



Original investigation

## Timing of reproduction and paternal cares in the crested porcupine

Emiliano Mori<sup>a,b,\*</sup>, Mattia Menchetti<sup>c</sup>, Mauro Lucherini<sup>d</sup>, Andrea Sforzi<sup>e</sup>, Sandro Lovari<sup>a</sup><sup>a</sup> Department of Life Sciences, University of Siena, Via P.A. Mattioli 4, 53100 Siena, Italy<sup>b</sup> Di.S.A.F.A., Entomology and Zoology, University of Turin, Largo Paolo Braccini 2, Grugliasco, 10095 Turin, Italy<sup>c</sup> Department of Biology, University of Florence, Via Madonna del Piano 6, Sesto Fiorentino, 50019 Florence, Italy<sup>d</sup> Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur—CONICET, San Juan 670, 8000 Bahía Blanca, Argentina<sup>e</sup> Maremma Natural History Museum, Strada Corsini, 5-58100 Grosseto, Italy

## ARTICLE INFO

## Article history:

Received 19 September 2015

Accepted 18 March 2016

Handled by Adriano Martinoli

Available online 13 April 2016

## Keywords:

*Hystrix cristata*

Monogamy

Paternal care

Birth periods

Cub guarding

## 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;

\* Corresponding author at: Department of Life Sciences, University of Siena, Via P.A. Mattioli 4, 53100 Siena, Italy.

E-mail addresses: [moriemiliano@tiscali.it](mailto:moriemiliano@tiscali.it) (E. Mori), [mattiamen@gmail.com](mailto:mattiamen@gmail.com) (M. Menchetti), [lucherinima@yahoo.com](mailto:lucherinima@yahoo.com) (M. Lucherini), [asforzi@gol.grosseto.it](mailto:asforzi@gol.grosseto.it) (A. Sforzi), [lovari@unisi.it](mailto:lovari@unisi.it) (S. Lovari).

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](http://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<sup>®</sup>, 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 <sup>4,5</sup>	7 months <sup>10</sup>	8–18 months <sup>3,11</sup>
	Female	12 months <sup>1,2,3</sup>	12–14 months <sup>4,5</sup>	9 months <sup>10</sup>	9–16 months <sup>3,11</sup>
Gestation period		105–110 days <sup>1,2</sup>	94 days <sup>6</sup>	90–112 days <sup>8</sup>	90–120 days <sup>3,12</sup>
Birth period peak		ND	from August to March <sup>7</sup>	March and September <sup>8,9</sup>	ND
Litter size	1 cub	ND	58.8% <sup>6</sup>	33.3% <sup>10</sup>	ND
	2 cubs	ND	32.1% <sup>6</sup>	44.7% <sup>10</sup>	ND
	>2 cubs	ND	9.1% <sup>6</sup>	21.9% <sup>10</sup>	ND
Average weight at birth		261 g (up to 450 g) <sup>1,2</sup>	330–440 g <sup>5</sup>	327 g <sup>10</sup>	350 g (up to 465 g) <sup>3,13</sup>
Inter-litter interval		142 days <sup>1</sup>	385 days <sup>5</sup>	130 days <sup>8</sup>	91–112 days <sup>3,13</sup>

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