Coming back home: recolonisation of abandoned dens by crested porcupines *Hystrix cristata* and European badgers *Meles meles* after wood-cutting and riparian vegetation mowing events

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Abstract

Semifossorial species excavate dens and thus are considered as landscape engineers, often responsible for soil oxygenation and shuffling, as well as for landslides and floods. The crested porcupine and the European badger are semifossorial mammals sharing dens in C Italy. Both species localise their setts mainly in densely vegetated areas, providing them with cover and protection from local predators and poachers. This is particularly evident for the porcupine, widely poached in central and southern Italy, whereas badgers may locally exploit burrows also in open and periurban areas. Wood-cutting and mowing of riparian vegetation surrounding den setts force both porcupines and badgers to leave their burrows. We evaluated the probability of den re-occupancy in the years following the vegetation removal, through intensive camera-trapping at 14 den setts monitored for 9 years. We performed GLMMs to test the annual probability of sett occupancy by the two species after vegetation disturbance events. The probability of re-occupying the burrow by porcupines increased with increasing time from the disturbance cessation. A similar pattern was also observed for the badger, which probability of den occupancy was also negatively correlated with the porcupine presence at the same den, confirming the aggressive behavior of this rodent. We also tested whether, since the first year after vegetation removal, the proportion of years of occupation by porcupines on the total of years has been affected by the disturbance repetition. This effect was found to be significant only for the badger. The crested porcupine, protected by international and national laws, is more sensitive than the badger, protected according to the Italian national law, to vegetation removal. A single disturbance event is sufficient to force it to abandon the den sett, followed by a slow recolonisation with growing vegetation. Conversely, the badger is sensitive to continuous vegetation removal whereas it can colonise porcupine dens abandoned after single disturbances.

Keywords: woodland management; den setts; habitat loss; recolonisation; *Hystrix cristata*; *Meles meles*.

Introduction

Habitat loss and fragmentation (e.g. due to urbanisation, infrastructure construction, agricultural expansion, and logging) have been reported to be the main anthropogenic disturbance to world ecosystems (e.g. Scott et al., 2006; Brodie et al., 2015; Khalatbari et al., 2018) and the main cause of the current global biodiversity crisis (e.g. Bright, 1993; Brooks et al., 2002; Fahrig, 2003). In the Mediterranean basin and in Central Europe, ecosystems were subjected to intensive human disturbance in the past 10,000 years and habitat fragmentation is a well-known driver of animal abundance and distribution (Mangas and Rodrìguez-Estival, 2010; Mortelliti et al., 2011; Thomas et al., 2018). If some species are potentially benefited by wood-cutting and agricultural/urbanisation intensification (Macdonald et al., 2007; Russo and Ancillotto, 2015), populations of forest-dweller species are generally negatively affected (Wilcove et al., 1986; Kouki et al., 2001; Mortelliti et al., 2011).

The European badger *Meles meles* and the crested porcupine *Hystrix cristata* are protected species in Italy; therefore, hunting against these species is not allowed in this country. Furthermore, the crested porcupine is also listed within the annexes of the Bern Convention and of the Habitat Directive. These species may be found in various habitat types ranging from woodlands to agricultural areas and human settlements (Mori et al., 2014a; Chiatante et al., 2017; Lovari et al., 2017; Geiger et al., 2018). Both species show semifossorial habits, i.e. they inhabit underground den systems (hereafter, "setts": Neal and Cheeseman, 1996) in daylight hours, which may be directly excavated or naturally present (Neal and Roper, 1991; Corsini et al., 1995; Roper et al., 2001; Monetti et al., 2005). Moreover, badgers and porcupines may share the same sett (Tinelli and Tinelli, 1980; Pigozzi, 1986; Zavalloni and Castellucci, 1994; Mori et al., 2015); however, during the reproductive period, crested porcupines tend to outcompete other species, dismissing them from the den (Mori et al., 2015). Given the high amount of energy required to dig dens (Vleck, 1979; Stewart et al., 1999), a strong den site fidelity has been reported for badgers and porcupines, who may occupy the same sett for many decades (e.g. Neal, 1986; Neal and Roper, 1991; Monetti et al., 2005). Even if both badgers and porcupines may attend a wide number of habitat types, their dens are mostly located within densely vegetated areas (e.g. scrublands and deciduous woodlands), often on limestone and in solid and steep soils (Neal and Roper, 1991; Doncaster and Woodroffe, 1993; Revilla et al., 2001a; Monetti et al., 2005). Conversely, pinewoods, human settlements and open habitats (farmlands and fallows) are largely avoided (Neal, 1986; Kurek, 2011; Revilla et al., 2001a; Mori et al., 2014a). Steep soils may guarantee den resistance, whereas the location within dense woodland and scrubland is functional to protect them from predators, extreme temperatures and poachers (Neal and Roper, 1991; Monetti et al., 2005; Lovari et al., 2017). Accordingly, it has been suggested that scrubland/woodland elimination (e.g for timber production or to increase agricultural areas/pastures for livestock) may force semifossorial mammals to locally abandon their setts (Feroe and Montgomery, 1999; Revilla et al., 2001a; Kurek, 2011; Lovari et al., 2017).

Due to their digging habits, both European badgers and crested porcupines have been suggested to be responsible for riverbank collapses, flooding and infrastructure damages, e.g. to railway embankments (Sforzi et al., 1999; Balestrieri and Remonti, 2000; Convito and Paci, 2003; Orlandini et al., 2015). In these cases, wood-cutting or riparian vegetation removal around dens has been proposed as a way to resolve conflicts with human activities and to mitigate damages without direct control intervention (Sforzi et al., 1999; Orlandini et al., 2015).

In this work, we aimed at assessing the pattern of recolonisation of den setts previously occupied by porcupines or by porcupines and badgers after vegetation removal in central Italy, also considering the interspecific interference occurring among these two semifossorial mammals. Given that badger setts may also occur in open areas (Tinelli and Tinelli, 1980; Pigozzi, 1986; Neal and Roper, 1991; Revilla et al., 2011a; Kurek, 2011), we predicted that wood-cutting may exert a stronger impact on the crested porcupine, which would recolonise abandoned dens in a longer amount of time.

Materials and Methods

Study area

Our study has been conducted on the Metalliferous Hills, in Central Italy (Provinces of Grosseto and Siena), along the Merse river valley (43.08°N, 10.09°E; 420-625 m a.s.l.: Fig. 1).

About 60% of the study area is covered by woodlands (mostly *Quercus cerris, Castanea sativa, Ostrya carpinifolia* and *Carpinus betulus*), surrounded by Mediterranean scrubland (*Juniperus* spp., *Rubus* spp. and *Spartium junceum*: about 8.5%). Open habitats (including fallows and cultivations) cover about the 25% of the study site. The remaining part of the study area (about 6.5%) is covered with coniferous woodlands (*Pinus nigra* and *Cupressus arizonica*). Average annual temperature was 16°C with summer peaks up to 33°C.

Camera trapping and vegetation control monitoring

Data were collected through a camera-trapping survey to study the spatiotemporal behaviour of the crested porcupine (June 2010-December 2018). We used 4 camera traps Ziboni Tecnofauna Explorer Case 1988 and 3 camera traps Multipir 12. Camera traps were located near the entrances of 16 den setts, i.e. all those detected within the study area, at a height of 20-50 cm above the ground level. All the setts were inhabited by reproductive groups of crested porcupines and 12 of them also hosted badger family groups (Mori et al., 2016). At least 57 individual crested porcupines and 46 badgers were camera trapped in our study site, i.e. at den entrances (cf. Balestrieri et al., 2016). Population densities cannot be reliably estimated, as both porcupines and badgers use also dense scrublands for denning, in our study area (Pigozzi, 1986; Mori et al., 2015; Lovari et al., 2017), which have not been surveyed because of their scarce accessibility.

Our survey included 3797 trap nights; each camera trap site was kept active for 28-52 nights/year, 24 hours/day, to take 3 pictures/event. Shortest monitoring times at den setts (i.e. 28, 32 and 34 nights/year) were due to camera-trap failures (because of dead batteries) and thefts. Camera traps were checked at least once every two weeks, to download photos and change batteries. Den setts were separated one-another by 800-1300 m and were considered as spatially independent one-another as each one hosted a familiar, reproductive nucleus of both the semifossorial mammals in at least one period of the year (Kruuk, 1989; Buesching et al., 2003; Mori et al., 2016).

In the study area, vegetation control (i.e. wood-cutting and removal of riparian plants along riverbanks) has been recorded and mapped once every three months. We recorded that it occurred several times during the study period, but always in early spring, in patches of up to 100 hectares.

Statistical analysis

To test the annual probability of den sett occupancy by porcupine after vegetation disturbance (i.e. wood-cutting or removal of riparian plants along riverbanks), we built a generalized linear mixed effect model (GLMM) with a binomial error distribution and a logit-link function. We considered each year as a sampling unit for each den sett and we assessed whether the den sett was occupied (1) or not occupied (0) by the crested porcupine. As explanatory variables, we used the year after the ceasing of vegetation disturbance and whether the den sett was occupied by the European badger in the same year. We controlled den sett occupancy from one to six years after vegetation disturbance; the latter case was available for only two den setts and, thus, we excluded it from the analyses. We used the den sett identity as a random intercept factor to account for the expected non-independence of occupancy pattern in different year in a determined den sett. We also conducted a specular analysis using the badger den sett occupancy as response variable (and the porcupine den sett occupancy in the same year as predictor).

Additionally, for both species, we tested whether the proportion of years of sett occupancy over the total years (starting to count from the year after the ceasing of the first vegetation disturbance) were affected by the number of years in which a vegetation disturbance event occurred. To do that, we used GLMs with binomial error distribution and a logit-link function. All the analyses were performed with R version 3.4.1 (R Core Team, 2017). GLM were run with the default *stats* package, whereas GLMMs were run with *glmmADMB* package (Skaug et al., 2015). Due to the low number of predictors tested in each model, we assessed the variables importance by hypothesis testing. The covariate significance was assessed by means of likelihood ratio chi square tests (for GLMs) or Wald's chi square tests (for GLMMs), performed with the R package *car* (Fox and Weisberg, 2011), because for nonnormal GLM(M)s, these tests are considered to be more reliable than the default statistics (Venables and Ripley, 2002; Assandri et al., 2017).

Predation pressure may influence the spatio-temporal distribution of prey species (e.g. Thaker et al., 2011; Prugh and Golden, 2014). However, local predation on porcupine is a very rare occurrence (i.e. by red foxes and grey wolves: Mori et al., 2014b). As well, badgers have been only occasionally detected in the local diet of the grey wolf, which may also take profit by road-killed badger/porcupine carcasses, thus not directly preying on them (Battocchio et al., 2017). Therefore, we excluded predation risk from predictors in our models.

Results

The crested porcupine was strongly and negatively affected by vegetation disturbance events. After those events, den setts regularly occupied for one or more years were regularly abandoned and then deserted (Fig. 2). As to the European badger, not all the monitored den setts were occupied before disturbance events, but a similar pattern of abandonment occurred. However, badgers may benefit from the (disturbed) porcupine deserted dens, recolonising them earlier than porcupines.

The porcupine probability of sett occupancy was significantly affected by the years after the ceasing of vegetation disturbance (χ^2 = 13.55, df= 4, p=0.008, n=63), but not by the badger sett occupancy (χ^2 =0.02, df=1, p=0.85, n=63). Less than 30% of the formerly occupied den setts were occupied again from the first year up to three after the ceasing of vegetation disturbance. From the fourth year, and more markedly during the fifth year, the probability of den sett occupancy increased up to a level of almost 70% (Fig. 3).

The badger probability of sett occupancy was significantly affected by the year after the ceasing of vegetation disturbance (χ^2 = 12.04, df= 4, p=0.01, n=53), and negatively (β = -4.69 ± 2.51), although marginally not-significantly, by the porcupine presence at sett (χ^2 =3.48, df=1, p=0.06, n=53). The badger, after a first year of very low occupancy probability (10%), rapidly occupied formerly abandoned den sett (about 50% in the third year) up to a maximum of about 80% of occupancy in the fifth year.

Considering the proportion of years of sett occupancy over the total years (after the first vegetation disturbance event), the crested porcupine was not significantly affected by the number of years in which a vegetation disturbance event occurred (β = -0.24 ± 0.27; LR χ^2 = 0.76; df = 1; p=0.38). Conversely, this variable significantly (and negatively) affected the European badger (β = -0.82 ± 0.33; LR χ^2 = 7.52; df = 1; p=0.006).

Discussion

Our results showed that both the European badger and the crested porcupine are sensitive to vegetation disturbance. However, we highlighted some interspecific behavioural differences. According to our predictions, the crested porcupine showed a higher sensitivity with respect to the badger, as it abandoned dens immediately after the disturbance and employed a higher amount of time for recolonisation. We are aware of the caveats related to our small sample size (i.e. 16 den setts); however, with a much greater number of experimental setts, a constant camera-trap monitoring, as the one we have used in our study but throughout a wider area, would have been particularly challenging. Furthermore, a reliable estimation of population density of crested porcupines and European badger would have only been possible through a capture-mark-recapture program (Pigozzi, 1988; Rogers et al., 1997; Sforzi et al., 1999; Tuyttens et al., 2001), but we are rather confident that most of locally available den setts have been monitored. However, some dens may have been located within dense scrubland, thus not detected (cf. Balestrieri et al., 2016; Lovari et al., 2017).

Despite crop damage by porcupine is very low in central Italy (Laurenzi et al., 2016), persecution and poaching against this species is still occurring because of popular beliefs, damage to small vegetable gardens and because it is considered as a food delicacy (Amori and Angelici, 1992; Cerri et al., 2017; Lovari et al., 2017). Poaching against badger seems to be a rare occurrence in central Italy. Illegal killings of badgers mostly occurred for pelts and fat (as folk medicine) before the 1970s (Kowalczyk et al., 2000). Sometimes, humans still kill badgers as a bycatch in hunting drifts to wild ungulates with hounds (Revilla et al., 2001b). Furthermore, in their native range (sub-Saharian Africa), crested porcupines are preyed upon by large carnivores (Mori et al., 2014b), which have brought this rodent to be evolved by thriving in concealed habitats (cf. Fattorini and Pokheral, 2012; Mori et al., 2014a). Conversely, badgers coexist with a number of small carnivores, but it has been reported to be the upper competitor (Macdonald et al. 2004; Trewby et al., 2007; Kowalczyk et al., 2008), as also being the largest in size (cf. Palomares and Caro, 1999; Donadio and Buskirk, 2006). Furthermore, it is only an occasional prey for the wolf (Gade-Jorgensen and Stagegaar, 2000; Battocchio et al., 2017). As a likely consequence of these factors, porcupine setts are for their vast majority located in dense scrubland and deciduous woodland (Monetti et al., 2005; Mori et al., 2014a), where their visibility is the lowest (Lovari et al., 2017). Conversely, although woodland and shrubs are also preferred by the badger (Tinelli and Tinelli 1980; Roper et al., 2001; Prigioni and Deflorian, 2005), this small carnivore might locate its dens also in agricultural areas or near human settlements (Neal and Roper, 1991; Balestrieri and Remonti, 2000; Remonti et al., 2006).

Our study points out that the European badger showed a higher speed in recolonising abandoned dens with respect to the crested porcupine. This behaviour may be due to the higher adaptability (according to vegetation cover) of badgers in den site selection (Neal and Roper, 1991; Monetti et al., 2005). Additionally, in our work, we observed that badgers occupied also dens previously used by porcupines, possibly favored by the “time lag” of porcupines in the occupancy rate and confirming the competitive supremacy of the large rodent (e.g. Mori et al., 2014b; Mori et al., 2015). Differently from the crested porcupine (Monetti et al., 2005), European badgers may stop the use of a den sett for short period, i.e. mostly outside the birth period, then coming back (e.g. Revilla et al., 2001a; Roper et al., 2001; Loureiro et al., 2007). However, we might exclude that this behaviour affected our interpretations, because of the strong temporal relationship occurring between vegetation removal and den abandonment.

Although crested porcupines and European badgers share communal den setts (Pigozzi, 1986; Mori et al., 2015), during the reproductive period crested porcupines increase the defence strategies inside and in the surroundings of the dens, attacking badgers and obliging them to search for other burrows, to the extreme consequence to kill them (Mori et al., 2014b; Mori et al., 2015).

In the last decades, damages to riverbanks and railway embankments due to European badger and crested porcupine digging behaviour resulted in high economic losses (e.g. Valdichiana Senese in the province of Siena, province of Modena: Orlandini et al., 2015; Mori, unpublished), due to flooding and landslides. Electric fences and individual removal are ineffective or show only a time-limited success (Massei et al., 2010; Laurenzi et al., 2016). Despite most damages to riverbanks are due to digging by coypus *Myocastor coypus* (Panzacchi et al., 2007), which burrows are sometimes used also by porcupine and badgers

(Sforzi et al., 1999; Mori et al., 2015), vegetation control (including mowing and wood cutting) has been proposed as a management strategy to reduce the presence of both badgers and porcupines (Sforzi et al., 1999). Our findings suggest that this management intervention, if not constantly repeated or maintained, is not successful as both species in five years almost completely recolonize formerly abandoned dens. Furthermore, vegetation disturbance may affect a number of other native species and may strongly threaten the environmental (e.g. riverbank) stability (Seymour and Simmons, 2008; Hubble et al., 2010). Thus, vegetation control should be considered only as an extreme management decision, when prevention, e.g. through fences partly buried, is not an effective strategy.

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Figures

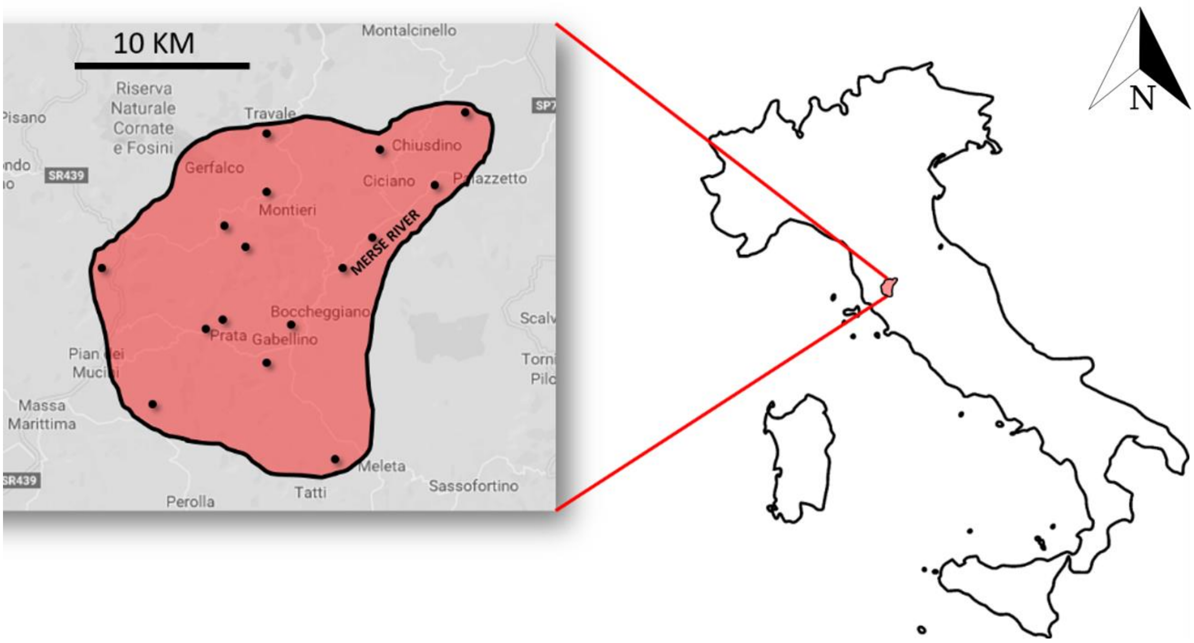

Figure 1. Location of the study area. Black dots show surveyed den setts.

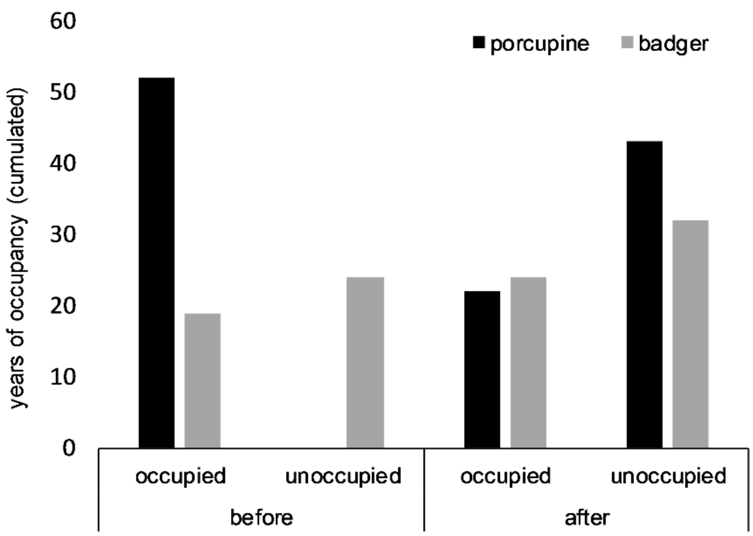

Figure 2. Years of den sett occupancy (cumulated for all den sett) by crested porcupines and European badger before and after vegetation disturbance events.

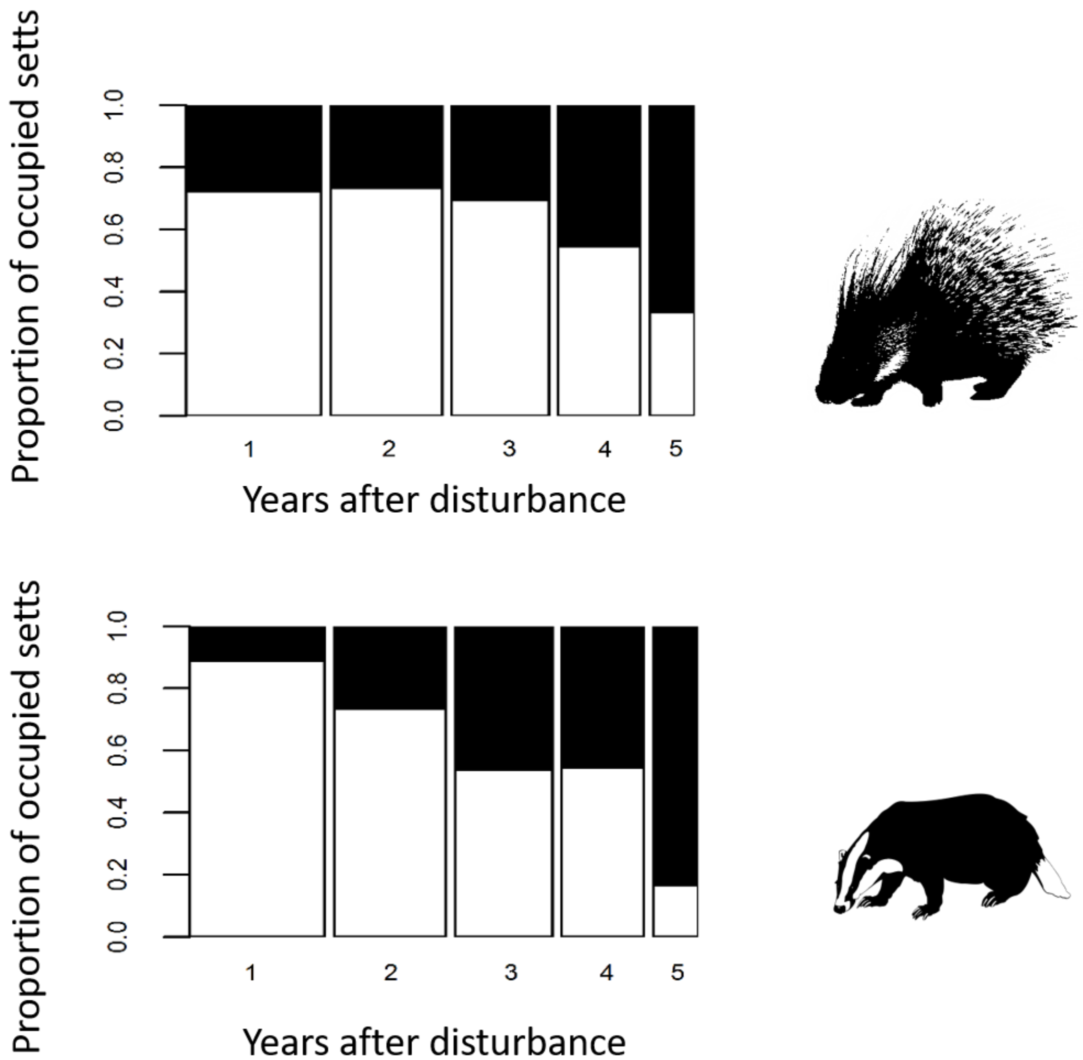

Figure 3. Proportion of dens occupied by crested porcupines (top) and European badgers (bottom), from one year to five years after the ceasing of vegetation disturbance. White = unoccupied; black = occupied. Bar width is proportional to sample size. $N_{porcupine}$= 63, N_{badger}=53.