



Original investigation

Timing of reproduction and paternal cares in the crested porcupine

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ABSTRACT

Old World porcupines are elusive, nocturnal rodents who pair for life, exhibiting frequent socio-sexual behaviour also outside the breeding period. Only anecdotal observations on captive individuals are available on the reproductive behaviour of the crested porcupine *Hystrix cristata*, a Sub-Saharan and North African large rodent probably introduced to Italy over 1500 years ago. Our work reports the first data on reproductive biology and paternal behaviour of free-living crested porcupines in Europe. A total of 44 litters was recorded at 4 den systems, over 3 years: 59% singletons, 32% twins, 9% triplets. Reproduction occurs throughout the year, but two significant birth peaks have been detected on February and October. The reproductive peak in October falls in the period of short rains in Sub-Saharan Africa, and coincides with the start of Autumn rains in Italy, thus preceding the vegetation regrowth in both areas, but especially in Africa. On the other hand, porcupines are unusual, as their “spring” peak of births in Central Italy falls actually in mid-winter (i.e. February), when snowfalls and the coldest temperatures tend to occur. By contrast, births in February anticipate the long rains in Sub-Saharan Africa by c. 30 days, when cubs leave the natal den for the first time and vegetation starts sprouting. Haphazard observations of cubs over 12 years ($N = 72$) have confirmed this pattern. Both partners ($N = 2$ radio-tagged pairs) share parental duties: alternation of cub guarding in den occurs in the first two months of life, i.e. when quills are still soft and relatively short, thus making cubs an easy prey for small and mesocarnivores.

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Introduction

Over 95% of mammalian species are polygynous (Kleiman, 1977), with males competing for mating rights and investing comparatively less than females in offspring (Trivers, 1972). As a consequence, paternal cares are rare in mammals and increase with increasing fatherhood probability (Trivers, 1972; Wuensch, 1985; Gubernick and Alberts, 1987; Syrůčková et al., 2015), along a gradient from polygyny to monogamy (Wittenberger and Tilson, 1980; Kleiman and Malcom, 1981). Although relevant quantitative studies are poor and mainly based on laboratory experiments (cf. Gubernick and Alberts, 1987), where male parental care may be induced by confinement to cages, paternal care has been observed in just 6% of rodent genera ($N = 443$; Dewsbury, 1985).

Old World porcupines *Hystrix* spp. (Rodentia; Hystricidae) usually pair for life (Kleiman, 1977; Morris and Van Aarde, 1985; Sever and Mendelssohn, 1988; Mori and Lovari, 2014). Den systems (hereafter, setts) are shared by a reproductive pair and several offspring (Smithers, 1983; Van Aarde, 1987; Felicioli and Santini, 1994). Activity rhythms (Corsini et al., 1995; Mori et al., 2014a) and home ranges (Mori et al., 2014b) of members of the same pair overlap greatly. There is no evidence of territoriality in genus *Hystrix*. Amongst monogamous mammals, only hystricomorphs have been reported to exhibit frequent socio-sexual behaviour, also outside the breeding period (Kleiman, 1974; Sever and Mendelssohn, 1988). A complex courtship pattern is shown by both sexes, involving allogrooming and sniffing before copulation (Morris and Van Aarde, 1985; Sever, 1991; Felicioli et al., 1997).

Collection of data on the reproductive biology of porcupines is challenging, especially in the wild, as they are burrow-living, elusive, shrubwood-dwelling and nocturnal animals. Some information is available for *Hystrix brachyura* (Gosling, 1997; Pedro de Margalhães, 2011), *Hystrix indica* (Ahmad and Chaudry, 1977; Greaves and Khan, 1978; Tohmè and Tohmè, 1980; Sever, 1985;

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Khaliq et al., 1991; Sever, 2003) and *Hystrix africaeaustralis* (Van Aarde, 1985; Van Aarde and Skinner, 1986), but only observations on the reproductive behaviour of captive individuals are available for *Hystrix cristata* (Mohr, 1965; Weir, 1974; Felicioli et al., 1997; Bartos, 2004; Amori et al., 2008: Table 1). A wealth of genetic (Trucchi and Sbordoni 2009; Trucchi et al., in press), palaeontological (Masetti et al., 2010) and parasitological (Mori et al., 2015) data suggest the African origin of the Italian population of crested porcupines, but see Angelici et al. (2003) and Bertolino et al. (2015).

While a reproductive season has been reported for some *Hystrix* species in the wild (Blanford, 1888; Van Aarde, 1985), the same species may breed throughout the year in captivity, with a constant food supply (Skinner et al., 1984; Van Aarde, 1985; Gosling, 1997). For free-living *H. cristata*, Santini (1980) reported several reproductive events in winter, an unusual biological feature for a rodent from a temperate country (Amori et al., 2008). Cubs of herbivores require milk during lactation and highly digestible plant material at weaning. Rains are necessary to trigger vegetation growth (Ellenberg, 1988), which in turn determines the birth period in herbivore mammals (Taylor and Green, 1976; Pettorelli et al., 2007).

In this paper, we have investigated the reproductive biology of free-living crested porcupines, with emphasis on paternal behaviour. We predicted that, in Central Italy, (i) crested porcupines should show reproductive peaks just before spring and autumn rains, and (ii) being monogamous mammals (Mori and Lovari, 2014), they should share biparental cares, especially when cubs are particularly vulnerable.

Material and methods

Birth periods

In a hilly area of Roccastrada municipality (Grosseto, West-Central Italy), detailed direct observations on number of litters and cubs/litter were conducted once a month throughout the year, at four large den setts on 2002–2003–2004 (R. Manetti, unpublished data). Each sett contained from one to three breeding pairs, at the same time. A mechanical system to explore burrows (Bassano and Peracino, 1997) was used to detect porcupine presence before pest control operations, under the aegis of the Provincial Council. If the den was inhabited, the porcupines were caught in live traps and relocated elsewhere. If cubs were present, the operations were delayed until cubs started following the pair members outside the den. Thus, data on litters were statistically independent of one another. Lactating females are easily distinguishable from males and non-lactating ones, because cubs strip quills surrounding the nipples of the mother, located in lateral position, to access the milk (Fig. 1). Mean peaks of rain in this area (1991–2011) occurred in February–March and in October–December (Meteorological station: Campiano, Municipality of Montieri, Grosseto, www.idropisa.it, downloaded on August 2012). The Rao's spacing test is used to assess uniformity of circular data (Batschelet, 1981) and was



Fig. 1. A road-killed lactating crested porcupine *Hystrix cristata*. Nipples are visible within the white circle.

performed to observe whether the number of litters was uniform throughout the year. The Watson's U2 test was then performed to see whether the distribution of litters over the year coincided with the unimodal distribution by Von Mises (Batschelet, 1981). Differences in number of cubs per litter between identified reproductive peaks were tested through a chi-square test. Haphazard observations of cubs were conducted in the wild, while radio-tracking porcupines, over 12 years (1990–2000 and 2011–2013), and were used for a comparison with the results of direct detailed records (see above). These observations were not included in the statistical analyses.

Paternal care

Out of a total of 13 pairs of radio-tagged crested porcupines, detailed data on cub presence could be assessed only for two pairs, producing one litter each. Porcupines were trapped in metal boxes, sedated (cf. Massolo et al., 2003) and intensively radio-tracked in Southern Tuscany for at least 12 months/individual (Lovari et al., 2013; Mori et al., 2014a,b), with a mixture of distance (1–2 fix/120 min; mean location error = 28.7–62 m) and homing-in locations (1 fix/15 min; mean location error = 14.28 m), for a mean value of 27–35 fixes/month/individual.

Pair 1 had its den in a suburban area (San Miniato, Province of Siena), whereas pair 2 lived in a deciduous woodland (Prata, Province of Grosseto). Temporal activity was assessed as described in Corsini et al. (1995) and Mori et al. (2014a); overlap between members of the same pair was estimated throughout the year from simultaneous radio-tracking data with circular statistics, through the R package CircStats (Agostinelli, 2009). Furthermore, a camera trap (Multipir 12[®], with infrared sensor) was activated full time

Table 1
Information on reproductive biology of Old World porcupines. ND, no data. (1) Gosling (1980); (2) Pedro de Margalhães (2011); (3) Mohr (1965); (4) Van Aarde and Skinner (1986); (5) Barthelmess (2006); (6) Van Aarde (1985); (7) Gaigher and Currie (1979); (8) Khaliq et al. (1991); (9) Ahmad and Chaudry (1977); (10) Tohmè and Tohmè (1980); (11) Bartos (2004); (12) Amori et al. (2008); (13) Weir (1974).

Species		<i>H. brachyura</i>	<i>H. africaeaustralis</i>	<i>H. indica</i>	<i>H. cristata</i>
Sexual maturity	Male	ND	8–18 months ^{4,5}	7 months ¹⁰	8–18 months ^{3,11}
	Female	12 months ^{1,2,3}	12–14 months ^{4,5}	9 months ¹⁰	9–16 months ^{3,11}
Gestation period		105–110 days ^{1,2}	94 days ⁶	90–112 days ⁸	90–120 days ^{3,12}
Birth period peak		ND	from August to March ⁷	March and September ^{8,9}	ND
Litter size	1 cub	ND	58.8% ⁶	33.3% ¹⁰	ND
	2 cubs	ND	32.1% ⁶	44.7% ¹⁰	ND
	>2 cubs	ND	9.1% ⁶	21.9% ¹⁰	ND
Average weight at birth		261 g (up to 450 g) ^{1,2}	330–440 g ⁵	327 g ¹⁰	350 g (up to 465 g) ^{3,13}
Inter-litter interval		142 days ¹	385 days ⁵	130 days ⁸	91–112 days ^{3,13}

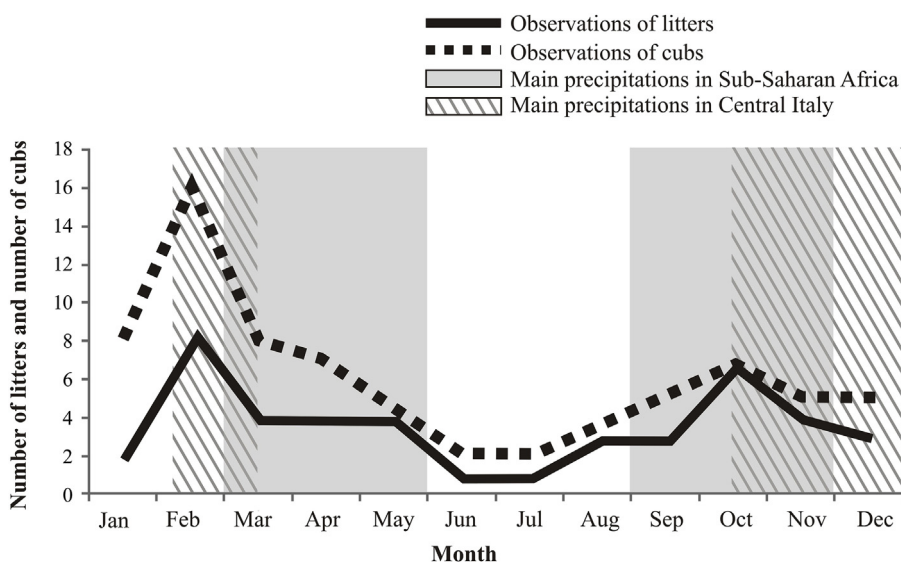


Fig. 2. Monthly distribution of litters of *Hystrix cristata*, Roccastrada (Central Italy). Main peaks occurred in February and in October, 2002–2003–2004 (pooled data). Peaks of rains are also reported for the Sub-Saharan African and the Italian distribution ranges of this species.

in front of the den of pair 2 (2.5 m from the main entry) to survey the movements of pair members and cubs in the surroundings of the den entry, also testing the presence of additional individuals. Porcupines were individually marked through a combination of radio-tags and coloured adhesive tapes applied to quills (Pigozzi, 1988).

Results

Birth peaks

A total of 44 pairs of crested porcupines with a litter was observed in three years (Sett 1, $N=10$; Sett 2, $N=14$; Sett 3, $N=12$; Sett 4, $N=8$): 59% singletons, 32% twins, 9% triplets. Births occurred throughout the year, with the highest number of litters in February and in October, as well as with the highest number of cubs in mid-winter (Fig. 2). Main rainy seasons for Sub-Saharan Africa and Central Italy are shown in Fig. 2. The Rao's spacing test showed that number of births was not uniform among months (Rao's $U=266.1$; $P<0.001$), whereas the Watson's U_2 test showed that the distribution of peaks was not unimodal, thus showing significant peaks in February and October ($U_2=0.145$; $P=0.04$). Number of litters composed by more than one cub was greater in October with respect to February ($N=7$ litters, 66%, in October; $N=8$ litters, 42%, in February; $\chi^2=11.36$, 1 df, $P<0.001$).

Paternal care

Temporal overlaps of activity rhythms, i.e. both members of a pair active at the same time (28–30 m distant one another outside the den), was high for both the pairs of crested porcupines in which cub presence was monitored intensively (pair 1, annual mean \pm SD = $54.47 \pm 23.51\%$; pair 2, mean \pm SD = $75.57 \pm 25.53\%$), ranging from 13.34% (pair 1) and 16.07% (pair 2), when cubs were in the den, to 86.99% (pair 1) and 94.76% (pair 2; Fig. 3).

Camera trapping showed that only the breeding pair was present in the den with cubs. We determined the approximate day of birth *a posteriori*, when cubs were recorded with the pair outside the den (cf. Mohr, 1965). Parents alternated at den, when cubs were present, thus significantly reducing the temporal overlap of their movements. Short camera trap videos (1 min., $N=47$) showed that parents moved together only in the immediate surroundings

of the den, when cubs were in the den. 75% of videos showed porcupines digging and possibly feeding; two copulations were also recorded. Cubs left the den for the first time when about 45–60 days old (Fig. 3), assuming that litters were born when parents started alternating in the den, and moved around with both their parents, while foraging. During the rest of the year, i.e. in absence of cubs in the den, 14 copulation events were recorded, but no litter was generated. Scent marking was never observed.

Time spent by the male of the pair in the den increased from $31.71 \pm 4.93\%$ (pair 1) and $24.93 \pm 2.37\%$ (pair 2) of the night, to $77.03 \pm 2.16\%$ (pair 1) and $68.93 \pm 7.46\%$ (pair 2) when cubs were present in the den. Similarly, time spent by the female in the den increased from $29.96 \pm 5.16\%$ (pair 1) and $22.85 \pm 1.89\%$ (pair 2) of the night, to $82.24 \pm 3.33\%$ (pair 1) and $74.86 \pm 4.58\%$ (pair 2) when cubs were present in the den. Members of the pairs stayed together with the cubs throughout the day and for $7.47 \pm 1.22\%$ (pair 1) and $6.81 \pm 0.98\%$ (pair 2) of the night.

Discussion

Our data show that reproduction of free ranging crested porcupines occurs throughout the year (cf. Felicioli et al., 1997, in captivity), with the higher number of reproductive pairs having litters in February, but producing mainly singletons, and the maximum number of twins and triplets in October. Reproductive peaks in mid-winter are unknown or rare for native rodents in temperate-cold countries, as offspring mortality would be increased (Amori et al., 2008). As to porcupines, the reproductive peak in October falls in the period of short rains in Sub-Saharan Africa and coincides with the start of Autumn rains in Italy, thus preceding the vegetation regrowth in both areas, but especially in Africa. On the other hand, porcupines are unusual, as their "spring" peak of births in Central Italy falls actually in mid-winter (i.e. February), when snowfalls and the coldest temperatures tend to occur (Meteorological station: Campiano, Municipality of Montieri, Grosseto, www.idropisa.it, downloaded on August 2011). By contrast, births in February anticipate the long rains in Sub-Saharan Africa by c. 30 days, when cubs leave the natal den for the first time (Mohr, 1965) and vegetation starts sprouting. On early Autumn, porcupines often gave birth to twins, whereas a significantly greater number of singletons occurred in February, in mid-winter, not an ideal time to optimise cub survival. If we assume that giving birth in February is a remnant

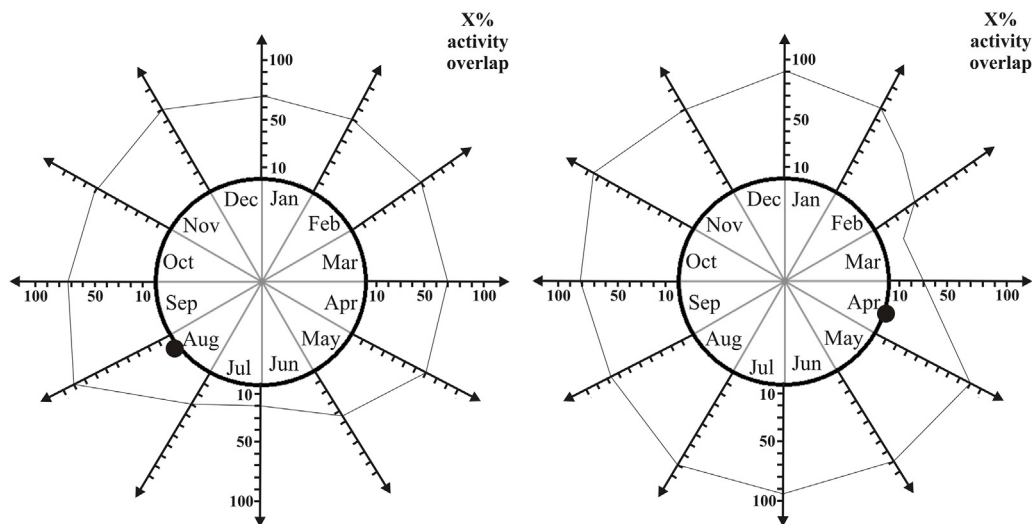


Fig. 3. Percent overlap of activity rhythms of members of the same pair of *Hystrix cristata* (left, pair 1; right, pair 2). Black dots show the first observations of cubs outside the den.

feature of the African origin of porcupines, this birth peak could be explained. Although, being in winter, when food resources are scarce and body weight of porcupines is significantly lower (males: $W = 101$, P -value = 0.003; females: $W = 138$, P -value = 0.046; Mori and Lovari, 2014), the production of twins or triplets may not be favoured by natural selection: singletons are preferred.

The den of pair 2, monitored by camera trapping, was inhabited only by the pair partners, with no subadults, nor other species (cf. Mori et al., 2014c,d), when cubs were born. This observation would confirm Van Aarde and Van Wyk (1991), who declared that reproduction in sexually mature females does not occur until their dispersal. Although copulations may occur throughout the year (in captivity, *H. cristata*: Santini, 1980; Felicioli et al., 1997; *H. indica*: Sever and Mendelssohn, 1988), the inter-litter interval detected for this species (91–112 days; Mohr, 1965; Weir, 1974) suggests that no more than 2–3 litters/year may be expected per pair. As the fertility period is short (approximately 9 h, i.e. 1.2% of the oestrous cycle; Morris and Van Aarde, 1985), copulations may help in maintaining pair-bonds throughout the year and thus ensure prompt fertilization of an oestrus female (Sever and Mendelssohn, 1988). No behavioural difference appears to occur between copulatory behaviour during the fertile and the non-fertile periods, i.e. when pregnancy follows or does not. Non-reproductive sex is quite rare amongst non-human mammals, but observed in some species, e.g. bonobos (Wrangham, 1996; Clay and Zuberbühler, 2011) and lions (Schaller, 1972). In mammals, most of the studies on parents-offspring bonds have been based on mother-cub relationships, neglecting paternal behaviour (Gubernick and Alberts, 1987). Male parental care appears to be critical for the survival of pups in several monogamous rodent species (e.g. *Peromyscus californicus*: Gubernick and Teferi, 2000; *Mus spicilegus*: Patris and Baudoin, 2000; *Microtus ochrogaster*: McGuire and Bemis, 2007, but see McGuire and Bemis, 2007 for variance on this behavioural feature) and in all the Old World porcupines as well (in captivity: Mohr, 1965). Sever and Mendelssohn (1989) observed seven male captive *H. indica* spending 30% of time alone with the newborns and 20% with both the female and their offspring. Biparental care intensively occurred also in free-ranging crested porcupines: our results indicated that the minimum synchrony in the activity rhythms of pair partners occurred during the first two months of life of cubs, fulfilling our prediction (ii). While coordination of care by members of breeding pairs has been well-documented for many monogamous avian species (e.g. Armstrong, 1965; Davis, 1982), this behaviour

is much less common among mammals (cf. McGuire et al., 2007), which are mainly polygynous (Kleiman, 1977). Presumably, the presence of the father in the den may increase cub survivorship (cf. Getz et al., 1992), both through warming up (e.g. by huddling) and through protecting cubs from intruding predators (e.g. red foxes and wolves: Lucherini et al., 1995; Mori et al., 2014c). At birth, crested porcupines have short and soft quills (Mohr, 1965), thus being more subjected to predation with respect to adults (Lucherini et al., 1995). When outside their den, young cubs tend to walk between their parents, who protect them (cf. Gosling, 1997; for *H. brachyura*; Mori, 2013, for *H. cristata*). In *H. africae australis* and in *H. indica*, both parents accompany offspring (≥ 2 months of age) in foraging excursions and rest together in burrows in daylight (Sever and Mendelssohn, 1985, 1989; Van Aarde, 1987).

Unguarded porcupine cubs should be an attractive prey for small/mesopredators (e.g. Canidae, Viverridae, Mustelidae), particularly numerous in the African distribution range of crested porcupines, which may have contributed to the evolution of protective behaviour by both parents.

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