

Short Note

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When quills kill: the defense strategy of the crested porcupine *Hystrix cristata* L., 1758

Abstract: Quills represent specialized morphological structures evolved by some mammal species to deter predators. Among quilled mammals, crested porcupines *Hystrix* spp. exhibit the most complex armor. The antipredator behavior of these rodents is poorly known. In this study, we describe in detail the defense strategies of *Hystrix cristata* when attacked by hunting dogs. We identified four kinds of display exhibited by porcupines. Tail rattling seems to be sufficient to repel solitary predators, while backyard/sideways attacks are exhibited only in extreme situations, or when numerical disparity among potential prey and predators occurs. We also report four cases of wild species killing by porcupines.

Keywords: antipredator behavior; backyard/sideways attacks; quill armor; tail rattling.

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Morphological mechanisms to deter predators, such as cryptic/confounding coat colors (Caro 2009) and quills (Sweitzer and Berger 1997, Zherebtsova 2000) have been developed by a few mammals. Quills are modified hairs that characterize the body of echidnas, hedgehogs, tenrecs, and New World and Old World porcupines (Zherebtsova 2000). These structures are coated with thick plates of keratin, which makes them similar to spines, and are embedded in the skin musculature (Chapman and Roze 1997, Zherebtsova 2000). Old world porcupine species included in the subgenus *Hystrix* (*Hystrix cristata* Linnaeus 1858; *Hystrix indica* Kerr, 1872; *Hystrix africaeaustralis* Peters, 1852) present the most complex and dense quill armor (Mohr 1965). Head, neck, feet, and belly are covered

with short, sturdy flattened spines and bristles (2–4.5 cm in length, 0.2 cm in width), back and sides with inflexible, circular true quills (up to 30–40 cm in length). An erectile well-developed crest of coarse hair (up to 50 cm in length) occurs from the top of the head to the shoulders and characterizes the morphology of the subgenus. Fuzzy bristles are present in the lumbar region. Rattle quills (5–8 cm in length) are attached to the tail and broaden at the terminal end (0.2–0.7 cm in diameter). Rattle quills have a circular, hollow, and capsule-shaped structure (Mohr 1965). When vibrated, these quills produce a typical rattling noise. The structure of subcutaneous muscles (musculi arrectores pilorum) and the well-developed integument smooth muscles are arranged to reflect the quills' arrangement along the back (Zherebtsova 2000). When a defense response against possible predators is triggered, the muscles contract and raise the quills (Woods and Howland 1977). Quills often remain stuck inside the muscles of the aggressor, provoking lethal wounds or infections (Mohr 1965). Microscopic spiny bristles are present on the quills' surface but oriented in the opposite direction, resulting in a sort of "harpoon effect" (Mohr 1965). Although popular beliefs attribute to porcupines the ability to shoot quills against possible enemies, quills are released only by contact or drop out when the animal shakes its body, as they are loosely rooted (Mohr 1965). Species belonging to subgenus *Hystrix* shed quills more frequently than other Hystricidae (Ellerman 1940). Although mainly nocturnal and cryptically colored (Corsini et al. 1995), crested porcupines are large-sized rodents and have short legs, which may, respectively, increase their visibility and limit escape success. Moonlight avoidance (e.g., Alkon and Saltz 1988) and ranging movements concentrated in thick vegetation areas (e.g., Corsini et al. 1995, Fattorini and Pokheral 2012) are not sufficient survival strategies against predators; the quill-armed body represents the primary mean of defense (Ellerman 1940). Crested porcupines have been reported to be a marginal component in the diet of some large and medium-sized carnivores (Table 1).

As for Italy, crested porcupine remains have been found in the feces of red foxes *Vulpes vulpes* Linnaeus,

Table 1 Species reported as predators of *Hystrix* spp.

Species	Predator	Geographical area	Main references
<i>Hystrix cristata</i>	<i>Panthera leo</i>	Cameroon	Breuer 2005
	<i>Lycaon pictus</i>	Cameroon	Breuer 2005
	<i>Vulpes vulpes</i>	Italy	Lucherini et al. 1995
	<i>Canis lupus</i>	Italy	Scandura et al. unpublished
	<i>Canis familiaris</i>	Italy	Monetti et al. 2005
	<i>Crocuta crocuta</i>	Cameroon	Breuer 2005
<i>Hystrix africaeaustralis</i>	<i>Panthera leo</i>	South Africa	Mills and Shenk 1992, Van Aarde, 1998
	<i>Panthera pardus</i>	South Africa	Van Aarde 1998
	<i>Vulpes chama</i>	South Africa	Klare et al. 2011
	<i>Canis mesomelas</i>	South Africa	Klare et al. 2011
<i>Hystrix indica</i>	<i>Panthera pardus</i>	Central and Southern Asia	Lovari et al. 2013
	<i>Panthera pardus</i>	Israel	Alkon and Saltz 1988
	<i>Hyaena hyaena</i>	Israel	Kerbis-Peterhans and Horwitz 1992

1758 (Lucherini et al. 1995) and, rarely, of wolves *Canis lupus* Linnaeus, 1758 (Scandura et al. unpublished data). Carcasses may be consumed by wolves, red foxes, Eurasian badgers *Meles meles* Linnaeus, 1758, stray cats *Felis silvestris catus* Linnaeus, 1758, common buzzards *Buteo buteo* L., 1758, magpies *Pica pica* Linnaeus, 1758, and carrion crows *Corvus cornix* (Linnaeus, 1758) (E. Mori, unpublished camera trap data). The crested porcupine has been reported to be part of the diet of the golden eagle *Aquila chrysaetos* (Linnaeus 1758) (Corsetti 1989), but we suggest that eagles may eat carcasses as they have different circadian habits from those of *Hystrix cristata*.

Predation seems to affect mostly younger individuals in *Hystrix* spp. (Mills and Shenk 1992, Monetti et al. 2005). Newborns are more vulnerable to predators, as they have softer quills, which develop into sturdy spines within the first 10 days of life (Mohr 1965). Predation is, however, poorly recorded, as cubs are always protected by at least one parent (Sever and Mendelssohn 1989). Male and female porcupines alternate in the den with cubs, while the other partner is out foraging (Mohr 1965); when outside the den, the offspring is always positioned between the two adults (e.g., Sever and Mendelssohn 1989). When threatened or harassed, porcupines defend themselves by erecting their quills and crest, and running sideways or backward into enemies, possibly leaving quills in what they run into (Ellerman 1940). Harassments by crested porcupines (quill/crest erection) have been observed against wild boars *Sus scrofa* in feeding areas (Figure 1A–D). Hunting dogs are often wounded by North American porcupine quills (Johnson et al. 2006), but no data are available about the interaction between *Hystrix cristata* and hunting dogs. In this study, we aimed to describe in detail the defense behavior of the crested porcupine to thwart attacks by hunting dogs. We also

report for the first time four cases of wild species killing by porcupines.

Observations occurred between November 2011 and February 2013 as part of a long-term research project about spatial behavior of the crested porcupine involving radio-tracking and camera-trapping monitoring; study site is located in a Site of Communitarian Importance in Tuscany, Central Italy (“Poggi di Prata,” Regional Law 56/2000; 42°55.90’N, 11°04.90’E), a ca. 1100 ha area located in the Metalliferous Hills. The study area was characterized by deciduous mixed oakwoods and fallows (Cantini et al. 2013). Possible predators of porcupines present in this area include red foxes and large-sized canids (wolves and/or hybrids wolf × dog). A torn carcass of *Hystrix cristata* was found inside the study area on 15th May 2012; the one responsible of the aggression might have been a large-sized canid (E. Mori, personal observation). Attacks by hunting dogs were observed during two wild boar hunting periods (1st November to 31st January), while wild species attacked/killed by porcupines were recorded during radiotelemetry procedures. When an interaction between a porcupine and a dog was observed, the number of individuals of both species involved was noted. The defense displays of *H. cristata* were described and attributed to one of the following four categories, characterized by increasing aggressiveness: (1) quill and crest erection; (2) tail rattling; (3) hind foot stamping and growling; (4) backyard/sideways attack. In addition, we recorded the outcome of the interaction, assessing whether the aggressor and/or the prey remained uninjured or they were wounded or dead. Twelve encounters between hunting dogs and crested porcupine have been observed on a total of 115 wild boar hunting days (Table 2). In 50% of the cases, the defense behavior of *H. cristata* was limited to quill erection and tail rattling and

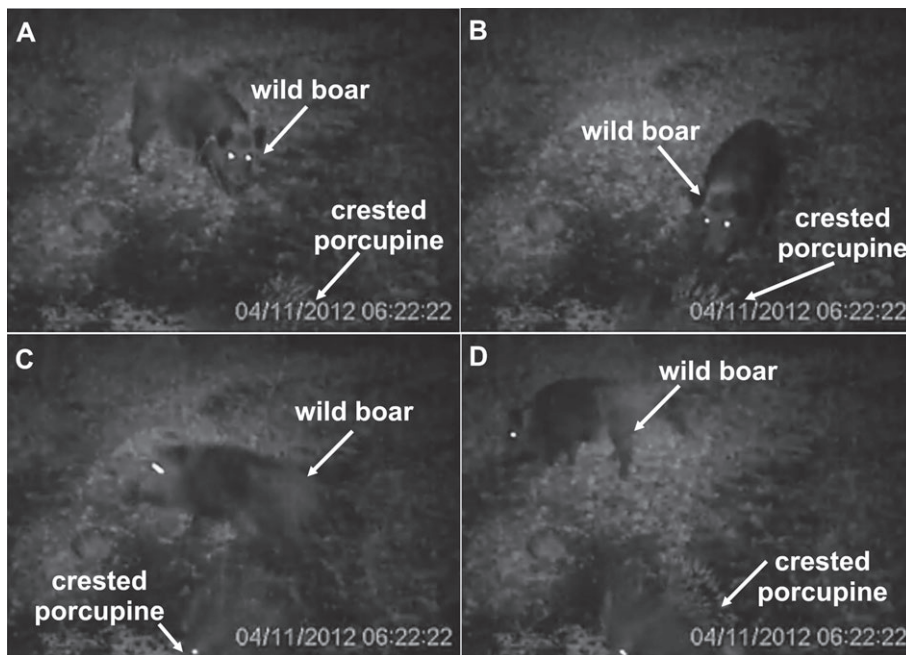


Figure 1 Harassment of a wild boar by a crested porcupine (Camera trap frames, Seravezza, Lucca, Northern Tuscany; 4th November 2012).

to the escape of the porcupines, when dogs approached them. Crested porcupines were attacked by dogs in 33.3% of the observations and only when the aggressors were more than one. In two of these cases, the porcupine (in both cases adult individuals) was killed. Four dogs were wounded by quills, and in one occasion, two crested porcupines, running backward, forced a young dog to take refuge inside their den, in which it was fatally impaled and injured by quills. Neither dogs nor porcupines were wounded when only quill/crest erection and tail rattling

were exhibited. In all but one case (but see 16th December 2012) in which hind foot stampings and backyard/sideways attacks were displayed, crested porcupines were in numerical disparity compared to dogs, and at least one contender was injured or died. During our study period, we recorded two cases of young red foxes (age determined from external appearance and teeth eruption: Harris 1978) and two of young European badgers (age determined by body size and teeth eruption: Neal and Cheeseman 1996, Revilla et al. 1999) fatally injured by the porcupine's quills

Table 2 Interactions hunting dog/crested porcupine observed in two hunting season. Numbers of involved individuals and outcomes of the interaction are reported.

Date	N° dogs	N° <i>Hystrix cristata</i>	Defense				Outcome of the interaction	
			1	2	3	4	Dog	<i>H. cristata</i>
1st December 2011	1	1	+				Uninjured	Uninjured
24th December 2011	4	1	+	+	+	+	1 Wounded; 3 uninjured	Dead
7th January 2012	1	1	+	+			Uninjured	Uninjured
28th January 2012	2	1	+	+	+	+	Uninjured	Wounded
3rd November 2012	1	2	+	+	+	+	Wounded	Uninjured
14th November 2012	1	1	+	+			Uninjured	Uninjured
21st November 2012	3	1	+	+	+	+	1 Wounded; 2 uninjured	Dead
5th December 2012	1	1	+	+			Uninjured	Uninjured
16th December 2012	1	1	+	+	+	+	Wounded	Uninjured
22nd December 2012	1	1	+	+			Uninjured	Uninjured
12th January 2013	1	2	+	+	+	+	Dead	1 Uninjured; 1 wounded
16th January 2013	1	1	+	+			Uninjured	Uninjured

Defense strategies are numbered according to the behavior displayed by the crested porcupine: 1, quill/crest erection; 2, tail rattling; 3, growling/hind foot stamping; 4, backyard/sideways attack.

(Figure 2). All these individuals were found dead in the proximity of the porcupine's den, with the only exception of a red fox. This last was observed moving slowly (after losing a large amount of blood in the proximity of the crested porcupine's den) with a quill embedded in the left side of the neck: we suppose that the fox eventually died.

In this paper, we report the first detailed descriptions of the antipredator behavior of crested porcupines and the first documented direct victims of the porcupine's quills in Italy. Growling/hind foot stamping and backyard/side-ways attacks were always shown, with the only exception of one case, when the number of porcupines involved in the encounter was different from the number of dogs. This seems to support the hypothesis that Old World porcupines' coloration may represent an aposematic signal (Caro 2009). We suggest that these behaviors are exhibited only in extreme danger situations (when porcupines are in minority) or when the probability of success is high (when porcupines are in the majority). In fact, most of the times when these displays were expressed, the predator (or at least one of them) was wounded. However, in these cases the porcupine as well was injured or even killed. On

the contrary, every time that both these behaviors were not exhibited, none of the opponents was wounded. Tail rattling seems to be sufficient to repel a solitary predator and may avoid the porcupines having to engage in a dangerous fight for self-defense, supporting the hypothesis of "acoustic aposematism". Hence, this "warning" signal (tail shocking to rattle) seems to be highly convenient in the evolution and self-conservation of the crested porcupine, as possible predators may learn, when young, to match that sound with a feeling of pain. Although direct interactions with other species have never been described in detail (Amori et al. 2009), adult crested porcupines are known to be highly susceptible animals (Ellerman 1940). Despite intensive observational effort during the whole period, encounters with hunting dogs were observed relatively rarely because of the mainly nocturnal habits of the crested porcupines (12 encounters on 115 hunting days). Such observations are useful to describe the porcupine's defense behavior because they happen during the day and are, therefore, easier to observe as opposed to encounters with other wild species that occur mostly at night. When dogs were more than



Figure 2 Above, the red foxes injured by crested porcupines (blood of the first on the left; carcass of the second individual on the right). Below, carcasses of the Eurasian badgers. Dates of the observations are reported.

one and the porcupine was alone (16.7% of observations), the porcupine run backward toward one of them, while the other dog(s) attacked the rodent in its less protected parts (head, neck, forelimbs) and killed it, before it was able to injure the first dog. Even though encounters with hunting dogs might be rare and limited to hunting season and to the daylight hours, we cannot rule out the possibility that crested porcupines could encounter feral dogs throughout the year and also during the night (Boitani and Ciucci 1995). We assume that the same range of behaviors would be displayed against nocturnal enemies, as our observations do not differ from anecdotal descriptions of the antipredator behavior of *H. africae australis* against large felids (Ellerman 1940). During this survey, we observed four young individuals of red fox and Eurasian badger that were killed following an encounter with crested porcupines. While the red fox is a known predator of *H. cristata* (Lucherini et al. 1995), the badger has been observed to feed just on porcupine's carcasses. All the killings described here occurred in the proximity of the den when cubs were present. We suggest that young, and thus inexperienced, individuals of Italian carnivores (e.g., red fox and Eurasian badger) may be attracted by

porcupines and attempt to prey on them, but are likely to experience injuries. This supports the hypothesis that the porcupine's behavior might be an aposematic signaling mechanism to the predator, as aposematism implies previous experience by the predator. The crested porcupine is a species of conservation concern in Italy, as it is listed in the Berne Convention (all. II) and the Habitat Directive (all. IV) and is protected by the Italian law since 1978 (National Law 968/1977). The eco-ethology of this species is poorly known, and further research is needed to better address management and conservation policies. This first approach to the study of defensive behavior should be implemented with additional studies and will need a larger small sample size in order to be better understood.

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