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Research Article

Spatial mark-resight models to estimate feral pig population density

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Abstract

Population size is a highly important parameter for wildlife management and conservation. However, its estimation can be challenging when a portion of the population is undetectable. Spatially explicit capture-recapture models are a precise approach to estimate wildlife population density while accounting for imperfect detection, but all animals must be individually identifiable. Spatial mark-resight models (SMR) allow the estimation of population sizes when only some individuals can be identified. This is the case in feral pigs (*Sus scrofa*), where some individuals are recognizable by natural marks. We compared two SMR approaches to estimate feral pig population density: SMR for an unknown number of marked individuals (SMR-UM) and SMR for a known number of marked individuals (SMR-KM). Both approaches are applicable in species with some individuals recognisable by natural marks, such as feral pigs. The SMR-KM is similar to a process of capture-mark-recapture of fewer individuals, which can be used in species with non-recognisable individuals (e.g., wild boar, *S. scrofa*). First, we fitted a SMR-UM using the complete capture history (individuals/traps/days) for all recognisable individuals (n=33) and the latent capture history (traps-days) for unmarked individuals throughout the entire sampling occasion (66 days). Secondly, we fitted SMR-KM dividing the sampling occasions into two periods: the sighting period (25 days) to identify individuals (n=13), and the resighting period (41 days) in which we used the complete capture and latent capture histories of the marked and unmarked individuals, respectively. We estimated very similar densities with the two approaches for feral pigs in our study area: 13.27 (SD=3.07) (8.12–20.02 95% BCI) and 12.87 (SD=2.21) (8.96–17.59 95% BCI) pigs/km^2, for SMR-UM and SMR-KM, respectively. Our results indicate that SMR models are an effective tool to monitor feral pig populations, as well as similar non-individually identifiable species, by tagging a small sample of the population.

Introduction

Wildlife population size is a highly important parameter for management and conservation. However, its estimation can be challenging. Determining population size can be a time-consuming and costly task, particularly for species that are not individually identifiable, have large spatial requirements (e.g. large mammals) or in situations of imperfect detection (Kendall and White, 2009). Moreover, these efforts do not always produce estimations with the precision and accuracy required for establishing effective management plans (MacKenzie et al., 2006). A plethora of methodologies is available to estimate both population abundance (i.e., relative index related to variation in population size or density) and the density in wildlife studies (Schwarz and Seber, 1999; Conroy and Carroll, 2009; Thomson et al., 2009). Their applicability depends on factors related to the peculiarities of the study (e.g. budget), the ecological traits of the species (e.g. body size, behaviour) and the particularities of the study population (e.g. detectability, expected density), among other factors (e.g. Acevedo et al., 2008).

The most generalised methodologies employed to estimate wildlife population size are the classic capture-recapture (CR) models (Buckland et al., 2000). Estimations of population density from CR models are the result of dividing the trappable population by the "effective trapping area", which is difficult to accurately define and measure (Efford, 2004). In addition, CR models have some implicit variability due the assumptions of the spatial relationships between activity centres of individuals and traps (e.g. MacKenzie et al., 2006; Borchers and Efford, 2008; Foster and Harmsen, 2012). In this context, spatial capture-recapture (SCR) models address both the technical problems and the conceptual limitations that arise when applying classical CR models (Efford, 2004; Royle and Young, 2008). SCR models allow for the estimation of the space use of animals and density simultaneously, while accounting for imperfect detection (Royle et al., 2014), even when working with non-territorial species (Royle et al., 2016). Recently, spatial mark-resight (SMR) models (Chandler and Royle, 2013; Sollmann et al., 2013; Royle et al., 2014; Kane et al., 2015) have been developed as an extension of SCR. SMR models use a combination of data from both marked/recognisable and unmarked/unidentifiable individuals. SMR models have improved the flexibility of spatially explicit modelling approaches as cost-effective tools to inform wildlife management and conservation (e.g. Kane et al., 2015).

Feral pigs (*Sus scrofa*) are listed as among 100 of the "world's worst" invaders by the IUCN's Invasive Species Specialist Group (Lowe et al., 2004). The negative effects of high-density feral pig populations are well documented and include damage to ecosystems, causing a reduction in plant (including crops) and animal abundance, the spread of zoonotic and shared diseases and vehicle collisions (Hone, 2002; Gortázar et al., 2007; Di Marco et al., 2012; Doherty et al., 2016). Population control is the most common intervention to deal with feral pig populations (Massei et al., 2011), but the success of these actions highly depends on precise and reliable estimates of population size (Ramsey

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Figure 1 – Details of two feral pigs. Spot patterns and marks allow for unambiguous identification of some individuals from photographic records.

et al., 2009; Massei et al., 2011). In addition, population density is a key parameter for the control of diseases, which is a major threat posed by this species (Hone, 2015). Nonetheless, the estimation of feral pig population size is an especially difficult task. This is a woodland species that is mainly nocturnal and has a particularly reduced visual detectability, in part owing to the absence of *tapetum lucidum* (Graves, 1984). Several methodologies to estimate population abundances have been applied to feral pigs (Engeman et al., 2013). However, because of these ecological peculiarities and the fact that not all animals can be individualised using natural marks (see Fig. 1), no methods to generate feral pig population densities have been validated (Gortázar et al., 2015).

In this context, the use of camera trapping in combination with SMR models may be a reliable and cost-effective alternative to estimating feral pig population density. Thus, the aim of this study was to assess the population status of a feral pig population using a cost-effective protocol based on camera trap surveys and SMR models. Two analytical approaches were comparatively performed: SMR for unknown numbers of marked individuals and SMR for known numbers of marked individuals. Both approaches are applicable in species with some individuals recognisable by natural marks, such as feral pigs. The last of the approaches is similar to a process of capture-mark-recapture of fewer individuals, which can be used in species with non-recognisable individuals (e.g., wild boar, *S. scrofa*). The ultimate goal of including SMR-KM in this study was to show its potential to be used in situations with a low number of recognisable/marked animals. A cost-effective protocol capable of generating precise estimates of population size has a high potential for use in broad-scale feral pig population monitoring. Given the relevance of this species, such a procedure could be applied worldwide, addressing both conservation and epidemiological issues.

Materials and methods

Study area

This study was carried out in a fenced estate in Andalusia, southern Spain (36°16′38″ N, 5°25′41″ O), covering a surface area of ca. 14000 ha within the Alcornocales Natural Park. Biodiversity conservation in this area is combined with traditional land uses, such as cork exploitation, animal husbandry and hunting. The habitat is a diverse Mediterranean woodland characterised by the presence of the cork oak (*Quercus suber* L.), the evergreen oak (*Q. ilex*) and the wild olive tree (*Olea europaea* var. *sylvestris*) with scrubland areas and scattered pastures. Large game species (red deer *Cervus elaphus*, fallow deer *Dama dama* and mouflon *Ovis aries musimon*) and livestock ("Retinta" cattle and "Merina" sheep) cohabit in the study area. The feral pig population originated from the escape of domestic pigs during the 20th century. The feral pig population is of no interest for hunting or livestock activities, and its eradication/control is a management objective for Spanish authorities, as pigs are important reservoirs of shared diseases and can serve as an epidemiological link between livestock and wildlife (Gortázar et al., 2007, 2016).

Sampling protocol

Based on a preliminary analysis of the animals' movements in the study area, we selected a territory of 415 ha for a camera trap survey (Sollmann et al., 2012; Sun et al., 2014). The surveyed territory is larger than the home range of the target species in Mediterranean habitats (Massei et al., 1996; Barasona et al., 2014) and in the study area (approx. 100 ha; the authors' unpublished data). We designed a 500 m grid to guide the location of the camera traps and each camera was located within a buffer of 100 m around the nodes of the grid selecting the best place to install each camera trap to optimize the captures and obtain a uniform distribution of the cameras (Fig. 2). Eighteen heat and motion infrared-triggered camera traps (HCO ScoutGuard and Ltl Acorn 5210A) were used to cover the sampling area (4.3 cameras per 100 ha). The final average distance between two consecutive deployed cameras was 397.8 m (SD=84.6; min=279.7; max=546.7). Given the home range of the species, and according to Chandler and Royle (2013), this sampling design increases the probability of capturing one individual with more than one camera (i.e., spatially correlated capture events). The cameras were located on posts 30–50 cm above the ground and were baited — from 2.5 to 4.5 m of distance from the camera — with corn to increase the potential of feral pigs being captured in photos (Meek et al., 2014). Cameras were set to take up to three pictures per minute. We checked the cameras every 10 days to change batteries and SD cards, as well as ensure proper functioning and baiting. We used a period of one day as a sampling occasion. The overall sampling period was 66 days starting on April 9^{th} 2014. To aid in the identification, we constructed a reference library for camera-trapping images (Supplement S1) highlighting the key features for identification using colouration patterns or natural marks and showing the individuals from several different angles (front, back, left and right sides; see Fig. 1). We

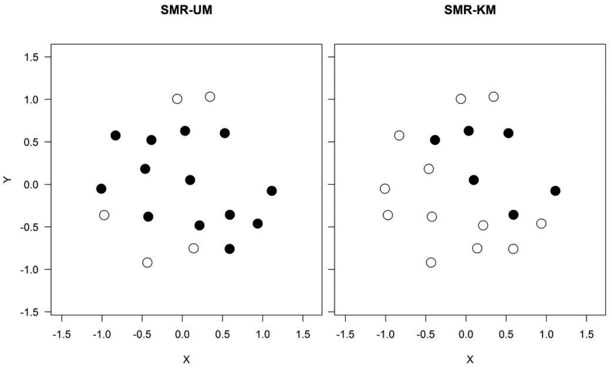

Figure 2 – Spatial location of traps with captures of marked animals (fill points) in Spatial Mark-Resight models for an unknown number of marked individuals (SMR-UM) (left) and Spatial Mark-Resight models for a known number of marked individuals (SMR-KM) (right).

Table 1 – Posterior summary statistics for Spatial Mark-Resight models for an unknown number of marked individuals (SMR-UM) and Spatial Mark-Resight models for a known number of marked individuals (SMR-KM) for feral pigs in the study area.

	SMR-UM		SMR-KM	
Parameter	**Mean±SD**	**q2.5–q97.5**	**Mean±SD**	**q2.5–q97.5**
N	336.62±77.80	206.00–508.00	160.98±27.63	113.00–220.00
Nu	303.62±77.80	173.00–475.00	147.98±27.63	99.00–207.00
D	13.27±3.07	8.12–20.02	12.87±2.21	8.96–17.59
lam0 (λ_0)	0.05±0.01	0.04–0.07	0.22±0.05	0.15–0.33
psi (ψ)	0.20±0.05	0.11–0.32	0.19±0.04	0.12–0.27
sigma (σ)	0.38±0.01	0.32–0.45	0.23±0.02	0.21–0.27
S	2536.9 ha		1244.7 ha	

Sigma (σ: Gaussian scale parameter) and *lam0* (λ_0: baseline capture probability) are the shared parameters for the analyses for recognisable and unidentifiable individuals in each model; *psi* (ψ) is the data augmentation parameter; *D* denotes the density (individuals/km^2) in the state space, *Nu* is the total number of unmarked animals, and *N* represents the total number of animals in the state space (*S*).

reviewed all images and recorded in a database the date, time, camera site, number of individuals observed, and the detection of the recognisable individuals. We employed a minimum time interval between consecutive pictures of 15 min, considered as independent events for analytical purposes. In those cases where several animals were captured in a picture, a different event was considered for each individual.

Spatial mark-resight analyses

The density of feral pigs was estimated by applying an SMR model. This spatially explicit approach can be used when part of the population is marked/recognisable and can be identified upon recapture (m), while the unmarked portion (U) remains unidentifiable, with the total population calculated as $N=m+U$. For the recognisable animals, we obtained 3D histories of individual spatially-explicit encounters (individual-traps-days), similar to those in a SCR study (Royle et al., 2014). For the unmarked portion of the population, we used camera-trapping data and occasions (η_{ik}) as reduced information of "latent" encounter 2D (traps-days) histories of individuals as accumulated counts ($\eta_{ik} = \Sigma y_{ujk}$). We assumed that the detections in each camera trap were spatially correlated with the density of the individual's activity centres (Chandler and Royle, 2013).

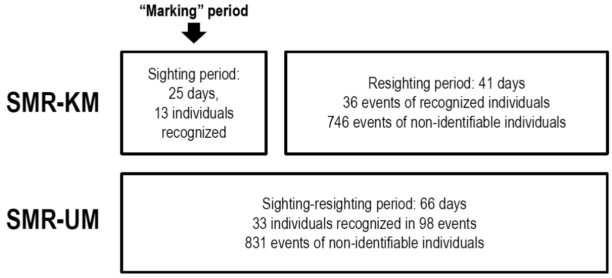

Figure 3 – Scheme of Spatial Mark-Resight models for an unknown number of marked individuals (SMR-UM) and Spatial Mark-Resight models for a known number of marked individuals (SMR-KM).

The same process in both marked and unmarked portions of the population was assumed, sharing the parameters sigma (σ: Gaussian scale parameter that determines the rate of decrease in detection probability between activity centres and traps) and lambda0 (λ_0: baseline probability of encounter) (Royle et al., 2014). Every individual i therefore has its own activity centre s_i and all activity centres are distributed across the state space (S) — defined as the area that includes the resighting grid and is sufficiently sizable to include all individuals potentially exposed to the survey. The position of the camera j is x_j, and the encounter histories for each recognisable individual i trapped by camera j on the occasion k is y_{ijk}, which is an array [i, j, k]. The number of times that an individual i was located by camera j has a Poisson distribution (i.e., multiple captures can occur by the same camera trap) with a mean λ_{ijk}, $y \sim Poisson(\lambda_{ijk})$. The link function between the location of camera traps and the activity centres follows a half-normal distribution: $\lambda_{ij} = \lambda_0 \times \exp(d_{ij}^2/2\sigma^2)$ (Royle et al., 2014), where d_{ij} is the distance between the activity centre for each individual s_i and the camera x_j, and λ_0 is the baseline probability of an encounter. The data model for the unmarked population also has a Poisson distribution, but in accumulated counts: $\sum_{k=1}^{K} n_{jk} \sim Poisson(K \times \lambda_0 \times \sum_{i=1}^{N} \exp(d_{ij}^2/2\sigma^2))$.

The total number of activity centres for unmarked individuals (U) was estimated in the model by applying the augmentation data approach (Royle et al., 2014) and by adding M potential individuals with all zero encounter histories. S was generated by buffering a distance function of λ_0 and σ from the trap array (Sollmann et al., 2013; Royle et al., 2014). Density was estimated by dividing the sum of the number of activity centres ($m+U$) by the total area of S. We assumed that recognisable feral pigs were a random sample from S because they were sighted throughout the extent of the trap arrays (see Fig. 2).

We used two different analytical approaches (Royle et al., 2014): 1) *SMR for an unknown number of marked individuals* (SMR-UM), using the 3D capture history for all recognisable individuals, and the latent 2D capture history for unmarked individuals throughout the period. 2) *SMR for a known number of marked individuals* (SMR-KM), dividing the sampling occasions into two periods: the sighting and the resighting periods (Fig. 3).

The sighting period should be long enough to recognise a set of individuals (m). We used the 3D encounter histories of the recognised animals and the latent 2D capture histories for non-recognised individuals throughout the resighting period. The first approach is useful when working with species with natural marks that make animals individually recognisable, such as feral pigs. However, not all species have such marks. To simulate the ability of SMR to work with species without natural marks (e.g. wild boar), we used a second approach that simulates the "capture and tagging" of a small sample m of the individuals in the population before the resighting period, and we compare the results using those procedures. For each approach, we calculated S because the number of marked individuals does not change with S as it does in SCR (Royle et al., 2014). Finally, the effort required and cost associated with each task involved in these sampling protocols, from camera acquisition to data analyses, were quantified in order to provide an estimate of the cost-effectiveness of the approaches.

Feral pigs are not a strictly territorial species (e.g. Hone, 2015). We hypothesised that differences in σ between SMR-UM and SMR-KM can be obtained due to the transient movement of the animals, which should be higher with SMR-UM due to the higher number of occasions. Given the relevance of σ to define S, we carried out a decomposition of σ using the SCR-Transience code from Royle et al. (2016), only with

Table 2 – Posterior summary statistics for parameters sigma for the Spatial Capture-Recapture allowing Markovian transience/dispersal for marked portion of the population.

Parameter	Mean±SD	q2.5%	q97.5%
sigma.rw (σ_{rw})	0.199±0.032	0.134	0.260
sigma.scr (σ_{scr})	0.224±0.034	0.165	0.299

Sigma.rw (σ_{rw}) is the random walk parameter generated by Markovian transience or dispersal, and *sigma.scr* (σ_{scr}) is the Gaussian scale parameter, related to the movements in the vicinity of the activity centre.

Table 3 – Analysis of sampling effort and associated cost of the different tasks carried out in the survey, including equipment and the tasks carried out to obtain information (field time) and processing of the data (setting data). Total costs for Spatial Mark-Resight models for known number of marked individuals (SMR-KM) and Spatial Mark-Resight models for unknown number of marked individuals (SMR-UM) are reported. We detailed the number of hours in camera checking (each 10 days) and the number of hours making a database and identifying the individuals.

Concept	Units	Unitary cost (€)	Total (€) SMR-KM	Total (€) SMR-UM
Equipment (camera traps)	18	180	3240	3240
Field time (hours)				
Camera installation and removal	32	20	640	640
Cameras checking (hours)	80; 130	20	1600	2600
Processing camera trap data (hours)	192; 375	20	3840	7500
Analysing data (hours)	42	45	1890	1890
		TOTAL	11210	15870

the recognised individuals. Two components of σ can be segregated: the "static" Gaussian scale parameter, related to the movements in the vicinity of the activity centre (σ_{scr}) and the random walk parameter generated by Markovian transience or dispersal (σ_{rw}).

We implemented these models in a Bayesian framework using Nimble 0.6 (NIMBLE Development Team, 2015; De Valpine et al., 2016) and R 3.3.1 (The R Development Core Team, 2017). For each analytical approach, we ran at least three chains of the MCMC sampler with 50000 iterations and burn-in 1000 iterations each. We checked for chain convergence by calculating the Gelman-Rubin statistic R-hat (Gelman et al., 2013). Values below 1.1 indicated convergence. Model specifications in R+Nimble are shown in Supplement S2. The code and datasets used in the analysis are available on request to the authors.

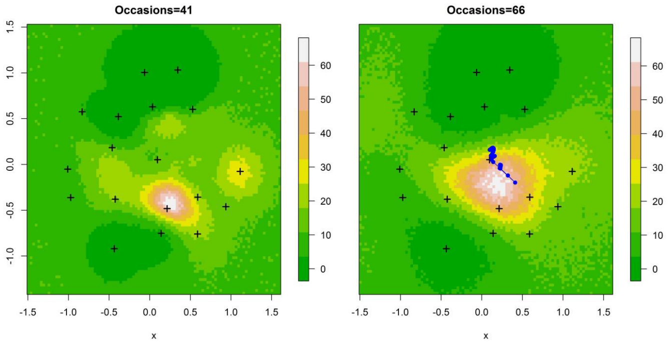

Figure 4 – Posterior probability distribution of the activity centre for feral pigs (individuals/km^2) based on Spatial Mark-Resight models for a known number of marked individuals (occasions=41) and Spatial Mark-Resight models for an unknown number of marked individuals (occasions=66) and movement trajectory of individual 14 throughout the period.

Results

All the cameras were operative for the entire study period. We obtained similar feral pig densities with SMR-UM and SMR-KM approaches. For the SMR-UM approach, the sampling effort was 1188 effective trap-days with a total number of independent capture events of 929 (a trap success of 78.19 pigs per 100 trap-days). Thirty-three animals were distinguished by means of singular colouration patterns or natural marks in 98 events. The other detections (831 independent events) were of unidentifiable pigs. Applying the SMR-UM approach, we estimated a feral pig density of 13.27 pigs/km^2 (SD=3.06; 8.12–20.02 95% BCI; 21% CV) (Tab. 1). We found poor mixing for σ_{rw} in the SCR-Transience model after running 3 chains of 750000 iterations. The difference in σ between approaches is due to the transience movement (Tabs. 1 and 2, Fig. 4).

Following the SMR-KM approach, during the sighting period (25 days) we individualised 13 individuals. Subsequently, in the re-sighting period (41 days), the total number of independent capture events was 782 (a trap success of 105.96 pigs per 100 trap-days), 36 and 746 events for "marked" and unidentifiable pigs, respectively. Using the SMR-KM approach, we obtained a density estimate of 12.87 pigs/km^2 (SD=2.20; 8.96–17.59 95% BCI; 17% CV) (1). Supplement S3 shows the derivations of S from σ for both SMR-KM and SMR-UM approaches.

The cost to estimate feral pig density was 11210 € (27.01 €/ha) for SMR-KM and 15870 € (38.24 €/ha) for SMR-UM (3). Once the equipment is amortized, the budget can be substantially reduced by 28.9% and 20.4%, for SMR-KM and SMR-UM, respectively. The most time-consuming task was the processing of camera trap data, which accounted for 34.2% and 47.2% of the total budget for SMR-KM and SMR-UM, respectively. The cheapest task was the data analysis (16.8% and 11.9% of the total budget for SMR-KM and SMR-UM, respectively).

Discussion

In this study, we describe a feasible and cost-effective sampling protocol to monitor feral pig population size. The density for this cryptic and elusive species, in which not all animals are individually identifiable, was addressed by identifying only a part of the population and using SMR models. Two approaches were compared: SMR for an unknown number of marked individuals, and SMR for a known number of marked individuals. The latter is equivalent to capturing and marking some individuals in a population, and was aimed to simulate a study with species without recognisable individuals (e.g. wild boar). The results of both approaches were equivalent, suggesting the ability of both SMR models to estimate reliable and precise population densities with fewer recognisable/marked individuals.

The density obtained in this study (approx. 13 ind/km^2; see Tab. 1) is within the ranges obtained for other feral pig populations worldwide (Tab. 4). Wildlife monitoring programmes are designed to detect differences in population size over time (i.e., population trends) and to establish effective management actions, such as defining adequate extraction quotas in the case of game species. The usefulness of a given monitoring programme therefore depends on the precision of survey estimates (Barnes, 2002), which is expressed with the coefficient of variation. From a management point of view, it is desirable to have as small a coefficient of variation as possible. However, high sampling efforts

Table 4 – Feral pig population density reported in previous studies.

Density - Study area	Method	Reference
6–14 ind/km^2 - Hawaiian Islands	Snaring	Anderson and Stone, 1993
7 ind/km^2 - Santa Cruz Island, California	Shooting / trapping	Parkes et al., 2010
3–8/12–43 ind/km^2 - New Zealand	Shooting	McIlroy, 1989
3–17 ind/km^2 - Galapagos, Ecuador	Shooting	Coblentz and Baber, 1987
27–47 ind/km^2 - Malaysia	Distance sampling	Ickes, 2001
10–20 ind/km^2 - South Island, New Zealand	Annual harvest	Clarke and Dzieciolowski, 1991

are required to obtain the desired coefficients of variation and accuracy (Taylor and Gerrodette, 1993; Nuno et al., 2013). As the coefficient of variation is clearly dependent on the number of occasions (related to the size of the population, the number of devices and occasions) and the number of recognisable individuals in the population, the more recognisable individuals, the more accurate and precise the estimates will be. In this study, we recognised approximately 10% of the individuals in S. According to the coefficient of variation obtained (17–21%), our sampling protocol was able to produce adequate management-oriented estimations of population size (White et al., 1982). The protocol described is, therefore, useful for deriving precise estimations in most contexts for these species, including wild boar, as was simulated with SMR-KM.

If we increase the number of occasions, σ will vary. We observed differences in the estimates for σ between SMR-UM and SMR-KM, which influenced the calculation of S (see Supplement S3). The reason for such differences may be due to the longer timeframe considered in the SMR-UM approach (66 days) since, considering feral pigs are not a strictly territorial species (Hone, 2015), some individuals may have dispersed or exhibited greater transience over the sampling period compared to the shorter timeframe considered for SMR-KM (41 days). Thus, their individual activity centres did not remain spatially stationary during the sampling period (Royle et al., 2016). Despite the poor mixing for σ_{rw}, our hypothesis is supported by the fact that the value for Gaussian σ obtained in SCR-Transience (σ_{scr}=0.22) was very close to the value for σ in SMR-KM (σ=0.23), and the difference in σ between SMR-UM and SMR-KM is due to the transient movements (Tab. 2 and Fig. 4).

A protocol based on camera trapping and SMR models involves two different phases of work, namely obtaining the data and then processing the data, deriving density information (Tab. 3). Camera trapping is a non-intrusive and cost-effective strategy with which to obtain data in wildlife monitoring programmes (Silveira et al., 2003). Devices are now cheaper and can operate for long periods, and the effort required to obtain information is notably reduced (Rovero et al., 2013). On the other hand, processing the information is a time-consuming task that exponentially increases with the density of the species and with sampling designs in which the probability of species detection is maximised by using attractants and/or monitoring highly used resources. However, the growing advances in data processing and computer-assisted photographic identification allow for the automation of deriving independent capture events from a set of photos (Morrison et al., 2016). Although the costs associated with this type of survey may be high at first, the use of innovative technologies may notably reduce costs in the future. In addition, some analytical approaches can be used to optimise the cost-effectiveness of the sampling protocol. For instance, in this study we showed that SMR-KM notably reduces the cost of the SMR-UM sampling protocol (29.4%) without compromising either precision or accuracy of the estimates.

The sampling protocol described here is a feasible and cost-effective tool for feral pig monitoring across different contexts. By recognising/tagging a small number of individuals in the population, the SMR-KM models provided precise estimations for species without identifiable individuals, including those with transience/dispersal movements. Thus, this sampling protocol is a promising approach for population estimations of related species such as the wild boar, for which there are currently no feasible and harmonised methodologies (Gortázar et al., 2015).

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Supplement S1 Reference library.

Supplement S2 Spatial Mark-Resight code in Nimble.

Supplement S3 Derivations of S from σ for both Spatial Mark-Resight models for an unknown number of marked individuals (SMR-UM) and Spatial Mark-Resight models for a known number of marked individuals (SMR-KM) approaches.