



Anthropogenic threats drive spatio-temporal responses of wildcat on Mt. Etna

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Abstract

Human expansion can cause disturbance and intrusion of invasive species, which are detrimental to small carnivores. We investigated how European wildcats responded to disturbance from mushroom collectors, cattle and feral pigs in Sicily, Italy. We used detections from 76 cameras over 2 surveys (2015–2016 and 2018; camera days = 1985) to run occupancy and co-occurrence models and estimate overlap in activity patterns between species pairs. During 2015–2016, wildcats were detected at the same location with cattle, mushroom hunters and feral pigs at 14.4%, 26.3% and 17.1% of cameras. During 2018, wildcats were detected at the same location with cattle, mushroom hunters and feral pigs at 7.8%, 19.7% and 6.5% of cameras. Dominant species (A; cattle, mushroom hunters and feral pigs) did not affect occupancy of the subordinate species (B; wildcats) during 2015–2016. In 2018, the effect of species A on wildcat occupancy was evident for cattle-wildcat and mushroom hunters-wildcat pairs and wildcat occupancy was higher at sites where species A was not present. Probabilities of detecting wildcats at sites where species A was not present or not detected were higher than probabilities of detecting wildcats at sites where species A was detected. Overlap in activity levels was low between mushroom hunters and wildcats and higher between cattle and wildcats, but varied between surveys for feral pig-wildcat pair. Although results differed between survey periods, we suggest that wildcats generally avoided cattle, feral pigs and mushroom hunters, at both temporal and spatial scales. Anthropogenic disturbance, livestock and invasive species are emerging threats to wildcats and future conservation actions should consider our results.

Keywords Activity · Camera-trapping · Cattle · Co-occurrence · Invasive species · Mushroom hunters · Wildcat

Introduction

Wildlife populations are suffering globally (Cardillo et al. 2008), mainly due to anthropogenic influences (Tucker et al. 2018) such as human expansion into natural habitat (Venter et al. 2016), cattle impacts (Lyndenmayer et al. 2018) and invasive species (Doherty et al. 2016). Anthropogenic disturbance can impact the behaviour of prey and predators (Muhly et al. 2011; Lesmeister et al. 2015; Whittington et al. 2019)

and, given the increasing rate of human visitations within protected areas (Balmford et al. 2009, 2015; Bötsch et al. 2018), this type of disturbance will likely become a major threat to wildlife (Marion et al. 2020) even within protected areas (da Silva et al. 2018). However, wildlife can adapt to humans by shifting their activity and occupancy patterns (Lee et al. 2019), avoiding areas heavily visited by humans (Whittington et al. 2019) and limiting their movements (Tucker et al. 2018). Such strategies affect individual fitness (Pirota et al. 2018; Gaynor et al. 2018), which ultimately influences species' persistence in area impacted by human influence.

The impact of cattle on wildlife is well documented (Vavra 2005; Schieltz and Rubenstein 2016; Anile et al. 2020b); negative effects include reducing population distribution of carnivores (Wolf and Ripple 2017), deteriorating habitat quality (Henkin et al. 2011; Lindenmayer et al. 2018) and competition (de Leeuw et al. 2001; Kinnaird and O'Brien 2012; Keesing et al. 2018). Moreover, the risk of disease transmission between wildlife and cattle and vice

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versa (Gortázar et al. 2007; Kamath et al. 2016; Miller et al. 2017) should further caution against allowing diffuse cattle grazing within protected areas (Soofi et al. 2018), especially when the same protected areas are exploited by humans while practising tourism and or recreational activities.

Invasive species are considered one of the most emerging threats to small carnivores and wildlife conservation globally (Doherty et al. 2016), because they usually outcompete native wildlife species (Santulli et al. 2014; Mazzamuto et al. 2017) and disrupt ecological process (Krull et al. 2013), hence triggering cascade effect on the whole ecosystem (Roemer et al. 2002). Feral pigs (*Sus scrofa*), along with the domestic cat (*Felis catus*), are one of the most widespread and highly impactful invasive species worldwide (Doherty et al. 2016). Their typical feeding behaviour (rooting; Elledge et al. 2013) causes severe modifications of soils, while also disrupting ground-nesting birds (Sanders et al. 2020) and rodent dens (Casula et al. 2017; Mori et al. 2020). Moreover, the gregarious social behaviour and the high reproductive output of feral pigs can strongly multiply the negative consequences of their impact on wildlife at several scales (Massei et al. 2011), and large solitary males can represent a serious threat to humans (*Homo sapiens*) (Mayer 2013).

The European wildcat (*Felis silvestris*, hereafter wildcat) is a small feline (3.7–4.9 kg) (Johnson et al. 2017) found in scattered populations across Europe (Anile et al. 2019). Its current status is defined in the IUCN red list as “Least concern”, but authorities warned of a decreasing population trend (Yamaguchi et al. 2015), even if some populations are expanding (Nussberger et al. 2018). However, several threats are currently recognized to pose a concrete risk to wildcat conservation; specifically, habitat fragmentation (Anile et al. 2019; Gil-Sanchez et al. 2020) and hybridization with the domestic cat (*Felis catus*) (Mattucci et al. 2013, 2016, 2019), roads (Klar et al. 2009), humans (Piñeiro et al. 2012; Anile et al. 2019) and competition with other wildlife species (Lozano et al. 2007) have also been documented to negatively affect wildcats.

Human activity can seriously alter wildcat behaviour even within natural protected areas, making them more prone to avoid human encounters and hence reducing wildcat detectability (Anile et al. 2019), similarly to what has been observed in caracals (*Caracal caracal*) (Ünal et al. 2020) and bobcats (*Lynx rufus*) (Clare et al. 2015), while also increasing their stress levels (Piñeiro et al. 2012). Although few studies have assessed whether cattle impact small cats, caracals and Geoffroy’s cat (*Leopardus geoffroyi*) seem to be negatively affected (Pereira et al. 2012; Ünal et al. 2020). Similarly, there is evidence that the presence of wild boar negatively affects wildcat occupancy (Lozano et al. 2007) as well as the detection frequency of caracals (Ünal et al.

2020). However, we are unaware of other studies that have assessed whether wild boars or feral pigs impact small carnivores, such as the wildcat.

We used detections collected by cameras placed at the same locations over two distinct survey period within the Mt. Etna regional park (Sicily, Italy) to investigate the following two hypotheses: (i) wildcats spatially avoid cattle, feral pigs and humans and (ii) wildcats temporally avoid encounter with cattle, feral pigs and humans. We expected wildcats would avoid cattle and feral pigs, given that grazing and rooting can both have drastic impact on the community of prey species usually consumed by wildcats (Singer et al. 1984; Mori et al. 2020). We also expected to find avoidance behaviour between wildcats and humans (in our case, mushroom hunters), given that their presence can be considerable in our study area and wildcats tend to avoid encounters with humans (Piñeiro et al. 2012; Anile et al. 2019).

Materials and methods

Study area

An extensive description of Mt. Etna (Sicily, Italy) is reported in Anile et al. (2019); the most remote areas (zone A) of Mt Etna were declared a World Heritage Site by UNESCO in 2013 (<<https://whc.unesco.org/en/list/1427>>).

Camera-trapping

We used camera traps in a replicated sampling design (i.e. same locations monitored during two different survey periods) [DFV® equipped with Sony® DSC-W55 (Fototrappolaggio, Forlì, Italy)]. During the first survey, we monitored 91 locations with seven arrays of camera traps from 2 July 2015 to 22 December 2015 (3 arrays with 15 cameras and 1 array with 12 cameras) and from 1 April 2016 to 1 July 2016 (2 arrays with 12 cameras and 1 array with 10 cameras (Anile et al. 2019)). The second survey occurred in 2018 and we monitored most ($n = 76$) of the locations monitored during the first survey and we deployed 7 camera arrays (6 arrays with 11 cameras and 1 array with 10 cameras) from 30 May to 14 November (Anile et al. 2020a). We hence truncated the data obtained during 2015–2016 realized during 2018 (i.e. we hence monitored the same 76 locations for the same number of camera-days in both survey periods). Across surveys, cameras were deployed at an average inter-camera distance of $791 \text{ m} \pm 28$ (SE; range = 273–1663 m), with the same local settings (e.g. height, inclination and orientation with respect to the trail/path) and with a delay time

of 10 min between successive bursts ($n=3$) of photos (Anile et al. 2019); no baits or lures were used to attract wildcats. Cameras were checked twice per week to ensure camera function, to change batteries and download data.

Pictures of humans (e.g. hikers, bikers and forest service employees) with clear evidences of mushroom hunting activity (e.g. a basket made of natural twigs is mandatory for any authorized mushroom hunters, though the illegal use of plastic bags is frequent and widespread) were classified as detection of mushroom hunters. Wildcat morphological identification was conducted according to Ragni and Posenti (1996) and used in several camera-trapping surveys conducted within our study area (Anile et al. 2019). Occasion length for the capture histories was set at 7 days, a mean of 3.7 ± 0.06 (SE; range = 1.2–4) occasions per camera. We calculated naïve occupancy (#sites occupied/#sites sampled) and RAI (Relative Abundance Index; #detections/100 camera-days) (Anile and Devillard 2015) for our target species.

Spatial avoidance

Single-species single-season occupancy

We used single-species single season occupancy models for assessing the scale and covariates which best explained occupancy and the detection of each species for each survey period; we then used those most-supported covariates in subsequent two-species occupancy models (Nagy-Reis et al. 2017; Ferreguetti et al. 2018). Our set of covariates for the single-species single-season models were based on Anile et al. (2019); specifically, the occupancy process was modelled using the following set of covariates; mf = % of km² of mixed forest; pf = % of km² of pine forest; me = % of km² of meadows; sh = % of km² of shrub vegetation; lf = % of km² of lava flows; $npmf$ = the number of patches of mixed forest patches; and ele = elevation. The detection process was modelled using the covariate $time$ defined as the number of days, since the first day of each year, for the time point located between the start and end dates of monitoring for each camera.

Single-species single-season occupancy models were run in *R* version 4.0.0 (R Core Team 2020) through the package *unmarked* (Fiske and Chandler 2011). First, the scale that best explained each species occurrence (Nagy-Reis et al. 2017) was assessed by running a set of models ($n=8$) in which the vegetation covariates were computed according to buffers with an increasing radius (from 100 to 700 with a step of 100 m, plus 750 m with all covariates being computed at the same scale within a given model), while keeping detection constant ($p \sim 1$). On the contrary, the occupancy process

was over-parameterized (i.e. an occupancy model formulation which included all the vegetation covariates as predictors, such as $\Psi \sim mf + pf + me + sh + lf$). The most supported scale was hence chosen for future modelling analysis, but when the null model ($p \sim \Psi \sim .$) was the most supported model among this first set of models, we selected the largest buffer within those supported ($< 2.00 \Delta AIC$) for that species during that survey (Nagy-Reis et al. 2017). We then ran a set of occupancy models to identify the covariates that best explained occupancy (hereafter bo for best occupancy); we kept the detection process constant and varied the occupancy process by using all possible combinations of covariates (mf , pf , me , sh and lf) for building models constituted of up to three terms for the occupancy process ($n=25$). The most supported models selected from this step were then ran in combination first with the covariate $npmf$ and then, after being ranked again, with the covariate ele to assess if model's performances (i.e. AIC) were improved by the addition of these two covariates for the occupancy process. Eventually, models were ranked again and the most supported were further ran in combination with the covariate $time$ for the detection process (i.e. $p \sim time \Psi \sim bo$). This set of a priori occupancy models (between 29 and 42 depending on the uncertainty around the occupancy process) were built with only additive combinations and we only considered models with full convergence. Goodness-of-fit for each most supported single-species occupancy model was assessed through the function *mb.test.gof* of the *R* package *AICcmodavg* (Mazerolle 2019); when overdispersion was detected, we adjusted model selection accordingly (MacKenzie et al. 2006).

Two-species occupancy

We used the software Mark (<http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>), accessed using the package *RMark* (Laake 2013) in the *R* environment, to run two-species co-occurrence models (Richmond et al. 2010). Given the striking differences in the body size of the species we studied, thereby more typical of a scenario with strong asymmetric interactions (i.e. species A can influence occupancy/detection of species B, but not vice versa), and the relative sparseness of our dataset, we opted to not use the co-occurrence model developed by Rota et al. (2016) which can account for scenarios when more than two species are interacting, albeit without assuming asymmetric interactions. Rather, we used the model developed by Richmond et al. (2010), which assumes, in pairwise cases, there is a dominant species (hereafter A; cows, mushroom collectors and feral pigs) and a sub-ordinate species (hereafter B; wildcats) and estimates the following parameters from a matrix of detection/non-detection data:

Ψ_A = probability of occupancy for species A;
 Ψ_{BA} = probability of occupancy for species B, given species A is present;
 Ψ_{Ba} = probability of occupancy for species B, given species A is absent;
 p_A = probability of detection for species A, given species B is absent;
 p_B = probability of detection for species B, given species A is absent;
 r_A = probability of detection for species A, given both species are present;
 r_{BA} = probability of detection for species B, given both species are present and species A is detected;
 r_{Ba} = probability of detection for species B, given both species are present and species A is not detected;
 $\Psi_{B\text{-hat}}$ = probability of occupancy for species B;
 $\Psi_{AB\text{-hat}}$ = probability of occupancy for both species; and
 SIF (species interaction factor) = a value ~ 1 indicates a random association, whereas a value > 1 indicates co-occurrence (i.e. no avoidance) and a value < 1 indicates avoidance.

We used the covariates previously identified as determinants of occupancy for each species during each survey period as predictors for our two-species co-occupancy models. We tested four ecological hypotheses: (i) whether the occupancy of species B was influenced by the occupancy of species A; (ii) whether the detection of species B was influenced by the detection of species A; (iii) whether occupancy of species B was influenced by the occupancy of species A, but detection of species B was not influenced by the detection of species A; and (iv) whether occupancy of species B was not influenced by the occupancy of species A, but detection of species B was influenced by the detection of species A. We used the following approach for identifying the most-supported models among the set of candidate models. In the first step of model selection, each model was ran assuming that (i) occupancy of species B was not influenced by the occupancy of species A, hence $\Psi_{BA} \neq \Psi_{Ba}$, or (i) occupancy of species B was influenced by the occupancy of species A, hence $\Psi_{BA} = \Psi_{Ba}$. Initially, we explored a set of models where the covariate *time* was allowed to vary for both species ($\Psi_A \sim \text{bo } \Psi_{BA} \sim \text{bo } \Psi_{Ba} \sim \text{bo } p_A \sim \text{time } r_A \sim \text{time } p_B \sim \text{time } r_{BA} \sim \text{time } r_{Ba} \sim \text{time}$) or for only one of them ($p_A \sim . r_A \sim . p_B \sim \text{time } r_A \sim . r_{BA} \sim \text{time } r_{Ba} \sim \text{time}; p_A \sim \text{time } r_A \sim \text{time } p_B \sim . r_A \sim \text{time } r_{BA} \sim . r_{Ba} \sim .$). The most-supported model selected from this step was then ran with the detection formulation including the covariate *days* = % of the ratio between days with at least one detection of species A and the effort (camera days) for each camera (Can et al. 2020); we hence further

tested whether the detection probabilities of species B were influenced by the detection (or non-detection) of species A. Ultimately, the most-supported model was then ran assuming that (i) occupancy of species B was not influenced by the occupancy of species A ($\Psi_{BA} \neq \Psi_{Ba}$) or occupancy of species B was influenced by the occupancy of species A ($\Psi_{BA} = \Psi_{Ba}$), but (i) detection of species B was not influenced by species A ($r_{BA} \neq r_{Ba}$) or detection of species B was influenced by species A ($r_{BA} = r_{Ba}$). Overall, we ran 13 models for each species pair, including a null model $\Psi_A \sim . \Psi_{BA} \sim . \Psi_{Ba} \sim . p_A \sim . r_A \sim . p_B \sim . r_A \sim . r_{BA} \sim . r_{Ba} \sim$ with $\Psi_{BA} \neq \Psi_{Ba}$ and $r_{BA} \neq r_{Ba}$ which represented our null hypothesis (i.e. occupancy of the two species was not influenced by any covariates and occupancy and detection of species B are independent from species A). We performed model selection using AICc and, when more than one model was supported by the data ($\Delta \text{AICc} < 2.00$), we accordingly averaged parameter estimates (Richmond et al. 2010). Goodness-of-fit for the best two-species occupancy model was then ascertained using a bootstrap procedure for calculating the variance inflation factor $\hat{c}$ (Cooch and White 2006). Specifically, we ran 1000 simulations in which (i) the values for the model parameters were used from the best two-species occupancy model and (ii) the capture histories of both species were randomly generated, although coherently with our raw results (i.e. detections occurred only at sites where detections were recorded with operational cameras). We based our inferences according to model performance and their parameter estimates; results are reported as mean plus standard error, unless explicitly stated.

Activity patterns

We used the R package *activity* (Rowcliffe 2019) to estimate the (i) activity level of each species pair for each survey and (ii) the coefficient of temporal overlap between species. The activity level was estimated by fitting a circular kernel density to radian time-of-day data, where the coefficient of temporal overlap indicated concordance in activity levels between species-pairs. The coefficient of temporal overlap (Δ_1) ranges from 0 to 1, so we distinguished three intensity levels for this coefficient (low < 0.33 ; 0.33 $<$ medium < 0.66 ; high > 0.66). Specifically, we first estimated the activity level and the respective 95% confidence intervals (hereafter 95% CI), for each species for each survey using the function *fitact* with 1000 bootstrap iterations. We then compared whether the activity levels of wildcats were significantly different from the dominant species for each survey using the function *compareAct*. We further tested whether the estimated

coefficient of overlap between species pairs was random using the function *compareCkern* with 1000 bootstrap iterations. Finally, we tested whether the coefficients of overlap between wildcats and the dominant species was statistically different between the two survey period (i.e. if 95% CI did not overlap) using the function *bootEst* with 1000 bootstrap iterations and the function *BootCI* from the R package *overlap* (Ridout and Linkie 2009).

Results

We accumulated 1985 camera-days for each survey (camera days per camera = 26.4 ± 0.4 ; range = 9–28). Average wildcat detections per cameras (considering only cameras with wildcat detections) were 1.71 ± 0.15 (range = 1–5) in the first survey and 1.28 ± 0.12 (range = 1–3) in the second survey. Similarly, wildcats naïve occupancy decreased from 0.50 to 0.27 as well as the RAI which decreased from 3.27 to 1.36 (Table 1). During both surveys, 48 locations were occupied by wildcats, with 10 locations occupied in both surveys, 11 locations occupied only in 2018, 27 locations occupied only in 2015–2016 and 28 locations were never occupied.

Cattle naïve occupancy and RAI increased from 0.23 to 0.46 and from 24.08 to 36.32, respectively, between survey periods. Similarly, mushroom hunter naïve occupancy and mushroom hunter RAI increased from 0.51 to 0.67 and from 16.72 to 42.72 between surveys (Table 1). On the contrary, feral pig naïve occupancy remained stable between surveys (0.27 and 0.26), but RAI decreased from 17.83 to 4.98 (Table 1). During the first survey, wildcats and cows were detected at the same location at 11 cameras (14.4%), wildcats and mushroom hunters at 20 cameras (26.3%) and wildcats and feral pigs at 13 cameras (17.1%). During the second survey, wildcats and cows were detected at the same location at 6 cameras (7.8%), wildcats and mushroom hunters at 15 cameras (19.7%) and wildcats and feral pigs together at 5 cameras (6.5%).

Table 1 Number of detections and cameras positive for the focal species obtained from two camera-trapping surveys (2015–2016 and 2018) conducted on Mt. Etna (Sicily, Italy) with 76 camera sites and 1985 camera-days per survey

Species	#Detections-# cameras positive first survey	#Detections-# camera positive second survey
Cattle	478–18	721–35
Mushroom hunters	332–39	848–51
Feral pigs	354–21	99–20
Wildcats	65–38	27–21

Spatial avoidance

Single-species single-season occupancy

Across surveys, the first set of models ran for identifying the most-supported scale of analysis highlighted a consistent signal (i.e. the same scale was selected in both surveys) for only one species (i.e. feral pigs, 700 m; [Online Resource](#)). For cattle and mushroom hunters, the most-supported models indicated that the best scale was that with the buffer radius of 750 m in 2015–2016 (although for mushroom hunters, the null model was best supported, we selected the larger buffer in this case) and 700 m in 2018 (Fig. 1). For wildcats, 400 m and 500 m were the most-supported buffers in 2015–2016 and 2018, respectively ([Online Resource](#)). Overdispersion was detected only for mushroom hunters in 2018 ($\hat{c} = 1.62$, $p = 0.013$). Top ranked single-season occupancy models are reported in Table 2.

Two-species occupancy

For 2015–2016, the most-supported model for the cattle-wildcat pair was that where occupancy and detection of species B was impacted by species A ($\Psi_{BA} = \Psi_{Ba}$, $r_{BA} = r_{Ba}$), although the associated SIF value was greater than 1 (Table 3). For the other two species pairs, the most supported models were those with $\Psi_{BA} = \Psi_{Ba}$, $r_{BA} = r_{Ba}$, although models with $\Psi_{BA} \neq \Psi_{Ba}$, $r_{BA} \neq r_{Ba}$ were supported as well (Table 3). We hence did not find evidence that species A influenced wildcat occupancy given that SIF values in 2015–2016 were above 1 (Table 4, Fig. 2). Nevertheless, probability of detecting wildcats at sites where species A (cattle and feral pigs) was present but not detected was higher than probabilities of detecting wildcats at sites where species A was detected ($r_{BA} = 0.27$, 0.15 vs. $r_{Ba} = 0.36$, 0.51). Furthermore, for the mushroom hunter-wildcat pair, probabilities of detecting wildcats at sites where mushroom hunters were not present ($p_B = 0.40$) were consistently higher than probabilities of detecting wildcats at sites where mushroom hunters were present and detected ($r_{BA} = 0.26$) or present and not detected ($r_{Ba} = 0.17$); Table 4, Fig. 2).

For 2018, the most-supported model for the cattle-wildcat and the mushroom-hunter pairs was that where occupancy and detection of species B was not impacted by species A ($\Psi_{BA} \neq \Psi_{Ba}$, $r_{BA} \neq r_{Ba}$), although models with $\Psi_{BA} = \Psi_{Ba}$, $r_{BA} = r_{Ba}$ were supported as well for the cattle-wildcat pair (Table 5). For the feral pigs-wildcat pair, the most-supported model was that with $\Psi_{BA} \neq \Psi_{Ba}$ but $r_{BA} = r_{Ba}$ (Table 5). We found evidence that both cattle and mushroom hunters negatively influenced the occupancy of wildcats (SIF = 0.88; 0.87), although we noted that the CI for the cattle-wildcat pair included the threshold

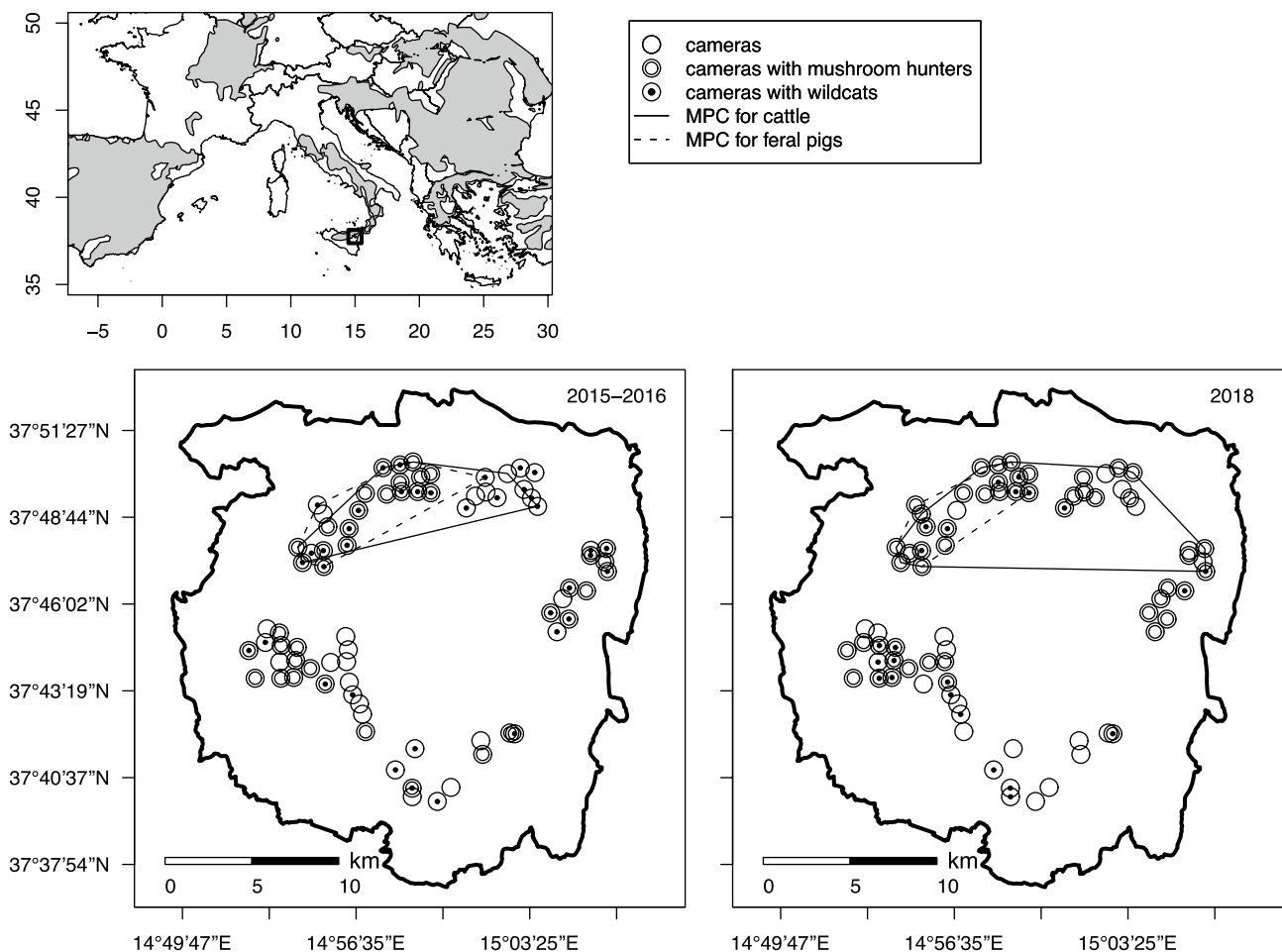


Fig. 1 Upper panel shows the approximate wildcat distribution in Europe according to the latest IUCN assessment. Lower panels show the 76 locations used in the two surveys (left panel=2015–2016; right panel=2018) on Mt. Etna. Cameras with detections of wildcats and

mushroom hunters are depicted, while for cattle and feral pigs, the MPC connecting the outermost cameras are shown (continuous and dotted, respectively)

of 1. Consistently with this result, occupancy of wildcats at sites where species A was not present was higher than the occupancy of wildcat at sites where species A was present ($\Psi_{Ba}=0.95$; 0.99 vs. $\Psi_{BA}=0.64$; 0.57 for cattle and hunters, respectively) (Table 6, Fig. 2). Probabilities of detecting wildcats at sites where feral pigs were not

present ($p_B=0.05$) were three times less than probabilities of detecting wildcats at sites where feral pigs were present, irrespective if they were detected or not ($r_{Ba}=0.16$, $r_{Ba}=0.15$; Table 6, Fig. 2). Goodness-of-fit for all two-species co-occupancy models indicated no overdispersion (all $p>0.05$ and $\hat{c}=0.99$ – 1.05).

Table 2 Most supported single-species single-season occupancy models for each species pairs based on camera-trapping data collected on Mt. Etna (Sicily, Italy) during two surveys (2015–2016 and 2018) with 76 locations for a total of 1985 camera-days per survey. The symbol between brackets indicates the direction of the relationship. Covariate descriptions as following: *mf*=% of km² of mixed forest; *pf*=% of km² of pine forest; *me*=% of km² of mead-

ows; *sh*=% of km² of shrub vegetation; *lf*=% of km² of lava flows; *npmf*=the number of patches of mixed forest patches, *ele*=elevation, *time*=number of days, since the first day of each year, for the time point located between the start and end dates of monitoring for each camera. Full model selection for each species and each survey is provided in [Online Resource](#)

Year	Cattle	Mushroom hunters	Feral pigs	Wildcats
2015–2016	$p \sim \Psi \sim mf(+) + me(+) + sh(+) + n$ $pmf(+) + ele(+)$	$p \sim time(+)$ $\Psi \sim mf(+) + pf(+) + npmf(+)$	$p \sim \Psi \sim mf(+) + me(+) + sh(+) +$ $npmf(+)$	$p \sim \Psi \sim sh(+)$
2018	$p \sim \Psi \sim mf(+) + sh(+)$	$p \sim \Psi \sim lf(-)$	$p \sim time(-)$ $\Psi \sim pf(-) + lf(-) + npmf(+)$	$p \sim \Psi \sim pf(-) + sh(-) + ele(+)$

Table 3 Model selection for the two species co-occurrence models for each species pair for the first survey conducted on Mt. Etna (Sicily, Italy) in 2015–2016 with 76 camera locations and 1985 camera-days. Models are reported until the 2 AICc points, plus the null model. Covariate descriptions as following: *mf*=% of km² of mixed forest; *pf*=% of km² of pine forest; *me*=% of km² of mead-

ows; *sh*=% of km² of shrub vegetation; *lf*=% of km² of lava flows; *npmf*=the number of patches of mixed forest patches, *ele*=elevation, *time*=number of days, since the first day of each year, for the time point located between the start and end dates of monitoring for each camera

Species pair	Model	npar	AICc	DeltaAICc	Weight	Deviance
Cattle wildcat	$\Psi A \sim mf + me + sh + npmf + ele \Psi BA = \Psi Ba \sim sh$	16	407.052	0.00	0.55	366.30
	$pA \sim time \ pB \sim . \ rA \sim time \ rBA = rBa \sim$					
	$\Psi A \sim . \ \Psi BA \neq \Psi Ba \sim$	8	418.92	11.39	0.00	400.77
Mushroom hunter wildcat	$pA \sim . \ pB \sim . \ rA \sim . \ rBA \sim \neq rBa \sim$					
	$\Psi A \sim mf + pf + npmf \Psi BA = \Psi Ba \sim sh$	14	519.22	0.00	0.26	484.33
	$pA \sim time \ pB \sim . \ rA \sim time \ rBA \neq rBa \sim$					
	$\Psi A \sim mf + pf + npmf \Psi BA = \Psi Ba \sim sh$	14	519.22	0.00	0.26	484.33
	$pA \sim time \ pB \sim . \ rA \sim time \ rBA = rBa \sim$					
	$\Psi A \sim mf + pf + npmf \Psi BA \neq \Psi Ba \sim sh$	15	520.84	1.62	0.11	482.84
	$pA \sim time \ pB \sim . \ rA \sim time \ rBA = rBa \sim$					
	$\Psi A \sim mf + pf + npmf \Psi BA \neq \Psi Ba \sim sh$	15	520.84	1.62	0.11	482.84
	$pA \sim time \ pB \sim . \ rA \sim time \ rBA \neq rBa \sim$					
	$\Psi A \sim mf + pf + npmf \Psi BA = \Psi Ba \sim sh$	15	520.94	1.72	0.11	482.94
Feral pig wildcat	$pA \sim time \ pB \sim . \ rA \sim time \ rBA = rBa \sim days$					
	$\Psi A \sim . \ \Psi BA \neq \Psi Ba \sim$	8	542.32	23.10	0.00	524.7
	$pA \sim . \ pB \sim . \ rA \sim . \ rBA \sim \neq rBa \sim$					
	$\Psi A \sim mf + me + sh + npmf \Psi BA = \Psi Ba \sim sh$	13	430.24	0.00	0.23	398.37
	$pA \sim . \ pB \sim . \ rA \sim . \ rBA = rBa \sim$					
	$\Psi A \sim mf + me + sh + npmf \Psi BA = \Psi Ba \sim sh$	13	430.24	0.00	0.23	398.37
	$pA \sim . \ pB \sim . \ rA \sim . \ rBA \neq rBa \sim$					
	$\Psi A \sim mf + me + sh + npmf \Psi BA \neq \Psi Ba \sim sh$	14	431.13	0.89	0.15	396.24
	$pA \sim . \ pB \sim . \ rA \sim . \ rBA = rBa \sim$					
	$\Psi A \sim mf + me + sh + npmf \Psi BA \neq \Psi Ba \sim sh$	14	431.13	0.89	0.15	396.24
	$pA \sim . \ pB \sim . \ rA \sim . \ rBA \neq rBa \sim$					
	$\Psi A \sim mf + me + sh + npmf \Psi BA = \Psi Ba \sim sh$	15	432.14	1.90	0.09	394.14
	$pA \sim . \ pB \sim time. \ rA \sim . \ rBA = rBa \sim time$					
	$\Psi A \sim . \ \Psi BA \neq \Psi Ba \sim$	8	450.27	20.03	0.00	432.12
	$pA \sim . \ pB \sim . \ rA \sim . \ rBA \sim \neq rBa \sim$					

Activity patterns

Most activity levels of species A were concentrated during the diurnal hours, whereas wildcat activity levels were more

strictly nocturnal (Fig. 3). The coefficient of overlap (Δ_1) was 0.33, 0.19 and 0.28 during 2015–2016 and 0.31, 0.22 and 0.56 in 2018 for the cattle-wildcat, mushroom hunters-wildcat and feral pigs-wildcat pairs, respectively. We did

Table 4 Parameters (95% confidence intervals are shown in brackets) from the best co-occupancy models for each pair of species from two replicated surveys conducted on Mt. Etna (Sicily, Italy) during 2015–2016 with 76 camera locations and 1985 camera-days

Real parameters	Cattle vs. wildcats	m. hunters vs. wildcats ^a	Feral pigs vs. wildcats ^a
ΨA	0.35 ± 0.14 (0.13–0.65)	0.61 ± 0.09 (0.41–0.77)	0.11 ± 0.06 (0.03–0.31)
ΨBA	0.90 ± 0.09 (0.49–0.98)	0.89 ± 0.11 (0.46–0.98)	0.74 ± 0.24 (0.17–0.98)
ΨBa	0.55 ± 0.19 (0.21–0.85)	0.66 ± 0.17 (0.30–0.90)	0.67 ± 0.15 (0.34–0.89)
$\Psi B\text{-hat}$	0.67 ± 0.12 (0.40–0.86)	0.80 ± 0.08 (0.53–0.93)	0.69 ± 0.38 (0.40–0.86)
$\Psi AB\text{-hat}$	0.31 ± 0.14 (0.10–0.64)	0.54 ± 0.08 (0.36–0.72)	0.09 ± 0.38 (0.02–0.28)
pA	1.00 ± 0.00 (0.99–1.00)	0.81 ± 0.67 (0.00–0.99)	0.19 ± 0.18 (0.02–0.71)
pB	0.24 ± 0.08 (0.08–0.42)	0.40 ± 0.08 (0.26–0.56)	0.31 ± 0.07 (0.18–0.47)
rA	0.22 ± 0.08 (0.09–0.44)	0.63 ± 0.05 (0.52–0.73)	0.71 ± 0.06 (0.56–0.82)
rBA	0.27 ± 0.10 (0.09–0.48)	0.26 ± 0.05 (0.16–0.39)	0.15 ± 0.07 (0.06–0.34)
rBa	0.36 ± 0.07 (0.22–0.52)	0.17 ± 0.06 (0.08–0.33)	0.51 ± 0.17 (0.20–0.81)
SIF	1.33 ± 0.25 (0.82–1.83)	1.10 ± 0.09 (0.94–1.27)	1.12 ± 0.40 (0.43–1.82)

^aModel average estimates for models within AICc < 2

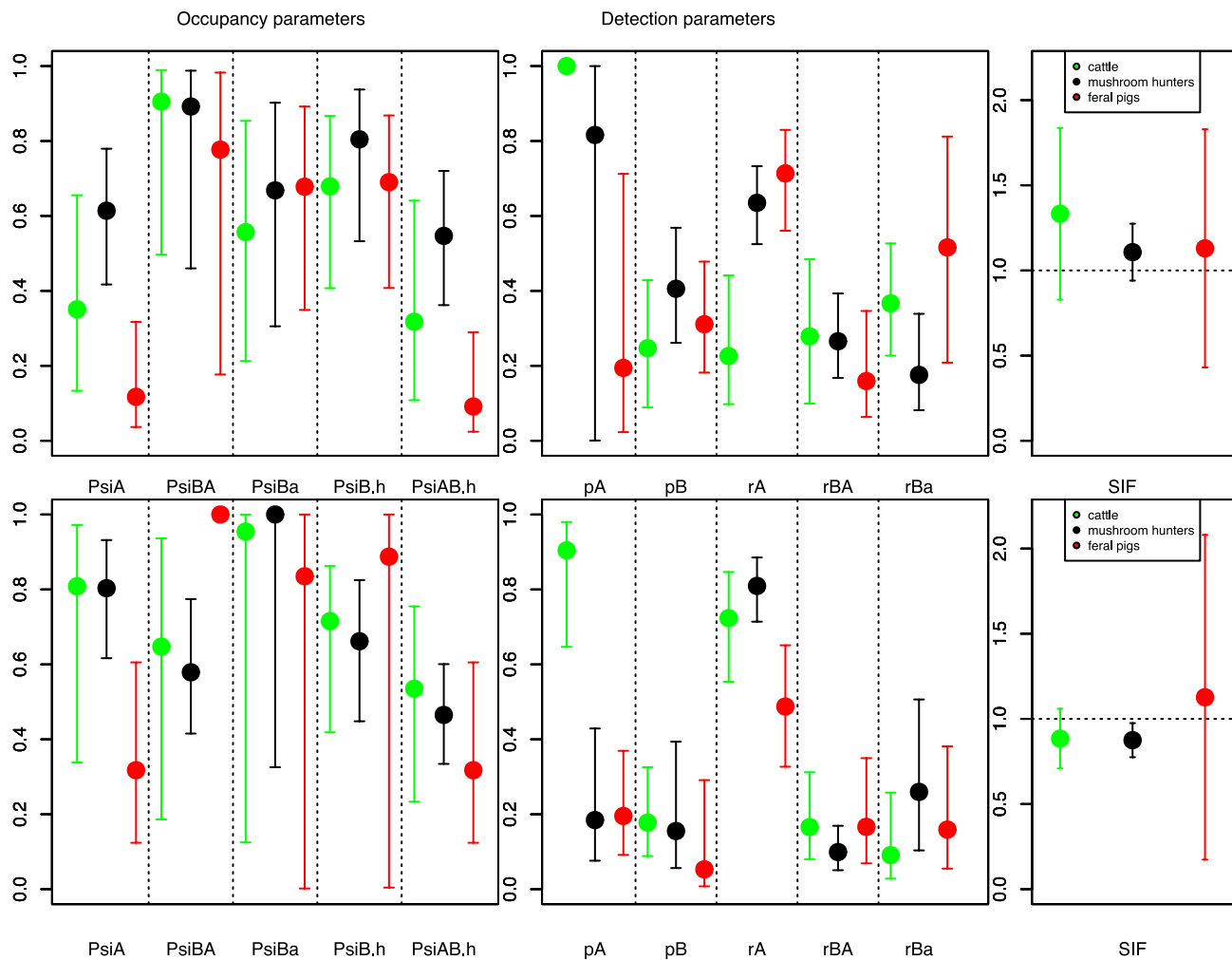


Fig. 2 Parameter estimates from two-species co-occupancy (species B is the wildcat) ran on detection data collected via camera-trapping on Mt. Etna (Sicily, Italy) during 2015–2016 (upper row) and 2018 (lower row) from 76 cameras. PsiB-h stands for ΨB -hat, similarly for PsiAB-h

Table 5 Model selection for the two species co-occurrence models for each species pair for the second survey conducted on Mt. Etna (Sicily, Italy) in 2018 with 76 camera locations and 1985 camera-days. Models are reported until the 2 AICc points, plus the null model. Covariate descriptions as following: *mf*=% of km² of mixed forest; *pf*=% of km² of pine forest; *me*=% of km² of mead-

ows; *sh*=% of km² of shrub vegetation; *lf*=% of km² of lava flows; *npmf*=the number of patches of mixed forest patches, *ele*=elevation, *time*=number of days, since the first day of each year, for the time point located between the start and end dates of monitoring for each camera

Species pair	Model	npar	AICc	deltaAICc	Weight	Deviance
Cattle wildcats	$\Psi A \sim mf + sh \Psi BA \neq \Psi Ba \sim pf + sh + ele$	18	378.68	0.00	0.43	330.68
	$pA \sim time \ pB \sim . \ rA \sim time \ rBA \neq rBa \sim$					
	$\Psi A \sim mf + sh \Psi BA = \Psi Ba \sim pf + sh + ele$	15	380.07	1.38	0.21	342.07
	$pA \sim time \ pB \sim . \ rA \sim time \ rBA \neq rBa \sim$					
	$\Psi A \sim mf + sh \Psi BA = \Psi Ba \sim pf + sh + ele$	15	380.07	1.38	0.21	342.07
Mushroom hunters wildcats	$pA \sim time \ pB \sim . \ rA \sim time \ rBA = rBa \sim$					
	$\Psi A \sim . \ \Psi BA \neq \Psi Ba \sim$	8	411.81	33.12	0.00	393.66
	$pA \sim . \ pB \sim . \ rA \sim . \ rBA \sim \neq rBa \sim$					
	$\Psi A \sim . \ \Psi BA \neq \Psi Ba \sim$	8	468.85	0.00	0.49	450.70
	$pA \sim . \ pB \sim . \ rA \sim . \ rBA \sim \neq rBa \sim$					
Feral pigs wildcats	$\Psi A \sim pf + lf + npmf \Psi BA \neq \Psi Ba \sim pf + sh + ele$	21	325.50	0.00	0.81	266.39
	$pA \sim time \ pB \sim time \ rA \sim time \ rBA = rBa \sim time$					
	$\Psi A \sim . \ \Psi BA \neq \Psi Ba \sim . \ pA \sim . \ pB \sim . \ rA \sim . \ rBA \neq rBa \sim$	8	357.91	32.40	0.00	339.76

Table 6 Parameters (95% confidence intervals are shown in brackets) from the best co-occupancy models for each pair of species from two replicated surveys conducted on Mt. Etna (Sicily, Italy) during 2018 with 76 camera locations and 1985 camera-days

Real parameters	Cattle vs wildcats ^a	m. hunters vs wildcats	Feral pigs vs wildcats
Ψ_A	0.80 ± 0.16 (0.33–0.97)	0.80 ± 0.09 (0.61–0.93)	0.31 ± 0.13 (0.12–0.60)
Ψ_{BA}	0.64 ± 0.24 (0.18–0.93)	0.57 ± 0.09 (0.41–0.77)	1.00 ± 0.00 (1.00–1.00)
Ψ_{Ba}	0.95 ± 0.11 (0.12–0.99)	0.99 ± 0.00 (0.32–0.99)	0.85 ± 0.55 (0.00–0.99)
$\Psi_{B\text{-}hat}$	0.71 ± 0.19 (0.41–0.86)	0.66 ± 0.10 (0.44–0.82)	0.88 ± 0.38 (0.00–0.99)
$\Psi_{AB\text{-}hat}$	0.53 ± 0.23 (0.23–0.75)	0.46 ± 0.06 (0.33–0.60)	0.31 ± 0.13 (0.12–0.60)
p_A	0.90 ± 0.07 (0.64–0.97)	0.18 ± 0.08 (0.07–0.42)	0.19 ± 0.07 (0.06–0.34)
p_B	0.17 ± 0.05 (0.08–0.32)	0.15 ± 0.08 (0.05–0.39)	0.05 ± 0.05 (0.00–0.29)
r_A	0.72 ± 0.07 (0.55–0.84)	0.80 ± 0.04 (0.71–0.88)	0.48 ± 0.08 (0.32–0.65)
r_{BA}	0.16 ± 0.05 (0.08–0.31)	0.09 ± 0.03 (0.05–0.16)	0.16 ± 0.07 (0.06–0.34)
r_{Ba}	0.09 ± 0.05 (0.02–0.25)	0.25 ± 0.10 (0.10–0.50)	0.15 ± 0.08 (0.05–0.38)
SIF	0.88 ± 0.14 (0.70–1.05)	0.87 ± 0.05 (0.77–0.97)	1.12 ± 0.48 (0.17–2.08)

^aModel average estimates for models within AICc < 2. SIF values below 1 are in bold

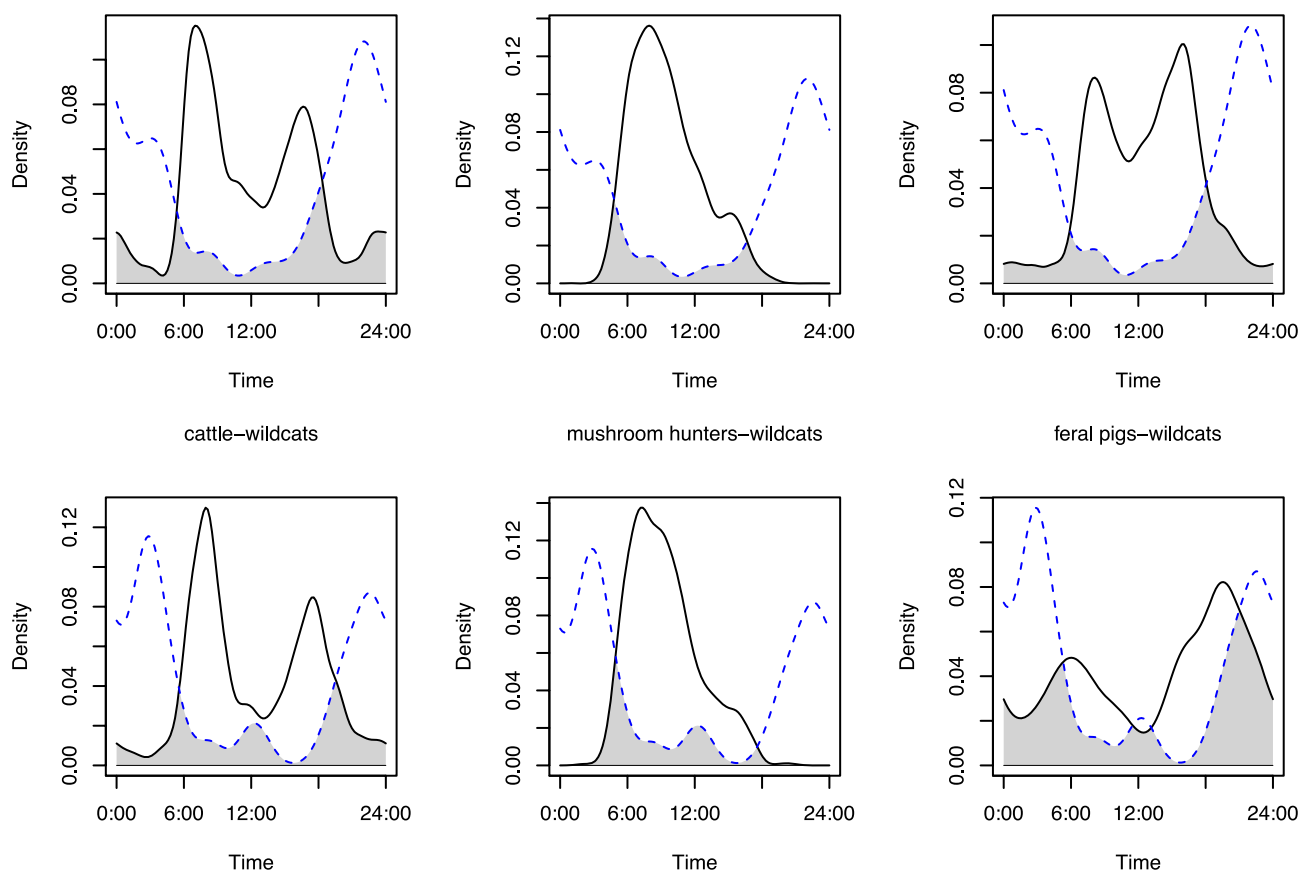


Fig. 3 Activity pattern and overlap of wildcats (dotted line) against cattle, mushroom hunters and feral pigs (continuous lines) from detection data collected via camera-trapping on Mt. Etna (Sicily, Italy) during 2015–2016 (upper row) and 2018 (lower row) from 76 cameras

not detect differences in activity levels between species A and wildcats during both surveys (all $p > 0.05$), but detected a change for feral pig-wildcat pairs (95% CI=0.15–0.32 in 2015–2016; 95% CI=0.39–0.66 in 2018), with feral pigs being more nocturnal in 2018.

Discussion

Cattle and mushroom hunters negatively affected wildcat occupancy during one of our survey periods (2018). Cattle numbers increased in 2018 (+44% detections and +49%

naïve occupancy); however, the reason for this increase was unknown given parcels of land within the park where livestock are allowed varies annually due to land rental patterns by farmers. Similarly, we cannot ascertain why mushroom hunters steadily increased in 2018 (+ 60% detections and + 23% naïve occupancy). Ideal mushroom-growing conditions (like precipitation, humidity, temperatures, moon cycle and acidity of the soil) can greatly vary across seasons, within seasons and also within a given area, making difficult, if not impossible, any accurate predictions relative to the numbers of mushroom hunters that can visit a certain area.

Cattle interactions with wildlife are usually negative (Schultz and Rubenstein 2016; Lindenmayer et al. 2018), and in our case, we suspect excessive grazing may have depressed the abundance and distribution of rodent prey (Torre et al. 2007; Bueno et al. 2012; Pereira et al. 2012) via reducing grass height (Davidson et al. 2010; Pereira et al. 2012), and hence reducing habitat suitability (Evans et al. 2006; Bueno et al. 2012; Rickart et al. 2013). Moreover, cattle grazing in Mediterranean ecosystems largely occurs in mixed forest areas (Schoenbaum et al. 2017), as we found during 2018; hence, cattle tend to occupy highly suitable wildcat habitat (Anile et al. 2019; Gil-Sanchez et al. 2020). This negative effect of cattle on small cats also has been described for caracals in Turkey (Ünal et al. 2020), for Geoffroy's cats in Argentina (Pereira et al. 2011, 2012) and for ocelots (*Leopardus pardalis*) in Mexico (Rorabaugh et al. 2020). Furthermore, the hunting strategy of wildcats strongly relies on their auditory system (Kitchener et al. 2010), and hence, the sound of the bells usually placed on cattle might further depress the chances of successful hunting, prompting wildcats to leave areas with widespread cattle numbers.

The negative impact of mushroom hunters on wildcat occupancy was evident in 2018. For both surveys, the probabilities of detecting wildcats at sites where mushroom hunters were not present was almost double the probabilities of detecting wildcats at sites where mushroom hunters were present and detected. Wildcats tend to minimize the risk of encounters with humans (especially when human presence is high as during 2018), as also found by Anile et al. (2019) and by Clare et al. (2015) for bobcats. Given that mushroom hunting seasons overlap with the critical period of raising cubs (Piñeiro et al. 2012), a better understanding of wildcat-human interactions is strongly needed. Camera-trapping can be a feasible tool to address this research need (Buxton et al. 2018; Lee et al. 2019), while also providing surveillance into illegal activities conducted by humans (Sandbrook et al. 2018; Meek et al. 2019).

We did not find evidence that feral pigs depressed wildcat occupancy; however, the effect of feral pigs on wildcat detection was strongly evident during our first survey. Indeed, probabilities of detecting wildcats at sites where

feral pigs were present but not detected were three times higher than probabilities of detecting wildcats at sites where feral pigs were detected. Furthermore, in Mediterranean habitat, feral pigs prefer large patches of forest populated by oaks (*Quercus* sp.) and mixed woods (Abaigar et al. 1994; Virgós 2002; Sütő et al. 2020), further increasing the chances of encounters with wildcats given the similarities in the habitat preferences (Anile et al. 2019). During our second survey, probabilities of detecting wildcats at sites where feral pigs were not present were three times smaller than probabilities of detecting wildcat at sites where feral pigs were present. Moreover, wild boars (*Sus scrofa*) are also known to negatively affect the distribution and detectability of rabbits (*Oryctolagus cuniculus*) (Lozano et al. 2007; Barros et al. 2020), which are the staple prey of wildcats when they are present (Lozano et al. 2006), as in our study area, and similarly to what was found for the crested porcupine (*Hystrix cristata*) in 2015–2016 (Mazzamuto et al. 2019). However, we did not account for interactions between multiple dominant species at camera locations; hence, the negative effects on wildcats we documented may be more severe given that cattle, feral pigs and mushroom hunters were also frequently detected at the same camera location.

Temporal overlap between wildcats and the other dominant species was generally minimal across surveys, but for feral pigs-wildcats pairs in the second survey, the overlap was medium (0.56): this increase in overlap was due to a change in the activity pattern of feral pigs, which were more crepuscular during 2018 than 2015–2016. Small cat species tend to be nocturnal (Cheyne and Macdonald 2011; Blake et al. 2016; Huaranca et al. 2020; Horn et al. 2020) and this process might be an adaptive response to avoid encounters with larger species during daylight hours (Davis et al. 2018). Nocturnality is one of the mechanisms that wildlife adopt to avoid encounters with humans (Gaynor et al. 2018; Nickel et al. 2020); however, the response seems to vary considerable across species (Frey et al. 2020; Haswell et al. 2020). Temporal segregation is hence employed by wildcats to minimize the risk of encounters with other apparently “competing” species (Sunarto et al. 2015).

Conclusions

Wildcat occupancy on Mt. Etna was affected by cattle and mushroom hunters, while feral pigs affected wildcat detectability. Future wildcat conservation actions should consider, and try to mitigate, these emerging threats to wildcats. With respect to cattle, a solution for mitigating their impact on wildcats could be to reduce the grazing intensity and local pressure by limiting stocking densities and herd persistence within the same area for a long time (i.e. rotational grazing (Schultz and Rubenstein 2016)). Feral pigs are an invasive

species, and hence should be eradicated as feasible (Keiter and Beasley 2017). Nevertheless, feral pigs in our study area are raised illegally; to address this long-term issue, an effective surveillance (e.g. establishment of nocturnal check points during critical periods and implementation of the patrol service) against illegal activities is urgently needed. Human pressure on natural ecosystem is increasing (Betts et al. 2017) and likely to continue (Balmford et al. 2009, 2015); hence, mitigation measures (e.g. limiting number of hikers and mushroom hunters) should be implemented to minimize human disturbance of wildcats, at least during the most critical period of their biological cycle (Piñeiro et al. 2012). Mt. Etna is a stronghold for the Sicilian wildcat population (Anile et al. 2020a); however, the emerging threats we have identified can seriously depress this population if the aforementioned suggested conservation measures are not undertaken in the near future.

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Author contribution Stefano Anile performed the field work and data analysis. All authors have participated in the writing of the manuscript.

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Declarations

Conflict of interest The authors declare no competing interests.

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