Ectoparasite load in the crested porcupine *Hystrix cristata* Linnaeus, 1758 in Central Italy

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Abstract The crested porcupine *Hystrix cristata* is a large body-sized rodent, occurring in Europe only in the Italian Peninsula, where it may have been introduced in early Medieval times. Its parasite fauna is currently poorly known and limited to few anecdotal observations. We have analyzed the ectoparasite load of 165 crested porcupines from Tuscany and Latium (Central Italy). Both captured and road-killed individuals were checked for fleas and ticks. Overall, only 39 porcupines were infested by four species of ticks and five of fleas. Abundance of ectoparasites was higher in areas with higher habitat richness, with respect to densely wooded areas. The most frequent species was the flea *Pulex irritans* (25 %), whose prevalence peaked in winter probably because of optimal abiotic conditions in the porcupine's den. The remaining species of both hard ticks (*Rhipicephalus bursa*, *Pholeoixodes hexagonus*, and *Ixodes ventalloi*) and fleas (*Paraceras melis*, *Ctenocephalides canis*, *Dasypsyllus gallinulae*, and *Hystrichopsylla talpae*), all with prevalence lower than 5 %, could be due to den sharing with other vertebrates, mainly carnivores such as, e.g., red foxes and badgers. The second most prevalent species was the generalist tick *Ixodes ricinus* (21 %). An adult male-biased parasitism for ticks has been detected, suggesting a possible role of testosterone related immune-depressive effect. The low richness in dominant ectoparasite species, built up by locally acquired generalist taxa, provides support to the allochthonous origin of this rodent in Italy.

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Introduction

Ectoparasite diversity in host communities is influenced by environmental variables and by the behavior of both host and parasite species (Poulin 1995, 1997; Romeo et al. 2013). Ectoparasites can be an important cause of illness and reduced fecundity in mammals (Krasnov et al. 2002, 2004a): this risk for the host health increases in group-living species which breed in the same den for several reproductive seasons (Hoogland 1979; Bordes et al. 2007). Among arthropods, fleas (Siphonaptera) most often represent ecologically specialized parasites (Beaucournu and Launay 1990) which alternate between periods of direct occurrence upon the host's body and

in the substrate of their dens, nests, or resting cavities. Thus, transmission and host-switching events are promoted when den setts are shared between different species (e.g., Kiviat 1978; Pigozzi 1986), resulting in an increase of parasite richness for each host species (e.g., Whitaker and Goff 1979; Altizer et al. 2003; Ancillotto et al. 2014).

The crested porcupine *Hystrix cristata* is a mainly nocturnal rodent (Mori et al. 2014a), which spends diurnal hours in underground dens (Monetti et al. 2005). Social organization of porcupines sharing the same lair includes a pair of adult individuals, subadults, and cubs, up to six to eight individuals (Monetti et al. 2005; Mori and Lovari 2014). It is the only porcupine species occurring in Europe, with a distribution range limited to Italy: this species may be native or introduced from North Africa (Mori et al. 2013). In Africa, this species is distributed in the Maghreb and south of the Sahara Desert, from Senegal to Central Tanzania, where its range overlaps with that of the congeneric *Hystrix africaeaustralis*. Six other species belonging to the genus *Hystrix* live in Eastern Asia, in complete allopatry with the crested porcupine.

The absence of sympatric congeners for crested porcupine in Italy is expected to significantly affect ectoparasite diversity (e.g., Krasnov et al. 2004b). On the other hand, this species may share its den sett with European badger *Meles meles* as well as red fox *Vulpes vulpes* (Mori et al. 2014b, c).

Currently, published information on parasitic arthropods of *Hystrix* spp. is scanty and mainly related to *H. cristata*. Toschi (1965) and Starkoff (1958) reported three hard tick species for *H. cristata* in Italy: *Ixodes ricinus*, *Pholeoixodes hexagonus*, and *Rhipicephalus bursa*. As for the North African range, Bailly-Choumara et al. (1976) detected two argasid tick species in *H. cristata* in Morocco: adult and immature stages of *Ornithodoros erraticus* and *Ornithodoros delanoei*. These two soft ticks are commonly found in burrows used by rodents, carnivores, and other mammals, although *O. delanoei* was only found in red foxes and porcupines' dens (Bailly-Choumara et al. 1976), suggesting that these hosts could be primary ones for this argasid tick. Concerning fleas, records of two species infesting the crested porcupine have been reported: *Pariodontis riggenbachi* covering the African distribution of this host and *Pulex irritans* which is a cosmopolite species primarily found on mammals and especially man (Beaucournu and Launay 1990), but no data on their incidence and prevalence on porcupines are available. *H. cristata* and *Ursus arctos* have been noted as secondary hosts for *P. irritans*, but whether these mammals are potentially primary hosts is still an open question (Beaucournu and Launay 1990). Together with the tick *Ixodes kaiseri* and *Ornithodoros tholozani*, the flea *P. irritans* has also been observed in *Heterorhabditis indica* (Theodor and Costa 1967).

In this work, we have improved information on ectoparasites of the crested porcupine in its Italian historical range (Mori et al. 2013) and providing the first data on their incidence and prevalence. We expected a low ectoparasite diversity, since no sympatric closely related species is present (Krasnov et al. 2004b; Romeo et al. 2013). On the other hand, parasite richness of this rodent in Italy could also be increased by possible host switching due to den sharing (Mori et al. 2014b). The effects of habitat and season, as well as of host-related variables (i.e., age and sex), on the specific richness and prevalence were also analyzed.

Materials and methods

Study site and parasite collection

Captures took place in the framework of a large research project on the ecology of this species between 1990 and 2014 (Lovari et al. 2013; Mori et al. 2014a). Permits for captures were provided by the Provincial Councils of Siena and Grosseto and the Environment Ministry, both granted by the approval of the National Institute for Environmental Protection and Research (ISPRA). Metal box trap baited with fruits and vegetables was activated for at least seven nights per month and checked at sunset and dawn during each trapping session. When an individual was captured, it was sedated before manipulation, according to a standard protocol (Massolo et al. 2003). The exact geolocation, sex, and age were recorded for each animal. An individual was considered as *adult* when maxillary teeth were erupted (Mori and Lovari 2014). A total of 67 captured and 98 road-killed crested porcupines from Tuscany and Latium (Fig. 1) were examined. Other 21 road-killed individuals were excluded from the analysis, as collected more than 1 day after death, a time long enough to allow ectoparasites to leave their host (Kinsella and Pattie 1967). Porcupines were collected throughout the year ($N=36$ in summer, $N=37$ in autumn, $N=50$ in winter, $N=42$ in spring). A total of 85 samples were collected from the province of Grosseto (10 captured and 75 road killed) and 70 from the province of Siena (44 captured and 26 road killed). The study area near Grosseto (Maremma Regional Park and Poggi di Prata; hereafter, area 1, cf. Fig. 1) is almost totally covered by deciduous woodland and scrubwood; individuals from Siena came from a multi-habitat made by suburban, agricultural, and small wooded areas (Le Malandrine estate—Buonconvento, Le Scotte—North Siena, and Calvaiano estate—Radicondoli; hereafter, area 2, cf. Fig. 1). The remaining 10 road-killed individuals came from neighboring provinces: six from Arezzo (hereafter, area 3, cf. Fig. 1), three from Florence (hereafter, area 4, cf. Fig. 1), and one from Rome (hereafter, area 5, cf. Fig. 1).

All the body regions were examined for arthropods. Collected ticks and fleas were stored in 100 % ethanol. Species identification was based on the morpho-anatomical examination of 89 specimens through an optical microscope

Fig. 1 Locations of the 165 crested porcupine captures and road kills analyzed in this work: *area 1* province of Grosseto, *area 2* province of Siena, *area 3* province of Arezzo, *area 4* province of Florence, and *area 5* province of Rome
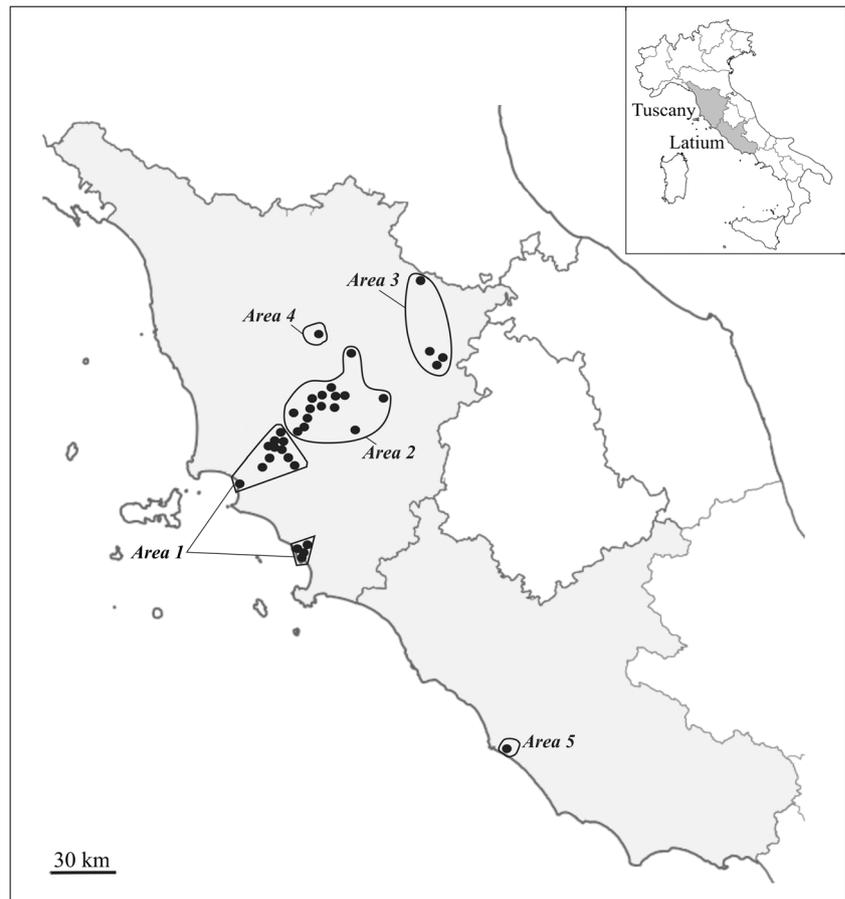
and referred to descriptions by Pérez-Eid (2007) for Ixodidae and by Beaucournu and Launay (1990) for Siphonaptera.

Data analysis

Variation of specific richness in arthropods, defined as the sum of all taxa recorded on a host, and prevalence in the total species of fleas and hard ticks were analyzed according to study areas, sex, and season. Since very few juveniles were infested (Table 1) and this could create recurrent biases in the model parameter estimates, only adult hosts were considered. To avoid outliers in residual variance errors, records from areas 3, 4, and 5 (Fig. 1, Table 1) were excluded from further analysis, since they were spatially isolated. Generalized linear models with Poisson errors, a log link function for specific richness, binomial errors, and log link for prevalence were carried out (Venables and Ripley 2002) and checked for variance error correctness (Zuur et al. 2009, 2010, 2013). Parameter estimates were associated to profiled 95 and 99 % confidence intervals (Kosmidis 2008; Johnson 2013). Multiple comparisons of parameter means were calculated using the contrast method of Tukey. All calculations were performed through software R 3.1.2 (R Core Team 2014).

Results

A total of 39 crested porcupines were infested by parasitic arthropod species (N=165, 24 %), in which there were 27 porcupine-harbored fleas (16 %) and 16 hard ticks (10 %). Parasites were uniformly divided between captured (58 %) and road-killed specimens (42 %). As to 69 juveniles (Table 1), only two females were infested: one in spring, hosting one specimen of *I. ricinus* along with more than five specimens of *P. irritans*, and another one in summer with more than five *P. irritans*. These young females were captured in the same locality (area 2), respectively, on April and August 1999. No juvenile males were infested by arthropod parasite species (Table 1).

Adults (N=96) were much more often infested (39 %) than juveniles (3 %; Table 1). A total of 78 specimens of ectoparasites were collected on 37 adult hosts (Table 1), and 21 were not identified to species level and only reported as *tick* or *flea* within capture/roadkill data sheets (samples were not available: Ixodidae and Siphonaptera; Table 1). Among the remaining 57 specimens, 38 were fleas (67 %) and 19 were hard ticks (33 %; Table 1). Within Siphonaptera, 22 specimens were identified as *P. irritans* hosted by 11 porcupines and 11 were *Paraceras melis* on seven hosts, 3 *Dasypsyllus gallinulae* on

Table 1 Number of hosts examined, averaged body mass (in kg), and number of hosts infested by ectoparasite species according to study area, age, and sex of crested porcupines between 1990 and 2014 in Central Italy

Province	Juveniles		Adults	
	♀	♂	♀	♂
Area 1	20	15	20	30
Body mass±SE	5.0±0.5	4.6±0.5	12.4±0.7	11.6±0.4
Pulex irritans	–	–	1 (2)	1 (6)
Paraceras melis	–	–	1 (2)	1 (1)
Unidentified flea	–	–	–	–
Rhipicephalus bursa	–	–	–	1 (1)
Unidentified tick	–	–	–	1 (2)
Area 2	18	14	27	11
Body mass±SE	4.6±0.6	4.8±0.4	11.3±0.5	11.8±0.5
Pulex irritans	1 (>5)	–	4 (1; 1; 1; 4)	1 (3)
Paraceras melis	–	–	2 (2; 2)	–
Pulex irritans+*Dasypsyllus gallinulae*	–	–	1 (1; 3)	–
Pulex irritans+*Ixodes ricinus*	1 (>5; 1)	–	–	1 (>5; >5)
Pulex irritans+unidentified flea+tick	–	–	1 (2; 1; 1)	–
Unidentified flea	–	–	2 (2; 3)	2 (1; 2)
Ixodes ricinus	–	–	1 (1)	3 (1; 2; 2)
Pholeoixodes hexagonus	–	–	1 (2)	1 (1)
Unidentified tick	–	–	2 (1; 1)	–
Unidentified flea + tick	–	–	–	1 (2; 2)
Area 3	0	0	2	4
Body mass	–	–	10.5; 13.0	9.5; 10.0; 13.5; 14.0
Paraceras melis	–	–	1 (1)	1 (1)
Hystrichopsylla talpae	–	–	1 (1)	–
Ctenocephalides canis	–	–	–	1 (1)
Ixodes ricinus	–	–	–	1 (2)
Ixodes ricinus+*Ixodes ventalloi*	–	–	–	1 (1; 2)
Area 4	0	2	0	1
Body mass	–	2.0; 3.0	–	10.3
Paraceras melis	–	0	–	1 (3)
Area 5	0	0	0	1
Body mass	–	–	–	14.5
Paraceras melis	–	–	–	1 (1)

Body mass is also reported (with standard errors for area 1 and area 2); the number of flea and hard tick specimens is presented in parentheses

one female host, 1 *Ctenocephalides canis* on one female, and 1 *Hystrichopsylla talpae* on an adult male. For Ixodidae, 14 were *I. ricinus* on seven hosts, 3 *P. hexagonus* on two hosts, and 1 *Ixodes ventalloi* and 1 *R. bursa* each on different male hosts.

Specific richness in parasitic arthropod species varied according to area, but not to sex or season (Tables 1 and 2): in wooded area 1 (N=50), adult porcupines hosted on average 0.2±0.1 arthropod species per individual, which was significantly lower than that on the localities from multi-habitat area 2 (N=38; 1.6±0.1; P<0.001).

Prevalence in fleas varied according to season and to study area (Table 1), but not to sex of hosts (Table 2): porcupines from area 2 hosted more frequently fleas (37 %) than those

from area 1 (10 %). Considering only individuals for which flea identifications were reached at species level, this was true for *P. irritans*, hosted by 25 % porcupines in area 2 versus 4 % in area 1. The prevalence in *P. melis* (Walker, 1856) was low in both areas (3 and 4 %, respectively; Table 1). Additionally, the prevalence (Prev) in fleas was lower in spring (N=33, Prev= 6 %) than in summer (N=22, Prev=32 %), autumn (N=23, Prev=26 %), and winter (N=18, Prev=61 %). This was mainly due to the variation in prevalence of *P. irritans* on crested porcupines from area 2, where five hosts out of 7 in winter harbored this species versus 3 out of 25 in the remaining seasons.

Prevalence of hard ticks varied according to study area and sex, but not according to season (Tables 1 and 2): porcupines

Table 2 Model parameter estimates (β) and profiled confidence intervals explaining the effect of sex, season, and region on the variation in total arthropod-specific richness and the prevalence of fleas and hard ticks separately on 96 adult crested porcupines in Central Italy (area 1 and area 2, cf. Fig. 1)

Source of variations	Arthropod species richness			Flea prevalence			Hard tick prevalence		
	β	95 % CI	99 % CI	β	95 % CI	99 % CI	β	95 % CI	99 % CI
Intercept	−2.41	−3.62; −1.40	−4.05; −1.11	−2.28	−4.05; −0.88	−4.71; −0.49	−6.70	−10.99; −3.73	−12.69; −3.00
Male sex	0.53	−0.18; 1.22	−0.41; 1.44	0.46	−0.86; 1.85	−1.27; 2.32	2.18	0.57; 4.12	0.10; 4.84
Season									
Spring	−0.27	−1.26; 0.76	−1.58; 1.11	−2.97	−6.02; −0.97	−7.47; −0.41	2.47	0.26; 5.77	−0.33; 7.28
Summer	−0.04	−1.17; 1.08	−1.56; 1.43	−0.53	−2.24; 1.09	−2.83; 1.60	1.23	−1.53; 4.66	−2.46; 6.17
Winter	0.76	−0.15; 1.75	−0.43; 2.10	1.09	−0.45; 2.75	−0.94; 3.33	1.37	−1.42; 4.82	−2.35; 6.34
Area 2	1.79	0.98; 2.72	0.75; 3.05	2.32	1.00; 3.87	0.61; 4.43	3.42	1.62; 5.78	1.13; 6.70

Non-zero parameters are presented in italics

from area 2 hosted more frequently hard ticks (29 %) than those from area 1 (4 %). Among infested porcupines from area 2, five male porcupines out of 11 and five females out of 27 hosted hard ticks (Table 1).

Discussion

A poor ectoparasite assemblage was found on crested porcupine in Central Italy, with two dominant species presenting prevalence above 20 %: one hard tick (*I. ricinus*) and one flea (*P. irritans*). The composition of ectoparasite communities varied across study areas: porcupines from area 2 harbored a more diverse arthropod parasite load than those from area 1. Although old road-kill individuals were excluded from the analysis, the higher number of captures in area 2 with respect to roadkill may have influenced this result. All the samples from area 1 came from scrubwood or deciduous woodland, while habitat types in area 2 were more diversified, with habitat ranging from deciduous woodlands to agricultural areas. This is probably at the origin of the observed difference in parasite diversity between the two areas.

Abundance of *P. irritans* and *P. melis* on porcupines in winter, with respect to the other seasons, may be related to behavior of these insects: they are nidicolous ectoparasites that can be found in nests/dens of host animals, particularly in winter (Cox et al. 1999; Rafinejad et al. 2013). Porcupines partly reduce their activity in cold months, thus resting longer in their underground dens (Corsini et al. 1995), where they may be more exposed to parasite infestation. Moreover, den sharing with badgers, foxes, and martens further increases the potential for parasite infestation (Tinelli and Tinelli 1980; Pigozzi 1986; Mori et al. 2014b). This may be particularly true for *P. melis* involving dens sharing between foxes and badgers with porcupines (Ancillotto et al. 2014).

Interestingly, this result is also supported by the anecdotal records of *P. hexagonus* which preferentially infest carnivores (Pérez-Eid 2007). Environmental conditions such as optimal temperature and humidity, and the durable presence of hosts wintering in dens, may also explain the observed seasonal pattern in prevalence by these fleas, especially for *P. irritans* which is most sensitive to cold and arid environments (e.g., Beaucournu and Launay 1990).

An adult male-biased parasitism for ticks (dominated by *I. ricinus*) has been detected. Spatial and temporal behaviors of paired male and female crested porcupine are almost completely overlapping (Corsini et al. 1995; Mori et al. 2014a, d); the species is thought to be monogamous (Mori and Lovari 2014). So, the higher tick load in males could not be due to any differences in their exploratory behavior compared to females. Hughes and Randolph (2001) claimed that testosterone levels deeply affect resistance to *I. ricinus* in rodent hosts. The lowest resistance to tick feeding occurs in sexually active males; therefore, a trade-off between mating success and parasitism may exist. A great consumption of fat reserves and high hormone levels due to the benefit of a high reproductive success could promote the suppression of immunological defense, thus a decrease in parasite resistance (cf. Corlatti et al. 2012; Romeo et al. 2013; Le Coeur et al. 2015).

Among rodents, parents groom the cubs (Gubernick and Alberts 1987), which may explain the low ectoparasite load of young porcupines. This habit, together with the small number of inhabitants in a porcupine den (on average, one breeding pair and one to two cubs; Mori and Lovari 2014), may militate against heavy infestations of the young. In facts, one could expect that cubs may be less resistant than adults to parasite infestations, thus making grooming by parents an advantageous behavior. It is likely that movements of young are shorter than those of adults, reducing the opportunity to come in contact with infesting stages of ectoparasites (cf. Le Coeur et al. 2015).

All other species we found on porcupines were occasional and related to co-inhabiting primary hosts as well as to the behavior in the space use of the crested porcupines, which often range in the surroundings of human settlements (Lovari et al. 2013; Mori et al. 2014d). Secondary hosts can sustain parasite species only if a primary host is present (Beaucournu and Launay 1990; Pérez-Eid 2007). This may explain the presence of the *R. bursa*, mainly encountered in open agricultural landscapes in the Mediterranean area, where wild or domestic Ungulates are presents, e.g., in area 1. It also supports the regular occurrence of *I. ricinus*, which distribution largely depends on wild or domestic ruminants; *H. talpae* is frequently found in nests inhabited by Microtinae, and its presence on porcupines indicates occasional frequentations of dens by these small rodents. *C. canis* is relatively specific to canid hosts, which again supports the regular frequentation of porcupines' dens by red foxes. Anecdotal information suggests that the densities of red foxes and badgers in area 1 are greater than those in area 2 (pers. obs.); *I. ventalloi* feed most preferentially on the rabbits, indicating that either rabbits could occasionally enter porcupine dens or that, conversely, porcupines may explore rabbit warrens. Interestingly, *D. gallinulae* is a species which infest nests of many small birds, but it may be encountered on mammals because of its dispersal behavior (Bates and Rothschild 1962).

The parasitic arthropod fauna of crested porcupines in Central Italy was composed by a relatively low number of dominant species, confirming and improving the scanty available information available on the parasites infesting this rodent (Starkoff 1958; Toschi 1965; Berlinguer 1965). All the ectoparasites detected on *H. cristata* were sourced from other mammals known to be primary hosts, mainly red foxes and badgers, and shared because of similar behavior in space use (cf. Mori et al. 2014b). This result matches what expected for an introduced rodent, locally acquiring relatively low specific arthropod ectoparasite taxa. Despite the long duration of the establishment of the crested porcupine in Italy, we found no arthropods infesting similar species on their native range, e.g., fleas belonging to the genera *Procaviopsylla* and *Pariodontis* (Beaucournu and Launay 1990). This result suggests a possible loss of ectoparasites during the history of introduction of *H. cristata* in Italy (e.g., Torchin et al. 2003). The introduction of alien species increases incidence, pathogenicity, and geographical range of native parasites locally acquired (Romeo et al. 2014). Therefore, if the crested porcupine keeps increasing its range, ectoparasite infestations in the newly colonized areas should be further investigated, with a special attention deserved to *P. irritans*, which has the human as a primary host (Buckland and Sadler 1989; Beaucournu and Launay 1990).

References

Altizer S, Nunn CL, Thrall PH, Gittleman JL, Antonovics J, Cunningham AA, Dobson AP, Ezenwa V, Jones KE, Pedersen AB, Poss M, Pulliam JR (2003) Social organization and parasite risk in mammals: integrating theory and empirical studies. Annu Rev Ecol Evol Syst 34:517–547

Ancillotto L, Mazza G, Menchetti M, Mori E (2014) Host specificity of the badger's flea (*Paraceras melis*) and first detection on a bat host. Parasitol Res 113:3909–3912

Bailly-Choumara H, Morel PC, Rageau J (1976) Sommaire des données actuelles sur les tiques du Maroc (Acari, Ixodoidea). Bull Ins Sci 1: 102–117

Bates JK, Rothschild M (1962) Field studies on the behaviour of bird fleas. I. Behaviour of the adults of three species of bird fleas in the field. Parasitology 52:113–132

Beaucournu JC, Launay H (1990) Les puces de France et du bassin Méditerranéen occidental. Faune de France 76. Fédération Française des Sociétés de Sciences Naturelles, Paris

Berlinguer G (1965) Aphaniptera d'Italia. Studio Monografico. Il Pensiero Scientifico Editors, Rome

Bordes F, Blumstein DT, Morand S (2007) Rodent sociality and parasite diversity. Biol Lett 3:692–694

Buckland P, Sadler J (1989) A biogeography of the human flea, *Pulex irritans* L. (Siphonaptera: Pulicidae). J Biogeogr 16:115–120

Corlatti L, Bethaz S, von Hardenberg A, Bassano B, Palme R, Lovari S (2012) Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs. Anim Behav 84:1061–1070

Corsini MT, Lovari S, Sonnino S (1995) Temporal activity patterns of crested porcupines *Hystrix cristata*. J Zool, London 236:43–54

Cox R, Stewart PD, Macdonald DW (1999) The ectoparasites of European badger, *Meles meles*, and the behaviour of the host specific flea, *Paraceras melis*. J Insect Behav 12:245-265

Gubernick DJ, Alberts JR (1987) The biparental care system of the California mouse, *Peromyscus californicus*. J Comp Psychology 101:169–177

Hoogland JL (1979) Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae, *Cynomys* spp.) coloniality. Behav 64:1–35

Hughes VL, Randolph SE (2001) Testosterone depresses innate and acquired resistance to ticks in natural rodent hosts: a force for aggregated distributions of parasites. J Parasitol 87:49–54

Johnson VE (2013) Revised standards for statistical evidence. Proc Natl Acad Sci U S A 110:19313–19317

Kinsella JM, Pattie DL (1967) Ectoparasites of small mammals of the alpine Beartooth Plateau, Wyoming. Can J Zool 45:233–235

Kiviat E (1978) Vertebrate use of muskrat lodges and burrows. Estuaries 1:196–200

Kosmidis I (2008) The profile model R Package: profiling objectives for models with linear predictors. R News 8:12–18

Krasnov B, Khokhlova I, Shenbrot G (2002) The effect of host density on ectoparasite distribution: an example of a rodent parasitized by fleas. Ecol 83:164–175

Krasnov BR, Khokhlova IS, Burdelova NV, Mirzoyan NS, Degen AA (2004a) Fitness consequences of host selection in ectoparasites: testing reproductive patterns predicted by isodar theory in fleas parasitizing rodents. J Anim Ecol 73:815–820

Krasnov BR, Shenbrot GI, Khokhlova IS, Degen AA (2004b) Flea species richness and parameters of host body, host geography and host "milieu". J Anim Ecol 73:1121–1128

Le Coeur C, Robert A, Pisanu B, Chapuis J-L (2015) Seasonal variation in infestations by ixodids on Siberian chipmunks: effects of host age, sex and birth season. Parasitol Res. doi:10.1007/s00436-015-4391-5

Lovari S, Sforzi A, Mori E (2013) Habitat richness affects home range size in a monogamous large rodent. Behav Proc 99:42–46

Massolo A, Sforzi A, Lovari S (2003) Chemical immobilization of crested porcupine with tiletamine HCl and zolazepam HCl (Zoletil®) under field condition. J Wildl Dis 39:727–731

Monetti L, Massolo A, Sforzi A, Lovari S (2005) Site selection and fidelity by crested porcupine for denning. Ethol Ecol Evol 17:149–159

Mori E, Lovari S (2014) Sexual size monomorphism in the crested porcupine (*Hystrix cristata*). Mammal Biol 79:157–160

Mori E, Sforzi A, Di Febbraro M (2013) From the Apennines to the Alps: recent range expansion of the crested porcupine *Hystrix cristata* L., 1758 (Mammalia: Rodentia: Hystricidae) in Italy. Ital J Zool 80:469–480

Mori E, Nourisson DH, Lovari S, Romeo G, Sforzi A (2014a) Self-defence may not be enough: moonlight avoidance in a large, spiny rodent. J Zool, London 294:31–40

Mori E, Menchetti M, Balestrieri A (2014b) Interspecific den sharing: a study on European badger setts using camera traps. Acta Ethologica. doi:10.1007/s10211-014-0197-1

Mori E, Maggini I, Menchetti M (2014c) When quills kill: the defense strategy of the crested porcupine *Hystrix cristata* L., 1758. Mammalia 78:229–234

Mori E, Lovari S, Sforzi A, Romeo G, Pisani C, Massolo A, Fattorini L (2014d) Patterns of spatial overlap in a monogamous large rodent, the crested porcupine. Behav Proc 107:112–118

Pérez-Eid C (2007) Les tiques: identification, biologie, importance médicale et vétérinaire. Lavoisier, Paris

Pigozzi G (1986) Crested porcupines *Hystrix cristata* within badger setts *Meles meles* in the Maremma Natural Park, Central Italy. Saugetierkd Mitt 33:261–263

Poulin R (1995) Phylogeny, ecology, and the richness of parasite communities in vertebrates. Ecol Mongr 65:283–302

Poulin R (1997) Species richness of parasite assemblages: evolution and patterns. Ann Rev Ecol Syst 28:341–358

R Core Team (2014). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Rafinejad J, Piazak N, Dehghan A, Shemshad K, Basseri HR (2013) Affect of some environmental parameters on fleas density in human and animal shelters. Am J Res Comm 1:2325–4076

Romeo C, Pisanu B, Ferrari N, Basset F, Tillon L, Wauters LA, Martinoli A, Saino N, Chapuis JL (2013) Macroparasite community of the Eurasian red squirrel (*Sciurus vulgaris*): poor species richness and diversity. Parasit Res 112:3527–3536

Romeo C, Wauters LA, Ferrari N, Lanfranchi P, Martinoli A, Pisanu B, Preatoni DG, Saino N (2014) Macroparasite fauna of alien grey squirrels (*Sciurus carolinensis*): composition, variability and implications for native species. PLoS One 9:e88002

Starkoff O (1958) Ixodoidea d'Italia. Studio Monografico. Il Pensiero Scientifico ed. Roma, Italy

Theodor O, Costa M (1967). A survey of the parasites of wild mammals and birds in Israel. Part one. Ectoparasites. The Israel Academy of Sciences and Humanity (Eds): 20

Tinelli A, Tinelli P (1980) Le tane di istrice e di tasso. Censimento e densità delle tane nella Riserva Presidenziale di Castelporziano per la conservazione dell'istrice e del tasso. Segretariato generale della Presidenza della Repubblica. Tenuta di Castelporziano, Rome, Italy

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421:628–630

Toschi A (1965) Mammalia. Lagomorpha, Rodentia, Carnivora, Ungulata, Cetacea. Collana Fauna d'Italia, Vol. VII. Calderini, Bologna, Italy

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York

Whitaker JO, Goff R (1979) Ectoparasites of wild carnivora of Indiana. J Med Entom 15:425–430

Zuur AF, Ieno EN, Walker N, Saveliev A, Smith G (2009) Mixed effect models and extensions in ecology with R. Springer, New York

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Meth Ecol Evol 1:3–14

Zuur AF, Hilbe J, Ieno EN (2013) A beginner's guide to GLM and GLMM with R: a frequentist and Bayesian perspective for ecologists. Highland Statistics, UK