagi® antennas (3 or 5 elements).

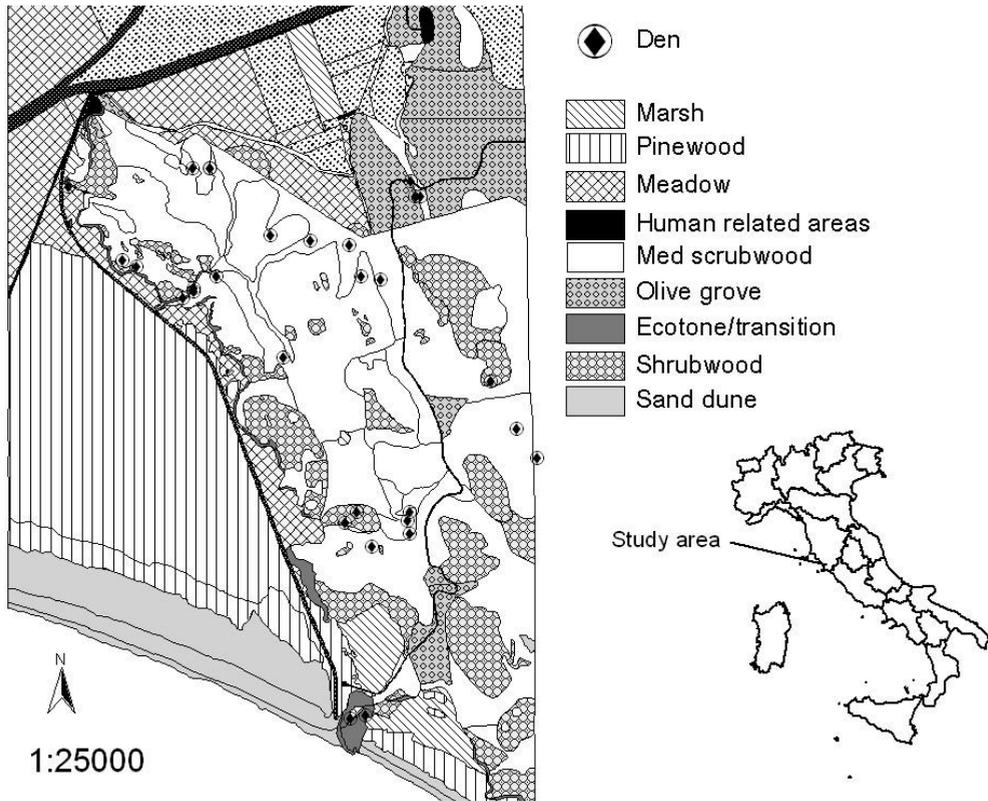


Fig. 1. — Study area in the Maremma Regional Park (Grosseto, Italy). Circles represent the locations of den sites of radio-collared porcupines from February 1998 to September 1999.

Each month, during daylight, we used the homing-in technique (KENWARD 1987) to locate the inhabited dens; each site was marked and geo-referenced. The entrances were precisely located, although no inference was possible regarding the chamber use.

We never found two den sites, used by radio-collared porcupines, closer than 150 m from each other, and entrances of the same den were never farther than 25 m apart. We arbitrarily defined a den site as a set of entrances no more than 30 m apart.

For each site, we measured slope angle, topography, habitat, as well as the main tree and shrub species in the environs of the site (10 m around each entrance). Den site was classified as exposed to the North (from 316-45°), the East (from 46-135°), the South (from 136-225°), and the West (from 226-315°). For each entrance, we measured the hole dimensions (height, width), internal and external slope angle (respectively, just inside and outside of the entrance), entrance floor and roof (rock, earth, or mixed). The slope angle of den sites was classified as A = 0-19°, B = 20-39° e C = 40-59°, whilst that of entrances was pooled in 2 classes: 1 = positive values (inside the entrance), 2 = negative values (outside the entrance).

The availability of sites with different aspect and slope angle was computed using a randomization procedure to sample 100 random locations in the study area (defined as the home range, MCP at 100%, of all radio-collared porcupines, increased by a peripheral buffer, 100 m wide). Availability of vegetation types was estimated using a Geographical Information System (ArcView 3.2 ESRI® for Windows).

A site fidelity index was calculated as the ratio between the number of den changes and the greatest possible number of changes (number of homing-in - 1); a value of 1 means that

porcupines changed den each month, 0 means that only one den was used. As crested porcupines are probably monogamous species (SANTINI 1980, CORSINI et al. 1995) and reproductive partners are usually found in the same den, we pooled the fidelity index values of mates. Furthermore, we estimated the proportion of dens used occasionally over the total number of used dens. A den site was considered as occasional if not used more than once. Finally, a pair bond index was computed for each paired porcupine as the proportion of times the animal was found in the den together with its mate.

### *Statistical methods*

We pooled data using the den sites as grouping variables, to avoid autocorrelation between entrances of same den sites, and then we used medians and Inter-Quartile distance (IQ) to describe data distributions (central tendency and variability, respectively).

The Chi-square test (SIEGEL & CASTELLAN 1988) was used to compare differences between frequencies of occurrence, in used and random sites, of different classes of aspect, slope angle and entrance features. The Mann-Whitney test was used to compare fidelity index for paired and solitary females (SIEGEL & CASTELLAN 1988). Exact significance levels were computed through permutation procedures, or estimated by Monte Carlo randomisation techniques (MEHTA & PATEL 1996, GOOD 2000).

We used the Bonferroni confidence intervals, based on a z-statistic, to test for selection of den site characteristics (aspect, slope angle, vegetation), when the chi-square test detected an overall significant difference in usage versus availability (NEU et al. 1974).

Statistical analyses were carried out using SPSS 9.01 (Statistical Package for Social Sciences, ©SPSS Inc., USA).

## RESULTS

We radiotracked 13 adult porcupines (5 MM, 8 FF), from February 1998 through September 1999. Most likely, our sample represented about 39% of the estimated adult population or, at least, of the trappable one ( $n = 33$ , Fig. 2).

Altogether, we located 30 different den sites of radio-collared porcupines, out of 56 den site records, over a total effort of 80 daylight trials. Most of the den sites (80.0%,  $n = 30$ ) were located mainly in the Mediterranean scrubwood. The habitats were not used according to availability ( $\chi^2 = 46.6$ , 10 df,  $P_{\text{Exact}} < 0.001$ ). The Bonferroni intervals (Fig. 3A) showed that porcupines significantly ( $P < 0.01$ ) preferred Mediterranean scrubwood, avoided cultivated land, marsh and pinewood, but they used as available the olive grove, the shrubwood and the garigue.

The vegetation cover of den sites was mainly represented by the ilex (41.3%) as the dominant tree species, and by the lentisk and the rosemary as dominant bushy species (51.9%).

Entrances had a median height of 24.0 cm (range = 13-72 cm; IQ = 14.0 cm), and a median width of 25.0 cm (range = 11-51 cm; IQ = 12.0 cm). The entry roofs were prevalently rocky ( $\chi^2 = 24.39$ , 2 df,  $P_{\text{Exact}} < 0.001$ ), whereas floors were mainly earthy ( $\chi^2 = 8.17$ , 2 df,  $P_{\text{Exact}} < 0.01$ ).

Slope angle of class B was preferred (20-39°;  $\chi^2 = 11.4$ , 2 df,  $P < 0.001$ ; Bonferroni confidence intervals,  $P_{\text{Exact}} < 0.01$ ). The Bonferroni confidence intervals also suggested a significant avoidance of flat terrains (slope angle class A: 0-19°). Steep slopes (class C: > 40°) were used as available (Fig. 3B).

Beyond the entrance, there was a significant ( $\chi^2 = 22.53$ , 1 df,  $P_{\text{Exact}} < 0.001$ ) tendency for porcupines to excavate descending tunnels (median = - 15.25°; IQ =

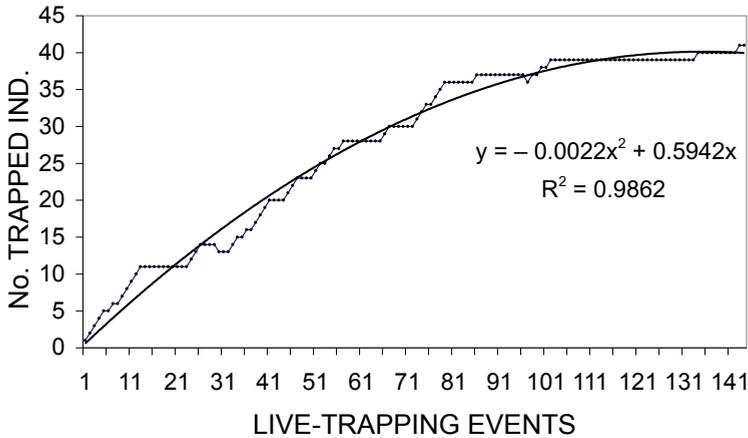


Fig. 2. — Total number (cumulative sum) of crested porcupines trapped during continuous live-trapping sessions in the Maremma Regional Park (Grosseto, Italy), from February 1998 to September 1999. Polynomial equation and the corresponding fit ( $R^2$ ) are reported.

15.25°). The spoil heap, dug out by the porcupine, in most cases (80.8%, 21/26) determined an inward slope angle (median = 11.00°; IQ = 14.10°;  $\chi^2 = 8.75$ , 1 df,  $P_{\text{Exact}} < 0.01$ ).

No significant differences were shown with regard to den site aspect ( $\chi^2 = 6.87$ , 3 df,  $P_{\text{Exact}} > 0.05$ ), but, when frequencies were compared to the availability of sites, we found a significant ( $P < 0.01$ ) avoidance of slopes exposed to the east and to the north (Fig. 3C).

As to den use, out of 56 locations, in 24 cases (42.9%) we found the same male-female pairs in the same dens, suggesting the existence of 5 reproductive units in our study area; in all other cases, only one collared individual was found in each den. Telemetry data (in prep.) would confirm the pair hypothesis, as usually porcupines belonging to the same pair were nearly always located together, even when outside the den.

During the study period, only 2 pairs (F15 & M12, F21 & M25) used only one den site. Pairs seemed to be more linked to den sites than unpaired porcupines (Fig. 4) used only one den site. The site fidelity index ranged from 0.22 to 1.00 for paired porcupines (mean = 0.73, SD = 0.30;  $n = 10$ ), whereas unpaired porcupines never used the same den site twice (site fidelity index = 0.00). Moreover, paired females showed a significantly higher fidelity than unpaired ones ( $U = 0.000$ ,  $P_{\text{Exact}} < 0.05$ ).

Most of the located dens (70.0%;  $n = 30$ ) were used only once (i.e. never longer than for 1 month) during the study period, whilst the others were used from 2 to 9 times.

Each den site was exclusive to one pair. In one case (3.3%;  $n = 30$ ), a den site was used by 2 females at different times, and never used by any other collared porcupine. The presence of uncollared porcupines in the dens we monitored can not

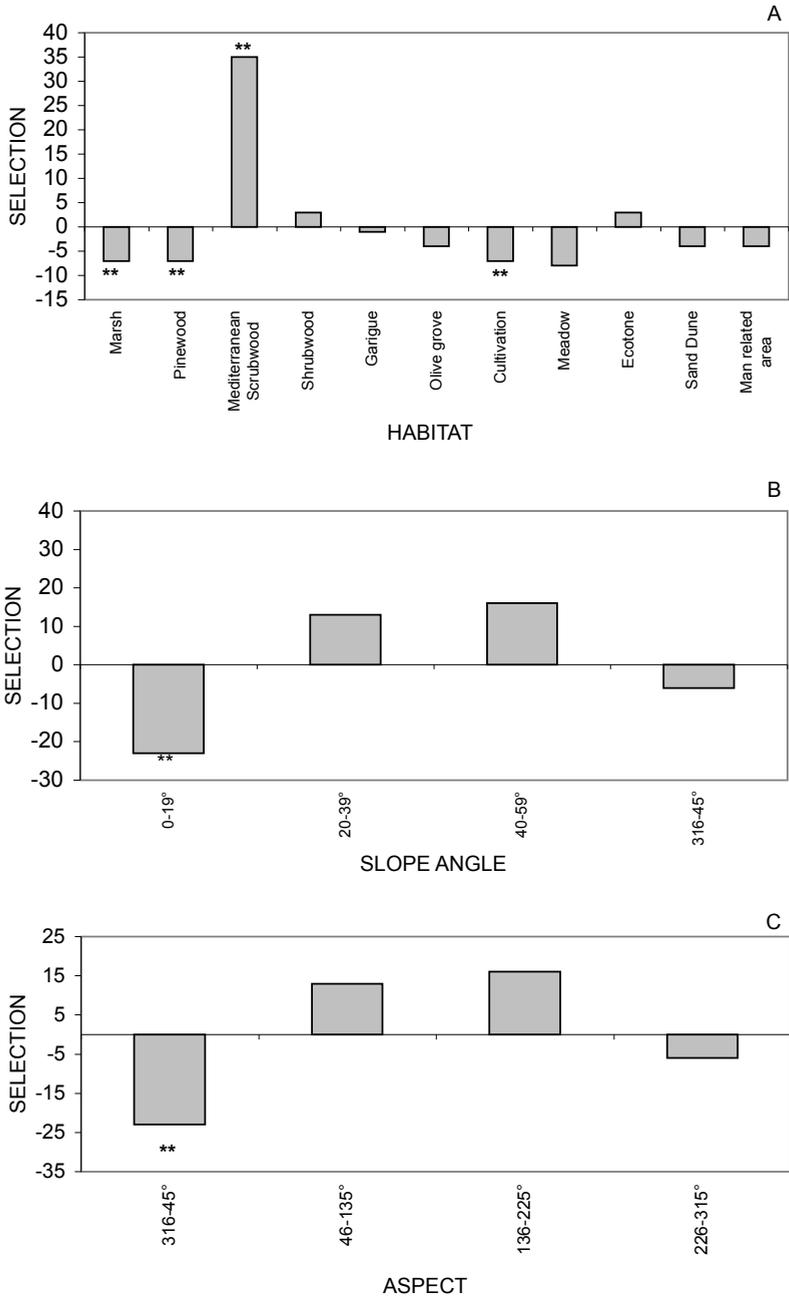


Fig. 3. — Results from a habitat selection analysis by the Bonferroni multiple comparisons method applied on a sample of den sites of 13 crested porcupines in the Maremma Regional Park (Grosseto, Italy), from February 1998 to September 1999. Selection is reported as the difference between the habitat use/category (expressed as percentage) and the availability. A, habitat type selection; B, slope angle selection; C, aspect selection. \*\*:  $P < 0.01$ .

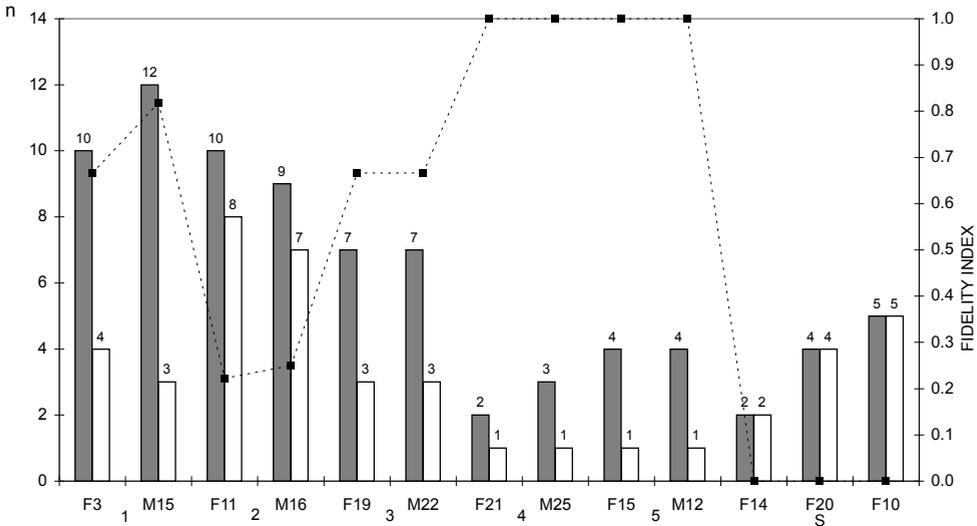


Fig. 4. — Number of homing-in sessions (grey bars), number of used dens (white bars), and fidelity index (black box, number of located dens over the maximum number of possible den changes) for each radio-collared crested porcupine in the Maremma Regional Park (Grosseto, Italy) from February 1998 to September 1999. Pair codes are marked beneath the individual codes (S = not paired individuals).

be ruled out, although we think it unlikely because no new adult individuals were caught in spite of our intensive trapping effort.

The mean pair bond index, as a proportion of the times when paired porcupines were found together, was equal to 0.69 ( $n = 5$ ,  $SD = 0.29$ ). Pair 2 (M16, F11) had a relatively low pair bond index (0.55 and 0.50 respectively), suggesting that the pair was not stable.

#### DISCUSSION

Our results show that crested porcupines preferred to den in areas covered with thick vegetation (Mediterranean scrubwood). TINELLI & TINELLI (1980) suggested that a protection effect of vegetation from adverse weather conditions might explain this preference for den sites covered with vegetation. Conversely, porcupines avoided moist terrains (marsh), bare areas (arable land) and sandy soils (pinewood). These results are consistent with the hypothesis that soil compactness, hence den stability, is important for den site selection. In our study area, the scrubwood was confined to the calcareous hills of the Uccellina, rich in natural caves and burrows. Beside the scrubwood, the garigue also occurs in the calcareous area, but it was not preferred by porcupines for denning (Fig. 3A). This rules out the alternative explanation that porcupines actually selected areas with suitable den opportunities, rather than vegetation cover. Both factors are likely to be involved

as vegetation cover may provide both protection from adverse climatic condition, and predation. Porcupine cubs are defenceless and vulnerable, especially in the first weeks from birth, and they may be easily predated in the den. LUCHERINI et al. (1991) reported some predation on young porcupines by the red fox. Cover provided by a thick vegetation may help the survival of cubs as well as adults. Porcupines are traditionally killed by man as a delicacy: despite being protected by the Italian law, particularly in a park such as our study area, incidents of poaching have been recorded (unpublished data).

Not all den entrances were used equally. The porcupines seemed to have dug several tunnels to get in/out of their den, but, later on, apparently selectively used only a few (cf. PIGOZZI 1984, for *Marmota marmota*). Selection may derive from the interaction of several factors, e.g. terrain slope angle, predator avoidance, number of individuals in the den, etc., but other factors may also be involved (e.g. likelihood of roof collapse).

The mean size of entrance holes was similar to the size of the porcupines, suggesting that they actively dug the connection tunnels to the chambers or, at least, the entrance holes. An abundant spoil heap could be found just outside each entrance, and the characteristics of the entrance holes (i.e. earthy ground and rocky roof) supports the above view. Appropriately sized entrances may be easily defended by a single porcupine, in case of a predator attack.

Other factors, such as terrain slope angle, may influence den site selection. These porcupines selected steep slopes for denning, possibly for a better rain drainage, but we cannot exclude that steep slope selection was a consequence of soil or vegetation preference. The slope angle of the immediate surroundings of the entrance (inner and outer) should depend on ecological factors other than just rain drainage, since both the inner and outer slope angle did not actually improve drainage. The inward slope angle may facilitate the porcupine entry or excavation activities, while the outer slope angle (inwardly directed) could be a direct cause of the excavation activity.

Porcupines also showed a clear avoidance of a northern aspect. FELICOLI & SANTINI (1994) suggested that porcupines might select south exposures to synchronize with sunset (*zeit geber* effect), but we believe that avoidance of a muddy ground, particularly in winter, may be a more likely explanation (cf. TINELLI & TINELLI 1988). No significant selection of a southern aspect was found, thus confirming our conclusion.

The fidelity index was greater than 0.65 for 8 out of 10 paired porcupines (i.e. they changed their den less than 35% of times), and much lower (from 0.0 to 0.25) for the other animals (3 unpaired females and 2 individuals of the same pair M16 and F11). The partners of the anomalous pair showed a very low fidelity index (0.22 and 0.25) and a relatively low pair bond index (0.50 and 0.55 respectively), suggesting that the pair bond was not as strong as that of the other pairs. Nonetheless, they showed a greater site fidelity than single porcupines. No data were available for single male porcupines. In *H. indica* adult females were reported to move between different den sites more than males (SALTZ & ALKON 1992), although this study related female transience to dispersal. As they followed their animals only for a short time (9 months), this limited sampling period may have biased their results. In the badger *Meles meles*, BUTLER & ROPER (1996) described frequent den shifting to reduce the ectoparasites in the chambers, i.e. the parasite burden. On the other hand, we did not find any ectoparasites on our porcupines, except for a very few fleas.

Paired crested porcupines showed a stronger site fidelity than single ones (most of whom were females), although our limited sample size calls for prudence. Site fidelity may increase as the pair bond strengthens (but see also CÉZILLY et al. 2000). This could depend on the presence of cubs in the den, if any. There is some evidence (unpublished data) that parents are likely to alternate in the den during the lactation period to protect cubs from predators, confirming this hypothesis. Another explanation is that the protection from local weather conditions and/or predators, and a strategic location of the den site (e.g. near abundant resources), would offer direct advantages to mates and so improve their breeding success. Most likely, both factors contribute to the overall reproductive success.

The distribution of porcupines in different den sites in our study area militates against the hypothesis that, in this species, communal living may play a critical role in communal predator defence or parental care (e.g. KINLAW 1999, EBENSBERGER 2001). In other areas (CORSINI et al. 1995, SONNINO 1998), the availability of den sites was limited by intensive human activities (e.g. cultivation and gardening) forcing porcupines to share the few available sites. In *H. indica* (SALTZ & ALKON 1992) and in *H. africae australis* (CORBET 1992), group living is common, but its origin has not been studied. In our study area, porcupines profited from the great number of natural burrows and, unlike other study areas, each den site was not shared by more than one reproductive pair and the yearlings. This suggests that, in the crested porcupine, social aggregation may be a consequence of resource distribution rather than of an antipredatory strategy. If so, this supports one of the predictions of the burrow-sharing hypothesis that states that a decrement of sociality is expected when the availability of burrows decreases (EBENSBERGER 2001). In areas with a scarce availability of den sites, crested porcupines may benefit from communal living, as the individual cost of burrowing may decrease with increasing sociality, but no data are available in this regard.

The only alternative hypothesis is that communal living may act as an antipredatory strategy (group defence), but, in our study area, predation apparently did not play a critical role, as adult crested porcupines are preyed mainly by Man and dogs (mainly hunting dogs), and predation risk is more intense for cubs and the young. Moreover, moonlight avoidance, reported for *H. indica* (ALKON & SALTZ 1988), was not reported for crested porcupines (CORSINI et al. 1995), possibly because the habitats typically preferred by porcupines, woody areas or woodland alternating with open areas, are characterized by dense vegetation cover that reduces visibility.

Thus, our results seem to support the burrow-sharing hypothesis that communal living in crested porcupines is possibly not influenced by predation risk, but, most likely, by resource (denning site) availability and distribution, although further research is needed to reject alternative hypotheses.

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