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ORIGINAL ARTICLE

The value of by-catch data: how species-specific surveys can serve non-target species

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Abstract

Camera trapping has a wide range of research application, but, while research designs are often focused on the study of a single focal species, cameras can also record other non-target species. Occupancy modeling using by-catch data can be a valuable resource to gain information on these species maximizing the scientific effort and efficiency of wildlife surveys. In this study, we used by-catch data from a European wildcat (*Felis silvestris silvestris*) survey in Southern Italy to assess the habitat covariates determinant for the occupancy of the crested porcupine (*Hystrix cristata*). We recorded 33 detections at 17 out of 51 cameras (naïve occupancy = 0.33). The best models fitted the data well, and porcupine occupancy estimate was 0.58 (SE ± 0.09) with a detection probability of 0.11 (SE ± 0.03). Average model showed that woodlands and number of shrub patches increased porcupine occupancy, while the reverse was true for altitude. Our results have improved the insights on the habitat use and ecological needs of this understudied species, and it is the first study that develops occupancy models for the porcupine using the presence/absence data obtained from a camera trap survey. Our study is an example of how camera trap surveys are often an under-exploited source of valuable information on a wider spectrum of sympatric species beyond the focal species for which camera traps were deployed. Minimum requirements for a camera trap survey to provide robust occupancy estimates for non-target species are discussed.

Keywords Camera trapping · Crested porcupine · Habitat use · Mt. Etna · Occupancy

Introduction

Scientific sound data on species presence, abundance, distribution, and habitat use is the basis for effective conservation and management actions. To gain this data in the last years, camera trapping has almost exponentially increased its use (Rovero and Zimmermann 2016) in the study of large to small mammals (e.g., O'Brien 2008; Glen et al. 2013), birds (e.g., Dinata et al. 2008), and reptiles (e.g., Welbourne et al. 2015). Camera trapping has a wide range of research application, and the majority of the studies involving camera traps aims to assess species detection and inventories, species occupancy, and density estimation (O'Connell et al. 2010; Rovero et al. 2013). Nevertheless, while research designs are often focused on the study of a single focal species (or a set of similar species), cameras can record also other non-target species generating the so-called "by-catch data" (Pamplin 2013; Burton et al. 2015; Anile and Devillard 2016). Edwards et al. (2018) demonstrated how it is possible to obtain important ecological information using data coming from camera traps deployed for another focal species. The use of by-catch data does not only maximize the scientific outcome, but can also increase the return on investment of the surveys (Pamplin 2013).

By-catch in the form of the presence/absence data can be analyzed through occupancy modeling (O'Connell et al. 2010; MacKenzie et al. 2017), a robust statistical framework for testing numerous hypotheses (e.g., Rovero et al. 2014;

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Ferreguetti et al. 2018). Occupancy is defined as the proportion of area, patches, or sample units (i.e., camera trap sites) occupied by a species, estimated whilst accounting for imperfect detection (MacKenzie et al. 2017).

In this study, we used data collected from a camera trap survey focused on the European wildcat (*Felis silvestris*) on Mt. Etna (Sicily, Italy), the highest active volcano in Europe and a recently declared UNESCO site. The wildcat survey had the goal to identify ecological drivers and human-induced determinants to estimate wildcat detection and occupancy (Anile et al. 2019), but we used by-catch data to identify the ecological features of detection and occupancy of the biggest Italian rodent, the crested porcupine (*Hystrix cristata*). The porcupine is mainly an elusive nocturnal animal whose direct observations are rare; hence, the use of camera traps is particularly suited to study its ecology. Its diet consists in underground plant storage organs and roots, as well as plant epigeal parts and fruits according to their seasonal availability (Bruno and Riccardi 1995; Mori et al. 2017). The porcupine has very few natural predators in Italy, since its remains have been found just in the feces of red foxes *Vulpes vulpes* (Lucherini et al. 1995) and, rarely, of wolves *Canis lupus* (Scandura et al. unpublished data). However, human-related activities as hunting with dogs and the presence of feral pigs can affect the porcupine activity (Mori et al. 2014b; Mori 2017). In Europe, the species is only present in Italy throughout the peninsula, in Sicily, and recently introduced in Sardinia, but historical and archeological evidence point out to an initial introduction of the crested porcupine in Italy in the Late Antique/early medieval period, or even in the early modern times in Sicily (Masseti et al. 2010). The crested porcupine is protected under the Berne Convention (Annex II) and the Habitat Directive (Annex IV) in Europe, and among the protected species within the National Law 157/1992 in Italy. Despite this legal protection, the species is still widely poached because of its meat and the supposed damage caused to the crops (Laurenzi et al. 2016; Mori et al. 2017; but see Lovari et al. 2017). The crested porcupine space and habitat use have been investigated in low elevation Mediterranean habitat and suburban areas in central Italy characterized by agricultural and woodland patches (Lovari et al. 2013, 2017; Mori et al. 2014a), but less is known about its habitat preferences and behavior in high altitude natural environments. Moreover, to the best of our knowledge, no scientific studies have explored the habitat use of this species in Sicily, the largest Italian region. In this study, we aim to demonstrate the possibility of using by-catch data to obtain reliable scientific information on other sympatric species. We will identify which factors influence the spatial distribution of the crested porcupine and assess the suitability of the habitat in the Etna Regional Park. The crested porcupine may play an important role in the preservation of the peculiar ecosystem on the volcano since it is the biggest seed disperser with dwelling habits (Bruno and Riccardi 1995; Monetti et al. 2005; Mori et al. 2017). Therefore, identifying the crested porcupine habitat preferences could lead to actions aimed at the preservation of the species in the Park. Based on what is known on the ecology of the crested porcupine in Mediterranean habitats, we predict that (1) woodlands and shrublands will promote the species occupancy because of food availability and suitable areas for denning; (2) habitat richness will positively affect the occupancy, while (3) the altitude negatively. Moreover, we expect that (4) the presence of feral pigs will negatively affect the crested porcupine detectability and/or occupancy. Finally, we will develop a porcupine occupancy model for the entire Etna Regional Park to elucidate the crested porcupine potential distribution.

Materials and methods

Study area

The Etna Regional Park (~ 590 km^2) covers the slopes of the biggest active European volcano, Mt. Etna. With an altitude range from 550 up to ~ 3360 m a.s.l, the Park is divided into four main management units (zones A, B, C, and D) according to different levels of protection. Our cameras were deployed within zone A and B; the "Integral reserve"—zone A—is subject to more constraints in order to ensure maximum protection of plants and animal species, and vehicle access is subject to permission and restricted to unpaved roads used for forest management, sheep farming, and tourism. The "General reserve"—zone B—is where educational activities and regular excursions are permitted. The most remote areas (zone A) of Mt. Etna have been declared a world heritage site by UNESCO in 2013.

The landscape is characterized by recent large lava flows and inactive secondary cones of different ages, intermixed with areas dominated by trees (Corsican pine *Pinus laricio*, different species of oak *Quercus pubescens*, *Quercus ilex*, chestnut *Castanea sativa*, aspen *Populus tremulus*, European beech *Fagus sylvatica*, and Mt. Etna broom *Genista aetnensis*). Forest cover usually lies between 1000 and 2000 m a.s.l., and areas at higher altitude are characterized by low shrub vegetation. The most widespread habitat within the forest cover range consists of large woodland patches intermingled with relatively small open fields, sometimes surrounded or interrupted by lava flows of variable extensions (Fig. 1).

The climate is typically Mediterranean at the lower altitudes with warm springs and hot dry summers. Rainfall is concentrated during autumn and winter with a yearly mean of 1000–1400 mm. Snow cover is common in winter and usually abundant at higher altitudes.

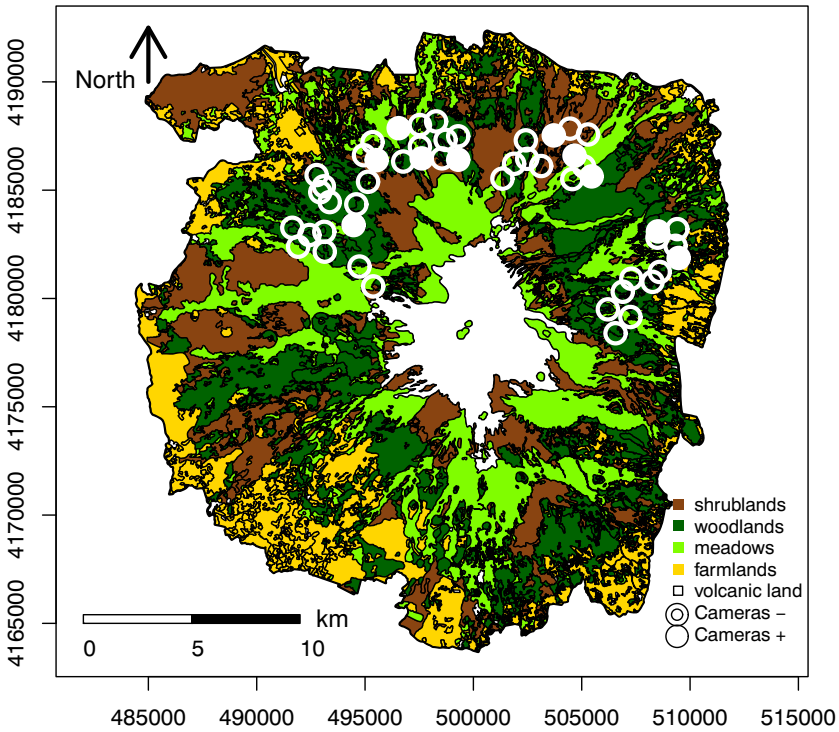

Fig. 1 Distribution of the habitat classes tested on Mt. Etna (Sicily, Italy). Camera traps are shown in the picture as positive if they ever detected the crested porcupine (solid white circle) and negative if they never detected it (white empty circle)

Camera trap survey

Cameras were initially set up to study the European wildcat in the area. We deployed camera traps along 4 arrays on the north side of the Park: one array of 15 cameras and one of 12 active between September and December 2015 and two arrays of 12 cameras active between April and June 2016. Within each array, cameras were randomly placed along unpaved road and trails, resulting in a spacing of 731 ± 200 m (mean ± SD; range 300–1114) between adjacent cameras, and at a mean elevation of 1328 ± 163 m a.s.l. (mean ± SD; range = 1108–1750). We used 15 digital cameras DFV® equipped with Sony®DSC-W55 (built-in flash Auto ISO: *W* 0.2–3.9 m; *T* 0.3–2.0 m) (Fototrappolaggio S.r.l., Forlì, Italy). Each camera was accommodated in an iron box, locked with a padlock, and tied to a tree with a chain at 50 ± 10 cm from the ground. Cameras had a 0.4 s trigger speed and we set them with a delay time of 10 min between successive bursts ($n = 3$) of photos. No lure or bait was used. Cameras were checked twice per week for camera functioning, batteries, and data download.

Covariates

Spatial analysis of habitat covariates was performed using the software QGIS v 3.4.5 (QGIS Development Team 2019) and its plug-ins. We expected the detection probability (p) to be influenced by the covariates reported in Table 1. The covariate *season* was classified as "cold" for September–December and "warm" for April–June (Mori et al. 2014a) as we expected that the porcupine activity may vary between the above periods. The covariate *feral_pig* refers to the number of pig detections per camera, and we did not calculate the RAI (Relative Abundance Index; O'Connell et al. 2010) for this metric as the mean number of functional days per camera was fairly constant (38.9 ± SD 5.2; range = 20–44). Ecological covariates to model the porcupine occupancy (ψ) (Table 1) were created from the land map "Nature map of the Sicilian region" at the scale of 1:50,000 created in 2008 with a resolution of 1 ha. Map accuracy was screened through extensive field-ground verifications. For each camera, we created a circular buffer of 793-m radius (197.99 ha) corresponding to the mean home range size of the porcupine in a Mediterranean habitat (Lovari et al. 2013; Mori et al. 2014a). The map included 41 different layers which we then merged into main habitat classes (Online Resource 1): woodlands, shrublands, and meadows (91% of the area of all camera buffers). The selection of these classes was made in accordance with the porcupine ecology (Lovari et al. 2013, 2017; Mori et al. 2014a); other habitat classes (e.g., farmland and anthropized areas) were not considered because they were not relevant for the species or not present/under-represented in the buffers' area. For each camera buffer, we extracted the following variables: (1) the area of each habitat class; (2) the number of the habitat classes as a proxy of habitat structure complexity; (3) the total number of patches per habitat as a proxy of fragmentation for a given habitat class; and (4) the number of all patches as a proxy of overall habitat fragmentation (Table 1). To avoid

Table 1 Covariates used to model the detection (p) and occupancy (ψ) of the crested porcupine on Mt. Etna (Sicily, Italy)

Model component	Covariate	Description
Detection (p)	*days*	Camera trap working days
	array	Categorical factor indicating camera trap array (1–4)
	season	Categorical factor (cold-warm)
	feral_pig	Number of detections of feral pigs per camera trap
Occupancy (ψ)	*woods* *shrubs*	Area per habitat class
	meadows	
	Nhabitat	Number of habitat classes
	Np_woods *Np_shrubs*	Number of patches per habitat class
	Np_meadows	
	Np_tot	Number patches of all habitat classes
	elevation	Altitude of each camera
	feral_pig	Number of detections of feral pigs per camera trap

multicollinearity, Pearson's correlation coefficient was used to test for non-independence between covariate pairs. Covariate pairs with ($r > |0.70|$) were considered highly correlated, hence only one covariate of the pair was included within our occupancy models. Before estimating the model coefficients, covariates were standardized to have mean 0 and unit variance by subtracting the covariate mean from each site value and then dividing the difference by the covariate standard deviation.

Occupancy modeling

Data were arranged in a detection matrix where each entry indicated if the porcupine was detected (score = 1) or not (score = 0) at the site during that occasion, in addition with an occasion matrix reporting if the camera was active (score = 1) or missing data because of malfunction (score = 0) (R package *camtrapR,* Niedballa et al. 2016). The detection matrix had a resolution of 8 days to minimize the risk of non-independent detections at each site. Although our survey was split into two non-consecutive periods, we used a single-season occupancy model, as adult porcupines are mostly territorial with minimal home range overlap; therefore, shifts in individual territories between seasons can be considered minimal (Mori et al. 2014a), and hence changes in occupancy between these two periods were assumed negligible. Based on the above considerations, we then run a single-species single-season occupancy analysis using the R package *unmarked* (Fiske and Chandler 2011).

A two-step approach was used to identify the most parsimonious occupancy models ($\Delta AIC < 2$) (MacKenzie et al. 2017). We first tested the effects of the covariates on the detection probability (p), whilst keeping the occupancy process (ψ) constant and over parameterized (all relevant habitat classes included as occupancy predictors, e.g., Strampelli et al. 2018). Covariates were tested both individually and in combination with the null model ($p(.)$), for a total of other 11 possible combinations investigated based on plausible ecological hypotheses (Table 2). In the second step, the best models for the detection probability were combined with a total of 28 occupancy models (Online Resource 2) which reflected a priori plausible ecological hypotheses about the porcupine occupancy in the study area. Potentially, occupancy processes were limited to a maximum of 3 additive terms. All models with convergence issues were discarded. We used the Akaike Information Criterion (AIC) to rank candidate models and calculate their Akaike weights (Burnham and Anderson 2004). Goodness of fit for the best models was checked with the function *mb.gof.test* (500 replicates) within the R package *AICcmodavg* (Mazerolle 2016) to test for overdispersion. The relative importance of covariates ($\mathcal{E}AICw$) was calculated for each covariate included in those models within the cumulative AIC weight of 0.95.

Finally, we mapped occupancy probability across Mt. Etna by deriving occupancy estimates from covariates computed on a spatial grid (n cells = 420) with a cell size of 1407 m (1.98 km^2) in accordance with the mean home range for a porcupine in a Mediterranean habitat (Lovari et al. 2013; Mori et al. 2014a). Elevation data was downloaded as GMTED (<https://earthexplorer.usgs.gov>), and the mean elevation value for each grid cell was extracted.

Results

The 51 camera traps set accumulated 1984 camera trap days with 58 events of porcupine recorded. One camera recorded 28 events of porcupine, so to remove the effect of this outlier, we kept only 5 events (maximum number of porcupine detections among the remaining cameras) from this camera, hence reducing the events

Table 2 Crested porcupine detection (p) models. Occupancy (ψ) is kept constant and overparametrized. Models with ΔAIC < 2 in italics

	nPars	AIC	ΔAIC	AICwt	cumltvWt	Rsq
Ψ (woods, meadows); p (feral_pig)	*5*	*169.76*	*0.00*	*0.3778*	*0.38*	*0.0695*
Ψ (woods, meadows); p (.)	*4*	*171.28*	*1.52*	*0.1768*	*0.55*	*0.0000*
Ψ (woods, meadows); p (feral_pig, season)	*6*	*171.69*	*1.93*	*0.1438*	*0.70*	*0.0708*
Ψ (woods, meadows); p (days)	5	172.18	2.42	0.1127	0.81	0.0223
Ψ (woods, meadows); p (season)	5	172.98	3.22	0.0754	0.89	0.0060
Ψ (woods, meadows); p (days, season)	6	173.59	3.83	0.0557	0.94	0.0340
Ψ (woods, meadows); p (feral_pig, array)	8	175.52	5.76	0.0212	0.96	0.0741
Ψ (woods, meadows); p (array)	7	176.96	7.20	0.0103	0.97	0.0065
Ψ (woods, meadows); p (feral_pig, season, array)	9	177.45	7.69	0.0081	0.98	0.0755
Ψ (woods, meadows); p (days, array)	8	177.65	7.89	0.0073	0.99	0.0328
Ψ (woods, meadows); p (days, array, season)	9	177.83	8.07	0.0067	1.00	0.0682
Ψ (woods, meadows); p (array, season)	8	178.75	8.99	0.0042	1.00	0.0107

to 33 independent porcupine detections from 17 camera traps (naïve occupancy = 0.33). Collinearity was detected for the following pair of covariates: *shrubs* and *Np_shrubs* ($r = 0.7$), *shrubs* and *woods* ($r = -0.8$), and *Np_woods* and *Np_tot* ($r = 0.9$) which therefore were independently included in our models. The detection process selection resulted in 3 top-ranking models (Table 2) which were then combined with the 28 a priori occupancy models, for a total of 84 models tested. Seventy-five models were discarded due to lack of convergence, and weighted model-averaging was used on the two top-ranking models (Table 3) to derive parameter estimates: porcupine occupancy estimate and detection probability were 0.58 (SE ± 0.09) and 0.11 (SE ± 0.03), respectively. Detectability was negatively affected, even if not significantly ($p > 0.05$), only by one covariate, *feral_pig*; hence, detectability decreased in sites with higher number of feral pig detections (Table 4; Fig. 2). We recorded feral pigs on 26 sites all part of the two camera arrays active September–December 2015; those cameras collected on average 17.54 ± SD 26.50 feral pig photos with 1.51 ± SD 1.19 individuals per photo.

The two top-ranking models did not show overdispersion (first model Table 3: $\chi^2 = 92.35$, $p = 0.38$, $\hat{c} = 0.98$; second model Table 3: $\chi^2 = 95.13$, $p = 0.31$, $\hat{c} = 0.97$). Occupancy was affected by three covariates: (1) the area of woodlands (*woods*), which had a positive effect, in which porcupine occupancy significantly increased in larger wooded areas; (2) number of patches of shrublands (*Np_shrubs*), which had a positive relationship (tough p was slightly above the 0.05 significance level) in which occupancy increased with a higher number of patches of shrub vegetation; and (3) altitude (*elevation*) which predicted a negative relationship with occupancy ($p > 0.05$) (Table 4; Fig. 2).

Spatially explicit predictions of porcupine occupancy for Mt. Etna (Fig. 3) showed that the distribution of cells with high predicted porcupine occupancy was widespread along the slopes of the volcano, with the majority of suitable cells located on the northern slope.

Discussion

In this study, we demonstrated the possibility of using data collected during a target species survey to obtain reliable scientific information on other sympatric species. In particular, even though the survey which generated our by-catch data was designed for the European wildcat, we were also able to study the occupancy and the detection probability of the crested porcupine, a different species in terms of ecological needs. However, this study was possible thanks to some survey characteristics suitable for both species. The wildcat and the porcupine have similar size, and both move along trails (Mori 2017; Anile et al. 2019); hence, camera trap displacement was appropriate to study both species and cameras were equally triggered. Moreover, the site spacing suited both the wildcat and the porcupine since the minimum home range for a

Table 3 Crested porcupine occupancy (ψ) models. Models with ΔAIC < 2 in italics

Model	nPars	AIC	ΔAIC	AICwt	cumltvWt	Rsq
Ψ (woods, Np_shrubs,elevation); p (feral_pig)	*6*	*162.04*	*0.00*	*0.513*	*0.51*	*0.25*
Ψ (woods, Np_shrubs); p (feral_pig)	*5*	*163.67*	*1.63*	*0.227*	*0.74*	*0.19*
Ψ (woods, Np_shrubs,elevation); p (.)	5	165.02	2.98	0.116	0.86	0.17
Ψ (woods, Np_shrubs); p (.)	4	165.83	3.79	0.077	0.93	0.12
Ψ (woods, Np_shrubs; Nhabitat); p (.)	5	166.92	4.88	0.045	0.98	0.14

Table 4 Results of the averaged best model describing the occupancy of the crested porcupine on Mt. Etna (Sicily, Italy)

Covariate	β	SE	z	p
Occupancy Ψ				
Intercept	15.499	11.606	1.335	0.1817
woods	26.729	13.443	1.988	0.0468
NP_shrubs	30.476	15.678	1.944	0.0519
elevation	− 14.871	0.9319	1.596	0.1105
Detectability p				
Intercept	− 20.518	0.3276	6.262	$< 2e^{-16}$
feral_pig	− 12.234	0.8164	1.498	0.1340

wildcat in a Mediterranean habitat (Monterroso et al. 2009; Anile et al. 2018) is about the size of the average porcupine home range (Lovari et al. 2013; Mori et al. 2014a). Finally, both species are associated to areas characterized by vegetation cover (Lovari et al. 2017; Anile et al. 2019). Future surveys that would have the porcupine as target species should survey woodlands and shrublands important for food sources and denning sites, respectively. Farmlands, even if not present in our surveyed area, should also be considered especially in the summer time (Mori et al. 2014a). Lastly, in the case of the presence of predators (e.g., red fox) and/or competing species (e.g., feral or wild Suidae), their occurrence should be considered in the analyses. In particular, the soil overturned by feral/wild Suidae nearby the camera site should be measured as a good proxy for indirect effect of Suidae on the porcupine.

The best models fitted the data well (as shown by the value of the test for the goodness of fit); this underlines the suitability of occupancy modeling as a tool to analyze bycatch data generated by camera-trapping surveys. Most of the covariates tested for the detection probability were not retained in the final model. Since the categorical factor indicating the camera trap array did not affect the detection, all the areas had similar probabilities to detect the porcupine indicating the adequacy of selected sites. We expected a reduced detection probability in the cold months because during the winter in Central Italy, the activity and the home range size of porcupines decrease (Corsini et al. 1995; Mori et al. 2014a; Mori 2017). Although the factor season was quite balanced among our cameras, it had no effect on the detection process. During our survey, the absence of snow on Mt. Etna may have not affected and reduced the activity of the porcupine.

As expected, the occupancy of the porcupine was significantly promoted by the presence of forested areas and by patches of shrubs. Space use and habitat selection of the porcupine are mostly affected by two limiting factors: food resources and den sites. Woodlands are the most suitable habitat for the exploitation of underground plant storage organs and roots, as well as plant epigeal parts and fruits according to their seasonal availability (Bruno and Riccardi 1995; Mori et al. 2017). The positive selection of woodlands has been recorded in Central Italy (Mori et al. 2014a; Lovari et al. 2017) and now also confirmed in Sicily. Moreover, during the daylight, this species rests in a den made of a network of chambers and tunnels with one or several entries (Monetti et al. 2005). The porcupines select steep compact soils covered in dense vegetation such as bramble thicket to dig its den, and it could explain why the occupancy was positively related to areas with a higher number of shrub patches (Monetti et al. 2005; Lovari et al. 2017).

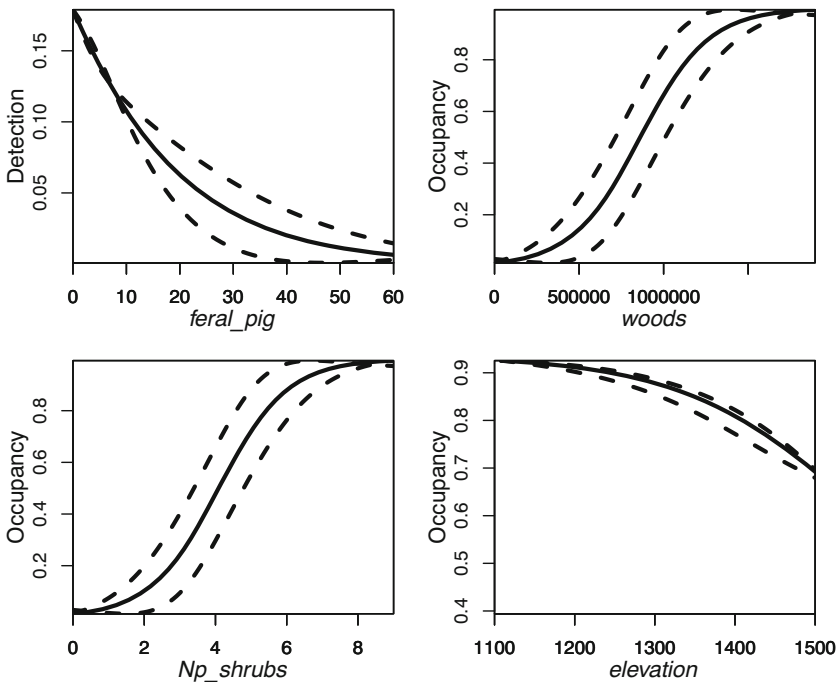

Fig. 2 Predictions from the best model Ψ (woods, Np_shrubs,elevation); p (feral_pig) describing the occupancy of the crested porcupine on Mt. Etna (Sicily, Italy). For definition of model covariates, see Table 1

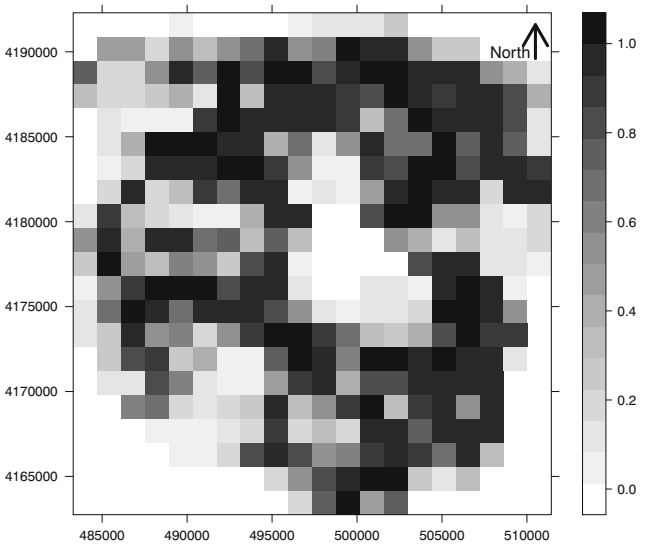

Fig. 3 Spatially explicit predictions from the best model Ψ (woods, Np_shrubs,elevation); p (feral_pig) describing the occupancy of the crested porcupine on Mt. Etna (Sicily, Italy)

Meadows did not explain the presence of the porcupine on Mt. Etna confirming a preference for covered areas (as the woods), as reported by Sonnino (1998). Our second hypothesis based on the habitat richness promoting the porcupine occupancy was not confirmed. Lovari et al. (2013) reported an inverse effect of the habitat richness on the home range size of the porcupine, with smaller home ranges when the number of habitat types per hectare was higher. We tested this covariate (number of habitat classes per camera buffer), but it was not retained in the average model (and neither in the best models). This difference we recorded might be explained, as in this study, we used macro-habitat classes to depict plant habit (e.g., woodland, shrubland, meadow) rather than the plant association (phytosociology sensu *strictu*). Therefore, we suggest that future studies should also consider a more detailed vegetation description to provide a deeper view of the plant association (and hence habitat richness) selected by the porcupine. The negative effect of altitude on the porcupine occupancy was confirmed by our by-catch data. Despite that we recorded the presence of the porcupine up to 1750 m a.s.l., its occupancy leveled at about 1500 m a.s.l., as also found by a previous study (Mori et al. 2013). Snow cover can represent an obstacle for locomotion, research, and exploitation of underground food resources as well as for the digging of the den (Mori 2017; Mori et al. 2018). This could explain the negative relationship between occupancy and altitude with a gradual reduction of the occupancy above 1200 m a.s.l. Mori et al. (2018) predicted that the ongoing global warming may help the porcupine in colonizing higher altitudes thanks to a reduction of the duration of snow and ice cover at the ground level and the shift of the forest distribution to high elevations. However, global warming can also result in more robust snowfall (Trenberth 2011; Kunkel et al. 2012), and hence, this hypothesized positive effect of global warming might be counterbalanced by periods of robust snowfall, which can increase the porcupine's mortality. More long-term studies are needed to further elucidate the role of global warming on the ecology of the porcupine, as unpredictable events (usually manifested with larger magnitude) can lead to contrasting effects.

Porcupine detection was negatively associated with feral pigs, but not the occupancy. The porcupine could be indirectly disadvantaged by the feeding habits, primarily rooting disturbance, of the feral pigs. In fact, Suidae overturn large patches of soil looking for plant underground storage organs (Barrios-Garcia and Ballari 2012; Gaskamp et al. 2018), and it could lead to a food resources or space competition (Mori et al. 2014b; Melletti and Meijaard 2017; Nie et al. 2019) in which the porcupine would avoid the areas with the presence of pigs. Contrary to our hypothesis, Mori (2017) hypothesized a possible positive/attractive effect of the rooting activity on the porcupine, because the turnover of the soil could enhance the access to food, especially when the ground is covered in snow. However, our results showed that the occupancy was not affected by the feral pig. On the contrary, the probability to detect the porcupine decreased with the increasing of feral pig detections, sign of an avoidance by porcupines of areas with high activity of pigs.

The map generated by our by-catch data showed a potential distribution of the porcupine on all slopes of the volcano, even if ample and well-connected areas of highly predicted occupancy occur more on the northern slope than on the southern one. In fact, the Southern slope of Mt. Etna is characterized by wider areas of farmlands and meadows at lower elevations, while the northern slope by well connected patches of forest and shrubs.

Conclusions

Our study is an example of how camera trap surveys are often an under-exploited source of valuable information on a wider spectrum of sympatric species beyond the focal species (if any) for which the camera-trapping was conducted. Researchers have deeply investigated the use of camera trapping in ecology (O'Connell et al. 2010; Rovero et al. 2013; Rovero and Zimmermann 2016), but future studies that wanted to make the most out of by-catch data should consider some sensitive factors while planning on the study design. Hofmeester et al. (2019) identified four main factors that can highly influence species detection at different spatial scales: animal characteristics (body mass, diet type, movement), camera trap specifications and set up, and environmental characteristics. Since the use of by-catch data implies a change in the specific research question compared to the one for which the cameras were initially deployed, corrections can be done using the appropriate covariates in a statistical framework (Hofmeester et al. 2019).

To our best knowledge, this is the first study that develops occupancy models for the porcupine using the presence/absence data obtained from a camera trap survey. Our results have improved the insights on this understudied species, and it is the first study reporting ecological information and needs of the porcupine on Mt. Etna and Sicily in general. Mt. Etna represents a good refuge for this species from the highly populated areas surrounding the volcano, and its unique environment should be kept highly protected to ensure the preservation of the porcupine, as well as of the wildcat. Since the woodlands represent the main habitat for the porcupine, logging should be avoided during its reproductive period to minimize the impact on the species and forest clearing should preserve patches of shrub to protect den sites. As the porcupine is the largest dwelling herbivore on Mt. Etna, its role into the ecosystem as seed disperser might be critical for the maintenance and persistence of the peculiar ecosystem found on the highest active volcano in Europe.

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References

Anile S, Bizzarri L, Lacrimini M, Sforzi A, Ragni B, Devillard S (2018) Home-range size of the European wildcat (Felis silvestris silvestris): a report from two areas in Central Italy. Mammalia 82:1–11. https://doi.org/10.1515/mammalia-2016-0045

Anile S, Devillard S (2016) Study design and body mass influence RAIs from camera trap studies: evidence from the Felidae. Anim Conserv 19:35–45

Anile S, Devillard S, Ragni B et al (2019) Habitat fragmentation and anthropogenic factors affect wildcat (Felis silvestris silvestris) occupancy and detectability on Mt. Etna Wildl Biol online first. https://doi.org/10.2981/wlb.00561

Barrios-Garcia MN, Ballari SA (2012) Impact of wild boar (Sus scrofa) in its introduced and native range: a review. Biol Invasions 14:2283–2300. https://doi.org/10.1007/s10530-012-0229-6

Bruno E, Riccardi C (1995) The diet of the crested porcupine Hystrix cristata L., 1758 in a Mediterranean rural area. Z Für Säugetierkd 60:226–236

Burnham KP, Anderson DR (2004) Multimodel Inference. Understanding AIC and BIC in Model Selection Sociol Methods Res 33:261–304. https://doi.org/10.1177/0049124104268644

Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Bayne E, Boutin S (2015) REVIEW: wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. J Appl Ecol 52:675–685. https://doi.org/10.1111/1365-2664.12432

Corsini MT, Lovari S, Sonnino S (1995) Temporal activity patterns of crested porcupines Hystrix cristata. J Zool 236:43–54. https://doi.org/10.1111/j.1469-7998.1995.tb01783.x

Dinata Y, Nugroho A, Haidir IA, Linkie M (2008) Camera trapping rare and threatened avifauna in west-Central Sumatra. Bird Conserv Int 18:30–37. https://doi.org/10.1017/S0959270908000051

Edwards S, Cooper S, Uiseb K, Hayward M, Wachter B, Melzheimer J (2018) Making the most of by-catch data: assessing the feasibility of utilising non-target camera trap data for occupancy modelling of a large felid. Afr J Ecol 56:885–894. https://doi.org/10.1111/aje.12511

Ferreguetti AC, Tomas WM, Bergallo HG (2018) Patch occupancy and activity pattern of the spotted paca (Cuniculus paca Linnaeus, 1766) in a protected area of the Atlantic Forest, Brazil. Mammalia 0:363–371. https://doi.org/10.1515/mammalia-2017-0095

Fiske I, Chandler R (2011) **Unmarked** : an *R* package for fitting hierarchical models of wildlife occurrence and abundance. J Stat Softw 43. https://doi.org/10.18637/jss.v043.i10

Gaskamp JA, Gee KL, Campbell TA, Silvy NJ, Webb SL (2018) Damage caused to rangelands by wild pig rooting activity is mitigated with intensive trapping. Cogent Environ Sci 4:1540080. https://doi.org/10.1080/23311843.2018.1540080

Glen AS, Cockburn S, Nichols M, Ekanayake J, Warburton B (2013) Optimising camera traps for monitoring small mammals. PLoS One 8:e67940. https://doi.org/10.1371/journal.pone.0067940

Hofmeester TR, Cromsigt JPGM, Odden J, Andrén H, Kindberg J, Linnell JDC (2019) Framing pictures: a conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. Ecol Evol 9:2320–2336. https://doi.org/10.1002/ece3.4878

Kunkel KE, Karl TR, Brooks H, Kossin J, Lawrimore JH, Arndt D, Bosart L, Changnon D, Cutter SL, Doesken N, Emanuel K, Groisman PY, Katz RW, Knutson T, O'Brien J, Paciorek CJ, Peterson TC, Redmond K, Robinson D, Trapp J, Vose R, Weaver S, Wehner M, Wolter K, Wuebbles D (2012) Monitoring and understanding trends in extreme storms: state of knowledge. Bull Am Meteorol Soc 94:499–514. https://doi.org/10.1175/BAMS-D-11-00262.1

Laurenzi A, Bodino N, Mori E (2016) Much ado about nothing: assessing the impact of a problematic rodent on agriculture and native trees. Mammal Res 61:65–72. https://doi.org/10.1007/s13364-015-0248-7

Lovari S, Corsini MT, Guazzini B, Romeo G, Mori E (2017) Suburban ecology of the crested porcupine in a heavily poached area: a global approach. Eur J Wildl Res 63. https://doi.org/10.1007/s10344-016-1075-0

Lovari S, Sforzi A, Mori E (2013) Habitat richness affects home range size in a monogamous large rodent. Behav Process 99:42–46. https://doi.org/10.1016/j.beproc.2013.06.005

Lucherini M, Lovari S, Crema G (1995) Habitat use and ranging behaviour of the red fox (*Vulpes vulpes*) in a Mediterranean rural area: is shelter availability a key factor? J Zool 237:577–591. https://doi.org/10.1111/j.1469-7998.1995.tb05016.x

MacKenzie DI, Nichols JD, Royle JA et al (2017) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier

Masseti M, Albarella U, Mazzorin JDG (2010) The crested porcupine, *Hystrix cristata* L., 1758, in Italy. Anthropozoologica 45:27–42. https://doi.org/10.5252/az2010n2a2

Mazerolle MJ (2016) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c)

Melletti M, Meijaard E (2017) Ecology, conservation and Management of Wild Pigs and Peccaries. Cambridge University Press

Monetti L, Massolo A, Sforzi A, Lovari S (2005) Site selection and fidelity by crested porcupines for denning. Ethol Ecol Evol 17:149–159. https://doi.org/10.1080/08927014.2005.9522604

Monterroso P, Brito JC, Ferreras P, Alves PC (2009) Spatial ecology of the European wildcat in a Mediterranean ecosystem: dealing with small radio-tracking datasets in species conservation. J Zool 279: 27–35. https://doi.org/10.1111/j.1469-7998.2009.00585.x

Mori E (2017) Porcupines in the landscape of fear: effect of hunting with dogs on the behaviour of a non-target species. Mammal Res 62:251–258. https://doi.org/10.1007/s13364-017-0313-5

Mori E, Bozzi R, Laurenzi A (2017) Feeding habits of the crested porcupine *Hystrix cristata* L. 1758 (Mammalia, Rodentia) in a Mediterranean area of Central Italy. Eur Zool J 84:261–265. https://doi.org/10.1080/24750263.2017.1329358

Mori E, Lovari S, Sforzi A, Romeo G, Pisani C, Massolo A, Fattorini L (2014a) Patterns of spatial overlap in a monogamous large rodent, the crested porcupine. Behav Process 107:112–118. https://doi.org/10.1016/j.beproc.2014.08.012

Mori E, Maggini I, Menchetti M (2014b) When quills kill: the defense strategy of the crested porcupine Hystrix cristata L., 1758. Mammalia 78. https://doi.org/10.1515/mammalia-2013-0126

Mori E, Sforzi A, Bogliani G, Milanesi P (2018) Range expansion and redefinition of a crop-raiding rodent associated with global warming and temperature increase. Clim Chang 150:319–331. https://doi.org/10.1007/s10584-018-2261-8

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. https://doi.org/10.1080/11250003.2013.857729

Nie Y, Zhou W, Gao K, Swaisgood RR, Wei F (2019) Seasonal competition between sympatric species for a key resource: implications for conservation management. Biol Conserv 234:1–6. https://doi.org/10.1016/j.biocon.2019.03.013

Niedballa J, Sollmann R, Courtiol A, Wilting A (2016) camtrapR : an R package for efficient camera trap data management. Methods Ecol Evol 7:1457–1462. https://doi.org/10.1111/2041-210X.12600

O'Brien TG (2008) On the use of automated cameras to estimate species richness for large- and medium-sized rainforest mammals. Anim Conserv 11:179–181. https://doi.org/10.1111/j.1469-1795.2008.00178.x

O'Connell AF, Nichols JD, Karanth KU (2010) Camera traps in animal ecology: methods and analyses. Springer Science & Business Media

Pamplin FA (2013) Optimising the value of by-catch from *Lynx lynx* camera trap surveys in the Swiss Jura region. University of East Anglia, MSc in in Applied Ecology and Conservation

QGIS development team (2019) quantum GIS. Open Source Geospatial Foundation Project

Rovero F, Martin E, Rosa M, Ahumada JA, Spitale D (2014) Estimating species richness and modelling habitat preferences of tropical Forest mammals from camera trap data. PLoS One 9:e103300. https://doi.org/10.1371/journal.pone.0103300

Rovero F, Zimmermann F (2016) Camera trapping for wildlife research. Pelagic Publishing Ltd, Exeter, UK

Rovero F, Zimmermann F, Berzi D, Meek P (2013) "Which camera trap type and how many do I need?" a review of camera features and study designs for a range of wildlife research applications. Hystrix Ital J Mammal 24:148–156. doi: https://doi.org/10.4404/hystrix-24.2-8789

Sonnino S (1998) Spatial activity and habitat use of crested porcupine, Hystrix cristata L., 1758 (Rodentia, Hystricidae) in Central Italy. Mammalia 62. https://doi.org/10.1515/mamm.1998.62.2.175

Strampelli P, Andresen L, Everatt KT, Somers MJ, Rowcliffe JM (2018) Habitat use responses of the African leopard in a human-disturbed region of rural Mozambique. Mamm Biol 89:14–20. https://doi.org/10.1016/j.mambio.2017.12.003

Trenberth KE (2011) Changes in precipitation with climate change. Clim Res 47:123–138. https://doi.org/10.3354/cr00953

Welbourne DJ, MacGregor C, Paull D, Lindenmayer DB (2015) The effectiveness and cost of camera traps for surveying small reptiles and critical weight range mammals: a comparison with labour-intensive complementary methods. Wildl Res 42:414–425. https://doi.org/10.1071/WR15054

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