Cohabitation of settlements among crested porcupine (*Hystrix cristata*), red fox (*Vulpes vulpes*) and European badger (*Meles meles*)

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In Italy, porcupines, badgers and red foxes share the same settlements. However, there is lack of information concerning their cohabitation. From 2012 to 2019, cohabitation by these three mammals was studied using camera-trapping and was found to occur only between porcupines and badgers, even in the presence of porcupettes. Cohabitation was associated with aggressive interaction between porcupines and badgers. Foxes were found to be scavengers of porcupine carcasses. Cohabitation among these semi-fossorial mammals and scavenging behaviour could play a role in disease transmission, including zoonotic diseases.

Keywords: Burrowing mammals, camera-trapping, cohabitation, scavenging, settlements.

AMONG mammals, at least 58% are known to exhibit burrowing behaviour[1]. Given the energetic costs associated with digging and limitations in the availability of burrowing sites, many species share the same den sites[2]. The coexistence of unrelated species and sharing of resources in a region have always been intriguing for ecologists to study the interactions between individuals of these species. Italy is the only European country in which the crested porcupine (*Hystrix cristata*), European Badger (*Meles meles*) and red fox (*Vulpes vulpes*) coexist, sharing the same burrows[3–5]. Therefore, Italy provides an ideal natural set-up of co-existence of these three species in a small area sharing common resources. For all these three species, burrows are the preferred sites for breeding, sleeping and hiding during daylight hours[6–8].

Despite the fact that these three species have mainly nocturnal habits, all of them show diurnal motor activities. The European badger shows a strong selection to night-time with little activity during the twilight periods and strong avoidance of daytime[9]. The red fox is a facultative nocturnal mammal that positively selects night-time[10]. The crested porcupine clearly shows a daytime motor activity, often performing sunbathing[11,12].

The hypogeous burrows of both badgers and porcupines can be a complex system of chambers and tunnels that show huge variation both in size and complexity[8,13,14]. The burrows open to the outside through holes at the ground level[13,15]. The settlement is a cluster of holes[3,8,13,15] that is commonly referred to as a burrow system, burrow site or den site[6,14,16–19], and could be used by both porcupine and badger. For porcupine and badger, the selection of burrow site follows the same criteria: a 10°–40° slope with sandy soil and dense vegetation cover in wooded areas[14,15,20]. A large soil heap, resulting from digging, is often visible in front of the ground holes[13,16]. Red fox burrows are mainly located in wooded areas with low vegetation and shrub cover[21]. Nevertheless foxes are reported to be opportunistic users of badger or porcupine burrows, mainly in spring, for breeding[14,21,22].

Observation of traces like footprints, quills and faeces of porcupine, red fox and badger in the same settlement, confirmed by the use of camera trapping, proved sett-sharing (co-use of the same settlement, though not simultaneously) by the three species[3,4,14]. However, no data are available on whether the three species cohabit (contemporary inhabitation) the same settlements.

Badger and fox are known to be predators[7,10]. Porcupine remains have occasionally been found in foxes faeces and it has been hypothesized that red fox is an occasional porcupine predator[23,24]. However, predation on porcupine by red fox has not been documented, and Mori *et al.*[4] hypothesized a mutual avoidance behaviour among the three species. The above factors could have implications on sett-sharing or cohabitation. Crested porcupines, at least in Italy, do not seem to have natural predators that are able to kill adult specimens[16,25]. Even predation of porcupettes is improbable because they are always protected by at least one adult[26–28].

In this long-term study we analysed cohabitation of the same settlement by crested porcupine, European badger

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and red fox using camera-trapping, in an area characterized by a high density of available settlements. We predicted that: (i) cohabitation of the same burrow between porcupines, badgers and/or foxes occur even if un-inhabited settlements are available in the same area and (ii) there is lack of aggressiveness and/or predation among these three species in order to allow cohabitation.

Methods

Study area and camera-trapping

The study was performed in a hilly area of 2548 ha in Crespina-Lorenzana (43.35412°N; 10.325052°E) in the province of Pisa, Tuscany, Central Italy, characterized by high biodiversity and environmental fragmentation. Camera trap monitoring was performed between 2012 and 2016 in two settlements. During October 2016 to November 2019, ten more settlements were included in the study, leading to a total of 12 monitored settlements (S1–S12) out of 67 present in the study area (2.6 settlements/sq. km; Figure 1 and Supplementary Table 1). The average distance between the settlements was 2.6 km (SD 1.4 km) and the minimum distance was 120 m. Distance and territory characteristics render impossible any direct underground connection among settlements. All ground holes of each settlement are known to be connected to each other and have existed for over 50 years.

Twenty-four camera traps (Num'axes PIE1009) with passive infrared sensors (PIRs) were used in order to assess inhabitation and/or cohabitation of settlements by the three studied species. Each settlement was sampled using two camera-traps in order to monitor the maximum number of holes used by the species (Supplementary Table 1). The camera traps were active for 24 h a day and were set to record 20 s video clips without time lapse. Video-trapping effort was indicated as number of trap days (TDs). The trap day is defined as a 24 h period in which a settlement has been continuously monitored by camera traps. Video-trapping effort was of 2662 TDs in S1 and S2, while in settlements S3–S12 it was 1028 TDs. Whenever possible, individual identification of badger, red fox and crested porcupine was made by detecting the presence of some phenotypic peculiarities (e.g. blindness, presence of wounds or injuries, particularity in coat coloration). Moreover, identification of nine crested porcupine individuals was possible as they were previously marked with coloured adhesive tapes on the quills, by white or black paint sprayed on the crest and/or on the tail, or by a combination of these methods. The video recordings from the camera traps were checked and filed on a weekly basis. Only those videos in which porcupines, badgers and red foxes were captured were analysed.

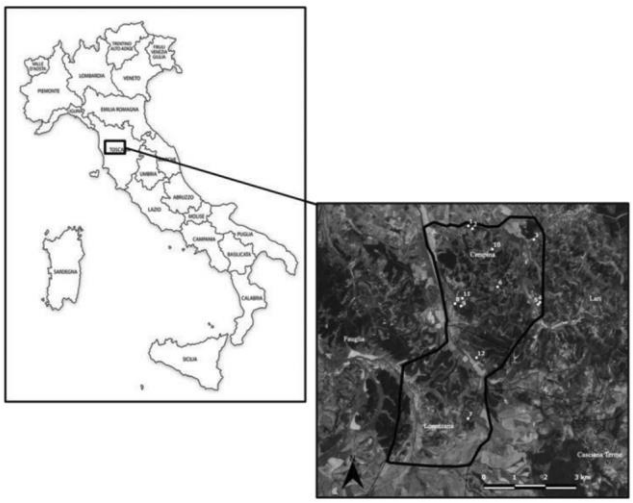


Figure 1. Map of Italy, and detailed map of the study area where camera-trapping was performed between 2012 and 2019. White spots indicate the 12 monitored settlements.

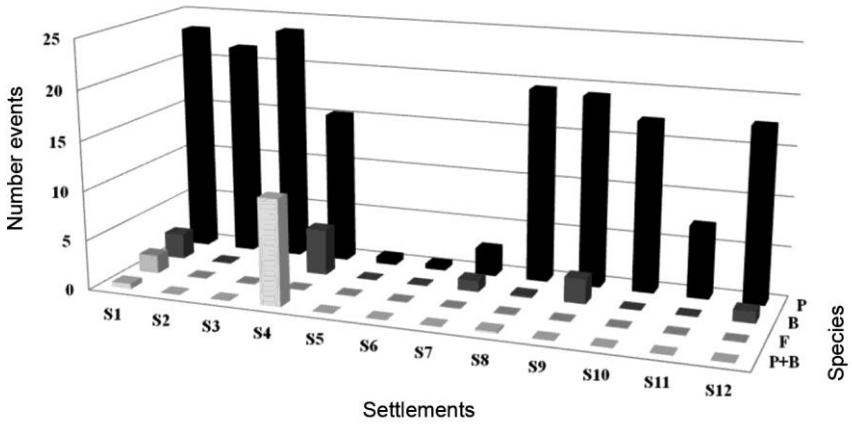
Inhabitation and cohabitation of settlements and interaction analysis

The use of settlements by each of the three studied species was assessed by the time of permanence in the burrow. Permanence is defined as the time continuously spent by the species inside or in front of the burrow (e.g. performing sunbathing and/or lactation) during daytime being longer than the minimum recorded time interval between the last going in and the first coming out of the burrow itself. Three possible types of settlement use were established: (i) inhabitation, (ii) cohabitation, and (iii) visit or exploration. The settlements were considered inhabited if the permanence of a monitored species in the burrow was confirmed. It was considered cohabited when at least two individuals of different species simultaneously inhabited the same settlement. Conversely, a settlement was indicated as visited or explored if permanence in the burrow was not recorded.

Cohabitation in the same settlement between porcupine and badger (P–B), porcupine and red fox (P–F), badger and red fox (B–F), and among porcupine, badger and red fox (P–B–F) was studied. For each cohabitation event, the simultaneous time of permanence in a settlement was

Table 1. Percentage use of the same and different burrow entrance holes during emerging from and returning to the burrow by porcupines and badgers in S1, S4 and S8. The single event of co-use of ground holes by both species is not reported here

Hole	S1	S4	S8
Same	2 (14.3%)	23 (21.3%)	2 (100%)
Different	12 (85.7%)	84 (77.7%)	0



	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12
P+B	0,5	0,0	0,0	10,7	0,0	0,0	0,0	0,2	0,0	0,0	0,0	0,0
F	1,8	0,04	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
B	2,6	0,1	0,0	4,7	0,0	0,0	1,2	0,2	2,5	0,0	0,0	1,2
P	23,3	21,6	23,6	15,3	0,7	0,5	2,7	19,5	19,2	17,1	7,2	17,5

Figure 2. Settlements inhabitation. Percentage of days of inhabitation of the 12 settlements by crested porcupines (P), badgers (B) and red foxes (F), and of cohabitation between porcupines and badgers (P + B) during 2662 trap days for S1 and S2 and, 1028 trap days for other settlements.

measured. In addition, use of the same and/or different burrow entrance holes during emerging from and returning to the burrow was assessed. The correspondence between early or late emergence of the species with the respective early and late return to the settlement on the same day was also assessed. The exclusive inhabitation of temporarily uninhabited porcupine burrows by red fox and badger was tested using chi-square test.

Presence of free settlements in the vicinity of those cohabited was checked in order to assess if cohabitation occurred only in a limited number of settlements.

All the videos in which at least two species were detected together were analysed for interactions. These were classified into two types: avoidance (AV) and aggressive (AI) interactions. AV was assigned when the two species, one individual in front of the other, change their direction respectively, with absence of aggressive behaviour. AI was assigned when at least one of the two species showed signs of aggression (e.g. quill erection, tail rattling, attempt to attack, approaching and biting).

Differences in the number of interactions in the dyads P–F and P–B in settlements not cohabited were analysed using chi-square test. Moreover, within the dyads that showed cohabitation among the same settlements, differences in the number of recorded interactions between settlements cohabited and not cohabited were also analysed using chi-square test.

Results

A total of 76,084 camera-trap videos were recorded of which 36,822 (48.4%) were those where animals were observed on camera. The target animals were recorded in 43.7% (33,292) of the total videos. The crested porcupine was observed in 25,807 videos (70.1% of 36,822), badger in 5336 (14.5% of 36,822) and red fox in 2149 (5.8% of 36,822). In addition to the nine marked porcupines, nine badgers, five red foxes and eight unmarked porcupines were identified (Supplementary Table 2). Moreover, seven porcupine families were recognizable. For each family, the porcupettes of the same litter were recognizable, while we had difficulties in the discrimination of siblings of the same litter. The minimum time of permanence was 10 h and 11 min, while the average time was 13 h and 44 min (SD 1 h and 26 min). The settlements were often explored by crested porcupines, badgers and red foxes during the same night, but at different times. Porcupines did not permanently inhabit all the monitored settlements. The red foxes inhabited only S1 and S2, when not used by porcupines. The badgers inhabited seven out of 12 settlements, four of them (S2, S7, S9, S12) in absence of porcupine and three (S1, S4, S8) in the presence of porcupines (Figure 2 and Supplementary Table 3).

Cohabitation was only recorded between badgers and porcupines during 2017–19 in 11.4% (n = 124 days) of TDs in S1 (n = 14), S4 (n = 108) and S8 (n = 2), each inhabited by a different recognizable porcupine family. Also, 8.9% (n = 11) of cohabitation events were recorded in 2017, 41.9% (n = 52) in 2018 and 49.2% (n = 61) in 2019. Cohabitation between porcupines and badgers was observed throughout the year (Figure 3 and Supplementary Table 4). In 74.2% of cohabitation days (n = 92), the event was observed in the presence of porcupettes. Cohabitation between badgers and porcupines with porcupettes

was recorded in all settlements in which cohabitation occurred. Porcupines and badgers in S1 used two out of four monitored ground holes; two out of five in S4, and one out of two in S8, for emerging from and returning to the burrow. Table 1 shows the percentage use of the same or different burrow entrance holes during emerging from and returning to the burrow. Only in one case in S4 the two species used both entrance holes without priority in the order of entrance of one species over the other. Within the cohabitation days (n = 124), badgers emerged from and returned to the burrow after the porcupines 30 times (24.2%); they emerged after and returned before the porcupines 62 times (50%); emerged before and returned after the porcupines 14 times (11.3%), and emerged and returned before the porcupines 18 times (14.5%). The average delay of first emergence between the two species was 46 min (SD 38 min). The last returning home event was recorded with an average delay of 41 min (SD 37 min). The average cohabitation time between the two species was 12 h and 40 min (SD 1 h and 6 min), from 10 h and 11 min to 16 h. The exclusive inhabitation of temporarily uninhabited burrows of porcupine by red foxes and badgers resulted in significant difference ($P < 0.001$, $\chi^2 = 52.26$). The red foxes exclusively inhabited the settlements in 100% of cases, while badgers both exclusively inhabited and cohabited with porcupines in 57% and 43% of cases respectively. Within a settlement, all the cohabitation events always occurred in the vicinity (no more than 250 m) of another available free/empty settlement. Totally 42 events of interaction were recorded. Table 2 shows the number and percentage of both types (AV and AI) of interactions for P–B, P–F and F–B. During three occasions, in S4, interactions between an adult badger and a four-month-old porcupette were recorded. The porcupette always drove away the badger by sideways attack, quill erection and tail rattling. Aggressive interactions between porcupines and red foxes were always recorded as a consequence of an intense exploratory activity of the red foxes just after the birth of porcupettes. No statistical differences were recorded in the number of interactions for P–F and P–B in settlements not cohabited, while statistical differences ($P < 0.01$, $\chi^2 = 7.27$) resulted in the number of interactions of the dyad P–B in the settlements cohabited and not cohabited.

Predation events on porcupine by both badger and red fox have never been observed. The scavenging of a porcupine carcass by a red fox was recorded during two occasions in S1 and S2 (Figure 4). In both cases the recorded videos clearly show the red fox sniffing and yelping before partially entering the ground hole and pulling out a dead porcupine from the burrow without any display of predatory movements.

Discussion

The results obtained in this study clearly indicate that red fox always inhabits exclusively the settlements, while both crested porcupine and badger can inhabit the same settlement both exclusively as well as together.

The results of this study reinforce the observations of Tinelli and Tinelli[14] on the opportunistic occupation of settlements by red foxes for breeding, as also hypothesized in studies performed in Poland and Belarus[22,29]. The potential cohabitation of settlements between red foxes and porcupines could arise with an increase in fox density.

Cohabitation between porcupines and badgers occurred several times during the whole year and also when porcupettes were present. The availability of settlements not inhabited in the vicinity of the cohabited settlements shows that cohabitation is not due to lack of settlements. Although the population density of porcupines and badgers in the study area is not known, cohabitation by these two species is intriguing and overcrowding does not seem to be the reason for the same. Cohabitation between porcupines and badgers may also not be due to the peculiar physiological state of the latter as overwintering. In the winter cohabitation periods recorded in this study, the

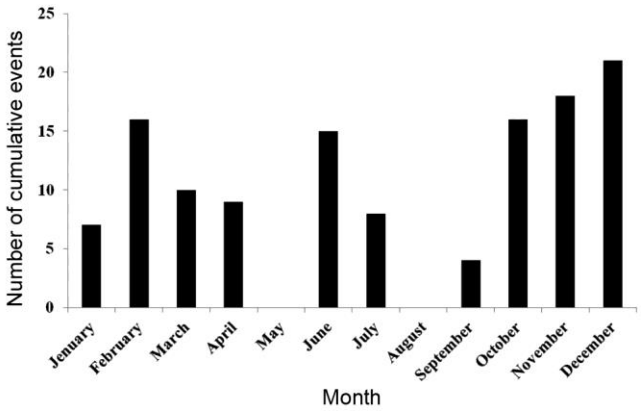


Figure 3. Number of cumulative monthly cohabitation events recorded during the whole period of monitoring.

Table 2. Number and percentage of avoidance (AV) and aggressive interactions (AI) recorded between porcupines and badgers (P–B), porcupines and foxes (P–F) and badgers and foxes (B–F) in the settlements

	Settlement	AI	AV	AI + AV
P–B	S1	0	8 (100%)	8
	S3	2 (50%)	2 (50%)	4
	S4	10 (40%)	14 (60%)	24
P–F	S1	0	1 (100%)	1
	S2	2 (100%)	0	2
	S3	0	1 (100%)	1
	S11	1 (100%)	0	1
B–F	S1	1 (100%)	0	1

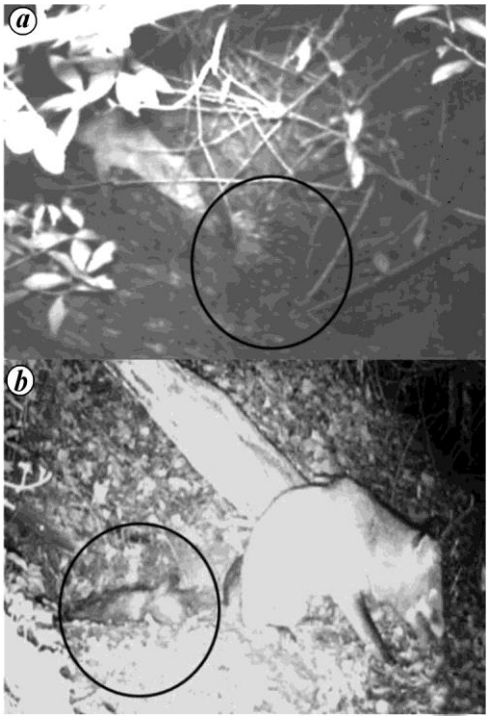


Figure 4. Scavenging of porcupine carcass by red fox. ***a***, Red fox (*Vulpes vulpes*) while pulling out the dead porcupine from the burrow. ***b***, Red fox while scavenging the porcupine carcass.

badger did not reduce its nocturnal activity indicating no overwintering at this latitude and altitude. In the study area in the cold season, the average nocturnal temperature was 6.8°C and occasionally reached a minimum of 3°C. According to Goszczyński and Wòjtowicz[29], the time spent by badgers in their settlements was closely dependent on the outside temperature. Inhabitation of the same settlement at different times (sett-sharing) between these three species was previously hypothesized by Pigozzi[3], as well as Tinelli and Tinelli[14], and confirmed by Mori *et al.*[4]. However, there is lack of information on cohabitation among these three species. Use of the same and/or different burrow entrances by both porcupines and badgers at different times during emerging from and returning to the burrow suggests that cohabitation is probably due to the possibility using different chambers.

Among the three settlements in which cohabitation occurred, in one of them (S1) not all ground holes were monitored; so in this case cohabitation could be underestimated.

Both AI and AV between porcupines and badgers resulted in significant higher cohabited settlements compared to exclusively inhabited ones. Conversely, no significant differences resulted in aggressive interactions in the dyads P–B compared to P–F. These results surprisingly disregard the prediction that absence of aggressive interactions permits cohabitation. To the best of our knowledge, scavenging of porcupine carcass by red fox has not been documented earlier. This suggests that the occasional presence of porcupine remains in red fox faeces[23,24] is more likely to be a consequence of scavenging on carcasses rather than of predation of juveniles or porcupettes, as hypothesized by Monetti *et al.*[16]. Since *Giardia duodenalis* and several serogroups of *Leptospira* were detected in crested porcupine[30–32], cohabitation among crested porcupine, badger and red fox and the scavenging behaviour of red fox on porcupine carcasses as well as of porcupine on carrions[33] could play a role in the spread of such zoonotic diseases. More studies are needed in order to assess the features of settlements that determine the choice by porcupines and badgers as well as the potential advantages of cohabitation for both species.

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