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RESEARCH PAPER

Combining N-mixture models with ecological niche modeling supplies a low-cost and fast procedure for estimating population size in remote areas

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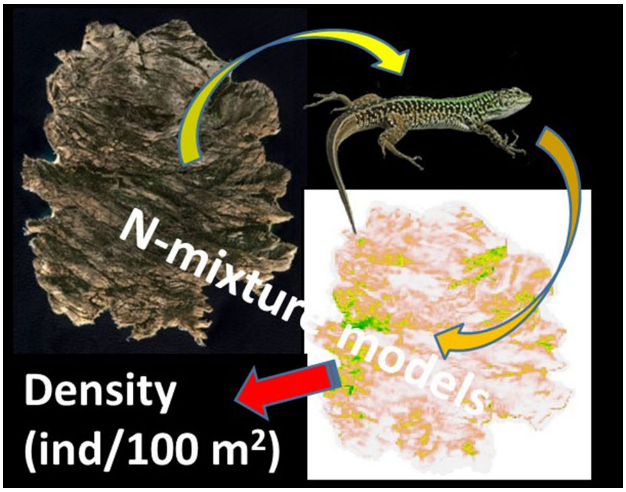
Abstract

Monitoring population changes and trends is a central task in conservation. However, obtaining detailed information for wide and low accessible areas, such as remote islands, is challenging, and cannot be achieved with conventional approaches, such as capture–mark–recapture protocols (CMR). In this paper, we show that combining N-mixture models with ecological niche modeling allows assessing reliable estimates of population size over large target areas on short time intervals. We used it to estimate the population size of a subspecies of the Italian wall lizards (*Podarcis siculus calabresiae*) endemic to the Island of Montecristo (10.39 km^2 in surface). During a single week, we first generated a niche model of the species based on satellite images sampled few days before sampling. Then, we estimated lizard abundance through Bayesian N-mixture models on repeated counts ($n = 3$) along transects ($n = 6$), settled in different areas of habitat suitability defined on the basis of the niche model. Finally, we estimated in approximately 20.000 the total number of lizards living in the Island by extrapolating the values computed on transects to the areas of the islands with the same suitability estimated by the niche model. The procedure can be easily repeated allowing monitoring the status of conservation of the species in the island of Montecristo. More in general, this procedure has the potential to be applied to monitor any other species of conservation interest in remote areas whenever detailed satellite images are available.

Graphical Abstract



Keywords Population estimate · N-mixture models · Ecological niche models · Remote islands

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1 Introduction

Monitoring of populations is a central task in conservation, as well as management of animal populations. Therefore, it is first mandatory to assess the conservation status of populations and species (Yoccoz et al. 2001; Reynolds et al. 2011; Ficetola et al. 2018). Second, it allows to highlight conservation priorities as well as to assess the efficiency of undertaken protection measures (Ficetola et al. 2021). Third, monitoring is also crucial to identify threats in order to deliver effective managing actions to deal with it (Nichols and Williams 2006; Purse and Golding 2015). Monitoring programs are particularly important in islands, where endemic species as well as endemic lineages of a species are particularly sensible to stochastic or directional threats than sister taxa occurring in the mainland (IUCN Standards and Petitions 2016; Ficetola et al. 2021).

Accurate information on population size is a central point to any monitoring programs. Population size estimates is one of the most important indicators on the conservation status of species, and is commonly used as a metric to define the conservation status of species (e.g., IUCN assessment and categorization). Despite its importance, obtaining detailed information on population abundances remains a difficult task, primarily for imperfect detection (Seber 1982; Williams et al. 2002). Assessing information on population size can be further limited by low accessibility, high costs, and low feasibility, particularly in islands, especially in small and remote ones (Ficetola et al. 2013; Yang et al. 2014; Marta et al. 2019). Consequently, species have received much less attention in islands than in mainland (Lamoreux et al. 2006; Rosauer and Jetz, 2015), and in general few information are available on population density in island populations, even for common and not endangered species.

Capture–mark–recapture (CMR) protocols are probably the most robust techniques for estimating population abundance, but are costly in term of time and field work. Namely, CMR protocols suffer reduced applicability when it is necessary obtaining population's density estimates over short time intervals on large areas (Costa et al. 2020). Such a kind of environmental constraints are particularly severe in islands (see for example, Ficetola et al. 2021). N-mixture models do not require capture, handling and marking, and are probably among the most cost-effective methods for estimating population size (Kéry ad Royle 2015; Ficetola et al. 2018; Costa et al. 2020; Rosa et al. 2022), having the potential to be applied in estimating population abundance in remote and low accessible areas. However, binomial N-mixture models have been recently disputed since their reliability decreases when parametric assumptions are not completely satisfied (Barker et al. 2018; Knape et al. 2018).

Ecological Niche Models (ENMs) are second tools which has proved particularly effective in the study of ecology and species distribution (Guisan and Thuiller 2005; Guisan et al. 2013). ENMs are computer algorithms used to predict the distribution of a species across geographic space based on using environmental data. They are largely applied in conservation biology to understand how environmental conditions influence the occurrence or abundance of a species, and predict species response to environmental changes purposes. ENMs ultimately are maps reporting the (environmental) suitability for a target species in a target area.

N-mixture models have already applied for large-scale abundance estimation in several taxa (Kéry and Royle 2015), including salamanders (Peterman and Semlitsch 2013) and lizards (Rosa et al. 2022), but have never been used in combination with ENM. Furthermore, no previous study has analyzed the application of N-mixture models on a short timeframe due to intrinsic difficulty of sampling individuals on remote and low accessible areas. In this paper, we combined N-mixture models with ENMs in order to obtain a picture of the population density of a model species over short time intervals (a week) on a large area with reduced accessibility (a remote island). The main idea is to split the study area into zones with increasing suitability and to perform population estimate through N-mixture models in each of them. This way, we should be able to estimate the entire population of the island, by extrapolating the estimates obtained by field sampling to the corresponding suitability zone.

As study area we selected the Island of Montecristo, a mountain island (645 m in height, and 10.39 km^2 in surface) with several rocky overhangs overlooking the sea and consisting almost exclusively of intrusive rock (granodiorite). The island is a Natural State Reserve (without public access) and belongs to the Arcipelago Toscano National Park.

The model species is the Italian wall lizard (*Podarcis siculus*), a small (50–70 mm in adult snout–vent length, SVL) diurnal lizard endemic to the Italian peninsula (Corti et al. 2011), with several different genetic lineages (Senczuk et al. 2017). The species occurs in a high variety of habitats, but it prefers open habitats, with tall vegetation and with high levels of insolation (Corti et al. 2011). The thermal optimum occurs between 33 and 36 °C (Avery 1978; Corti et al. 2011), and the activity is fundamentally diurnal. Several subspecies have been described, most of them from insular systems (Corti et al. 2011), even if not always supported by molecular analyses (Senczuk et al. 2017). In particular, the population of the island of Montecristo has long been recognized as a subspecies (*P. s. calabresiae*) endemic to the island (Taddei 1949). However, to date, no information is available on density and potential distribution of this subspecies on the island.

The objective of this study was, therefore, to estimate the whole number of Italian wall lizards occurring on the Montecristo Island during spring, 2021.

2 Methods

2.1 Data sampling

Field work on the Montecristo was carried out on between 16 and 22 May, 2021. We defined six linear transects (mean ± sd: 348 m ± 94 m, 240–490 m), two each within the three main habitats of the island, i.e., the stream bed, dense shrub, and open and rocky shrub. Lizards were not captured, but only counted on sight. Transects were run by two people at constant speed who counted all lizards observed within 10 m distance from the transect. The location of each individual was taken using a GPS, and the starting hour, track and time spent for each survey was recorded. Each transect was repeated three times in three different days, between 9:00 and 17:00, with constant meteorological conditions (similar temperature; no rain; low or absent wind). We also performed additional not standardized surveys in the west portion of the island in order to collect data on the occurrence of the species in all habitats available in the island.

2.2 Population size estimation

Population size was estimated using Poisson N-mixture models for closed population (Royle 2004; Ficetola et al. 2018) on the data set collected through each repeated transect. To help stabilizing the numerical optimization algorithm, we standardized all the covariates. Detection was modeled in function of track (meters), hour and survey duration (minutes), whereas abundance was modeled in function of the habitat only. We defined three main habitats (i.e., stream bed, dense bush, and open bush), corresponding to the three main zones of habitat suitability according to the output of niche modeling (see next sections).

It is general recognized that a low number of spatial replicates provide unreliable estimates and identifiability problems (Dennis et al. 2015; Kéry and Royle 2015), although some applications of N-mixture models based on few spatial replicates are present in the literature (Ficetola et al. 2018, 2021; Kidwai et al. 2019). However, fitting the model within a Bayesian framework still provides unbiased estimates even with low number of replicates since it has the great advantage of being exact for any sample size (Kéry and Royle 2015), and supplies the possibility of checking model adequacy with posterior predictive checks (Conn et al. 2018). Therefore, models for lizards were fit in the Bayesian analytical framework available through the R (v. 3.6.3) package R2jags (Su and Yajima 2015), which uses the samplers implemented in JAGS 4.3.0. Since lizards were detected in every survey, we did not include into the model a layer of hierarchy accounting for zero-inflation. By contrast, to account for over-dispersion, we included a random survey effect in the observation model. Uninformative normal priors ($\mu = 0$ and $\sigma = 0.0001$) were used for model's coefficients, and a uniform prior ($a = 0$ and $b = 3$) was used for the random survey effect (σ). Three independent chains were run, with 340,000 iterations each. The first 40,000 values were discarded, and thinning was set to 10 in order to break within-chain autocorrelation. Convergence was checked via visual inspection of results, and violations of one or more model assumptions were analyzed though a goodness-of-fit test aimed to assess if simulated data differ from the real data in some systematic way (Conn et al. 2018). Results from the posterior distribution are reported as the half sample mode (HSM, Bickel and Frühwirth 2006) with 95% and 50% highest density intervals (HDI_{95}, Meredith and Kruschke 2018).

2.3 Ecological niche models

In order to obtain a fine-grained model of the ecological niche of the species, we used a Sentinel-2 satellite image of the island taken on 13th May, 2021. The Sentinel-2 satellites each carry a single multi-spectral instrument with 13 spectral channels in the visible/near infrared and short wave infrared spectral range. Spectral images provide geographical information specifically designed for applications in land monitoring, including data on land cover and variables related to such topics as vegetation state and the water cycle. In our analyses, we used all the 13 spectral bands (SBs) as variables to model the niche, and the optical image (i.e., the orthophoto) to interpret the model and identify the preferred environments by the species. Images were cut out on the study area, and map resolution was set to 25 m. Presence data were resolved to the same spatial scale of SBs and duplicated records within grid cells were deleted, leading to a sample of 208 presence records. We used presence-only modeling method as implemented in Maxent 3.3.3.k software (Phillips et al. 2006) by using the package "dismo" (Hijmans et al. 2017). Models were validated using cross-folding: the set of occurrences was divided at random into five equal-sized subsets, each having the same distribution of presence/background samples; in turns, four subsets were used for model generation and the fifth used for testing. Discriminating performance was estimated using AUC (Area Under the receiver operating characteristics Curve), which is a threshold-independent measure of the ability of the model to discriminate between background and presence sites (Liu et al. 2005). However, the AUC did not take into account spatial autocorrelation due to both cross-validation procedure (i.e., spatial sorting bias; Segurado et al. 2006; Veloz 2009) or geographical clustering of the presence points

(Hijmans 2012). Following Hijmans (2012), we therefore also computed three additional AUCs, accounting for spatial autocorrelation (pwdAUC), geographical clustering (null model AUC or nAUC), and the calibrated AUC (cAUC) by the combination of pwdAUC and nAUC. Additional details on AUC estimation are provided elsewhere (Sacchi et al. 2022).

3 Results

3.1 Population size

During the 18 repeated counts, we obtained 176 detections of adult lizards in 6 replicated transects, with a minimum of 4 and a maximum of 32 for single survey. On average, we observed 15.4 lizards/man-hour of survey.

The Poisson model with over-dispersion had a good fit, since simulated and observed data were very similar (goodness-of-fit test: $P_{\text{simulated>fitted}} = 0.478$). The observational model showed that both the hour and survey duration affected the detection probability, since the posterior probability distributions of the corresponding beta coefficients largely deviated from zero ($P_{\beta<0} = 0.979$, HDI_{95}: − 1.56, − 0.11; $P_{\beta>0} = 0.966$, HDI_{95}: 0.06, 2.20, respectively), By contrast, any effect was not evident for the track ($P_{\beta>0} = 0.506$, HDI_{95}: − 0.81, 0.61). In detail, the detection probability was highest early in the morning, and increased with sampling effort. The Bayes estimates indicated population size between 5 and 38 individuals/site (Table 1), but the model showed that the abundance differed among habitats (Table 1). Indeed, lizards were more abundant in the stream bed with respect to both open ($P_{\text{stream>open}} = 0.999$, $\text{HDM}_{\text{difference}} = 1.46$; HDI_{95}: 0.91–2.10) and dense ($P_{\text{stream>dense}} = 0.999$, $\text{HDM}_{\text{difference}} = 1.59$; HDI_{95}: 1.01–2.24), while any difference did not occur between open and dense shrubs ($P_{\text{open>dense}} = 0.618$, $\text{HDM}_{\text{difference}} = -0.12$; HDI_{95}: − 0.79–0.53).

Table 1 Bayesian estimates of the abundance of Italian wall lizards in each sampling site

Transect	Nmax	HDM (HDI_{95})	Area (m^2)	Density (ind/100 m^2)
Dense shrub 1	5	5 (5–26)	1790	0.28 (0.28–1.45)
Dense shrub 2	11	11 (11–32)	1221	0.90 (0.90–2.62)
Open shrub 1	5	7 (5–28)	1543	0.45 (0.32–1.81)
Open shrub 2	7	8 (7–29)	1001	0.80 (0.70–2.90)
Stream bed 1	22	33 (22–157)	3017	1.09 (0.73–5.20)
Stream bed 2	32	38 (32–156)	3529	1.08 (0.91–4.42)

Nmax is the maximum sights over the three replicates

3.2 Habitat suitability

The ENM obtained through Maxent obtained an AUC value of 0.91 ± 0.02, while sensitivity and specificity were (mean ± SD) 0.846 ± 0.043 and 0.852 ± 0.016, respectively. Overall, the model was able to capture the relationship between the presence of lizards and the environment. The nAUC did not deviate from 0.50 (0.56 ± 0.03), suggesting that spatial autocorrelation due to the coordinates alone was negligible. By contrast, the pwdAUC value (0.55 ± 0.04) was about 39% lower than AUC, suggesting that spatial autocorrelation in SBs causes an overestimate of the ability of the model to discriminate presence/absence of morphs when using training AUC. Given the lack of any effect of spatial correlation alone, the cAUC value (0.48 ± 0.04), supplied the same conclusions of pwdAUC.

The projection of the model onto the orthophoto of the island of Montecristo (Fig. 1a, b) showed that most suitable areas for the Italian wall lizards correspond to the valley floors and the vegetated slopes immediately associated with them. Elevated rocky areas, with scarce vegetation appeared, by contrasts, low suitable for the species. In general, the occurrence of the species was predicted highest in the area were water and wet environment are maximally available.

Among the 13 SBs, the B8A, B12, B11, and B06 supplied the highest percentage contributions to the model, but also the B08 and B04 had a certain effect. The combination of B8A, B12, and B11 pointed in particular on stream beds and small water collections of the island (Fig. 1c). The combination of the B12, B04 and B8A relays with the Short-Wave-Infra-Red (SWIR) bands (Fig. 1d), which are commonly used for monitoring open water bodies, whereas the combination of B8A and B11 is commonly used as moisture index (Fig. 1e). Finally, the composition of the B08 and B04 generate the Normalized Difference Vegetation Index (NDVI, Fig. 1f), which is commonly used as an indicator of the greenness of biomes.

We cut the habitat suitability map according to cell scores estimated by Maxent. Cells scored with low than 0.20 were regarded as not suitable at all for the species. They represented the white to grey areas in the suitability map (Fig. 1b) and covered the 77.9% of the whole island. Cells with a score between 0.20 and 0.40 were regarded as low suitable for the species and corresponded to the pale-brown regions of the suitability map (Fig. 1b), covering the 14.7% of the whole island. This portion of the island included open and dense shrubs. Finally, cells with a score higher than 0.40 were considered highly suitable for the species, and corresponded to the yellow-green portions of the suitability map (Fig. 1b), being only the 7.4% of the whole island.

Basing on the estimates we obtained through N-mixture models, we computed an overall estimate of the number of lizards inhabiting the island of Montecristo by assigning the

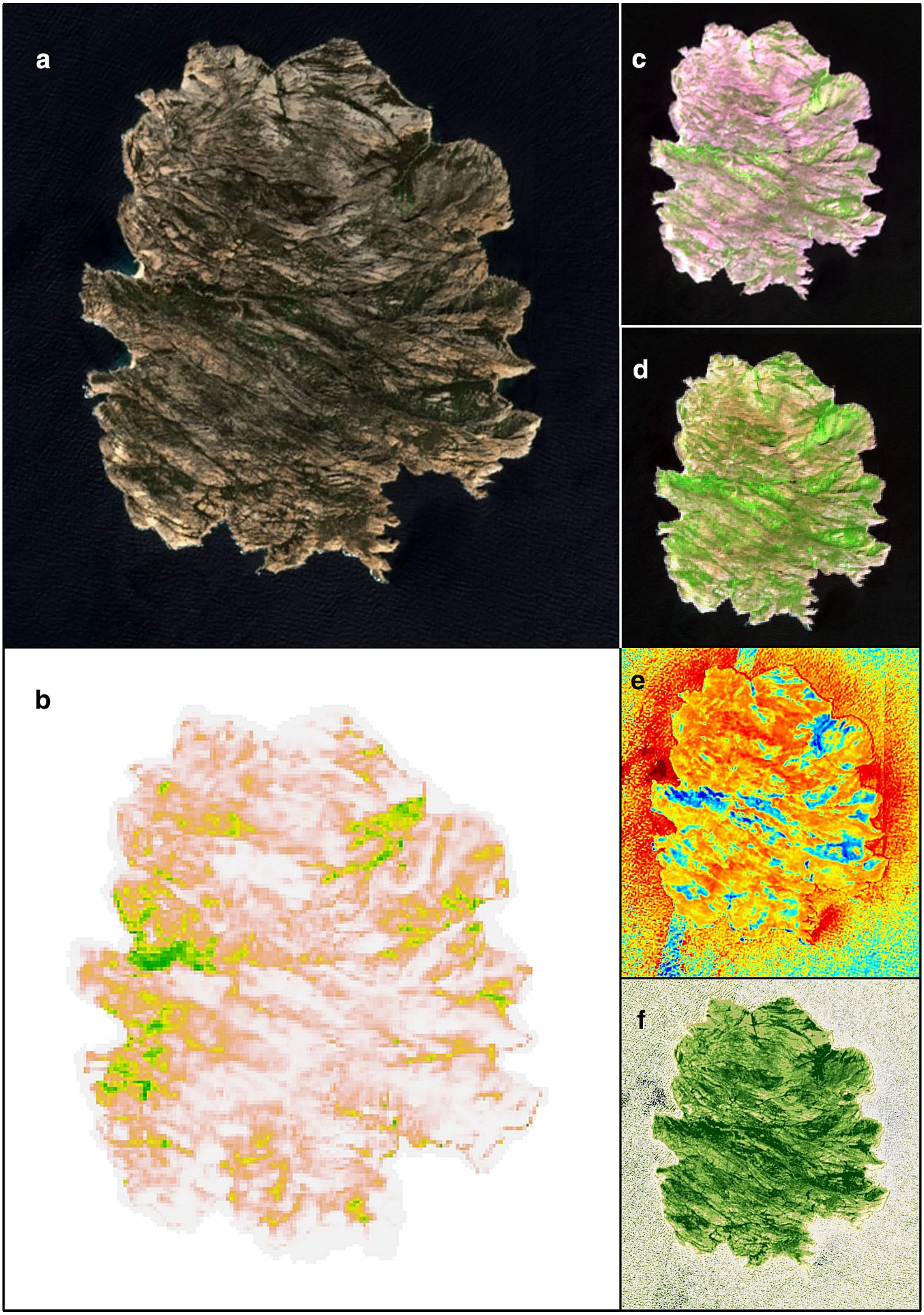

Fig. 1 Ecological niche models for Italian wall lizards at Montecristo Island; **a** orthophoto of the island taken at 17/05/2021; **b** suitability map for the species based on the 13 spectral bands images of the island taken at 17/05/2021; **c**–**f** spectral images in false colors of the island obtained by combination of spectral bands: c) image obtained by the overlap of the B8A, B11 and B12 spectral bands; **d** SWIR image obtained by the combination of the B08, B12, and B04 spectral bands; **e** moisture index obtained by the combination of the B8a and B11 spectral bands; **f** NDVI image (greenness of vegetation) obtained by the combination of the B08 and B04 spectral bands

mean values of lizard densities estimated for open and dense shrubs to the low suitable cells, and the mean value of lizard densities estimated for stream beds to the high suitable cells (zero lizards were assigned to not suitable cells). This approach leads to an estimate (HDM) of 19,266 individuals (HDI_{50}: 17,378–23,313; HDI_{95}: 16,053–73,519).

4 Discussion

N-mixture models are a reliable procedure for obtaining population density estimates when robust CMR protocols are not applicable (Ficetola et al. 2018; Costa et al. 2020). However, N-mixture models also have limited application when the target area is too large or characterized by low accessibility, high costs, and low feasibility. Indeed, with increasing the size of the target area (as well as being it less accessible), the number of transects required for covering it increases and, at the same time, the number of replicates for each transect decreases reducing the assessment of reliable estimates. In summary, in larger (or low accessible) target areas N-mixture models will suffer reduced applicability as CMR protocols do for small study areas. In this paper, we showed that combining N-mixture model protocols with ENMs offers a reliable short cut for obtaining population size estimates in large and low accessible target areas. A further point of merit of our approach is the fact that we performed field sampling in only one week, and we used satellite images collected exactly during the field work period. This allows obtaining a picture of the state of the population in a given period, in a way that, by replicating the sampling (and the modeling), it is possible to follow population trend in detail, and, consequently, to identify threats early enough to deliver effective managing action to deal with it.

Our study case, with the Italian wall lizard on the island of Montecristo, is a good example of the kind of information that we can obtain by combining N-mixture models with ENMs, other than the estimation of the population size living on the islands. First, we estimated the total number of lizards living on the island as approximately 20.000 in less than 25% of the island, that is for its majority rocky and unsuitable for the species. The mean density within the suitable portion of the island was approximately 1 individual/100 m^2. This is the first study reporting population density estimates for small lacertid lizards in a very large area, notably the whole population inhabiting a small and remote island. Data on population size for lacertids still now published refer to very small areas, both because they involved CMR methods, or population size estimate was not the primary endpoint of the research (i.e., CMR methods were applied to study species breeding biology). Despite this, our estimates for the Italian wall lizard on the island of Montecristo are fully consistent with previous data reported on other lacertid species. Bayesian hierarchical distance sampling model have been used to estimate the individual density of the Common wall lizard (*Podarcis muralis*) in wooded habitats of Northern Italy (1–3 ha in size), supplying values between 0.14 and 0.47 individuals/100 m^2 (Rosa et al. 2022). Using CMR methods in a 0.52 ha study area in central France, the population density of the common wall lizard (*Podarcis muralis*) was estimated in 5.3 individuals/100 m^2 (Barbault and Mou 1988). In Spain on the contrary, using the same methods on a 0.27 ha plot, the density of adult Bocage's wall lizard (*P. bocagei*) was estimated between 2.8 and 6.9 individuals/100 m^2 (Galán 1999). Still in central Spain, the population density of the eyed lizard (*Timon lepidus*) in a 7 ha plot was estimated in 0.032 individuals/100 m^2 (Díaz et al. 2006). Again, using CMR in a small plot (0.25 ha), the population density of the Fitzinger's algyroides (*Algyroides fitzingeri*) in central Sardinia was estimated in less than 1 individual/100 m^2 (Capula et al. 2002).

Estimates for population density of lacertid lizards on large study area have been achieved, but not using CMR methods. For example, the population densities of three lacertid species, i.e., *P. siculus*, *P. muralis*, and *Lacerta bilineata*, have been obtained in two large areas (850 ha and 4696 ha) of Mediterranean central Italy through distance sampling, and ranged between 0.05 and 0.48 individuals/100 m^2 (Maura et al. 2011). In particular, values for *P. siculus* ranged from 0.05 to 0.24 individuals/100 m^2.

Previous studies aimed at estimating population density of lacertid lizards on islands involved only small islets around the main island, and did not used CMR methods. The approach in those cases based on repeated sampling without marking lizards, and multiplying the number of lizards estimated for spatial units (e.g., ha) and for the total surface of the isles. For example, using N-mixture model on the Capo Grosso peninsula (0.08 ha) of the island of Vulcano (Sicily), the population density of the endemic Eolian lizard (*P. raffonei*) resulted in 35 individuals/100 m^2 (Ficetola et al. 2018, 2021), which is the largest density reported for insular population of any lacertid species. Using distance sampling, the population density of the endangered Balearic lizard (*P. lilfordi*) inhabiting the coastal islets of Mallorca, Menorca and the Cabrera archipelago (Balearic Islands), was estimated on average in 15 individuals/100 m^2 (Pérez-Mellado et al. 2008).

All above studies well exemplify as all previous study on lacertid lizard supplied robust estimates of population density, which are limited to very small areas (with few exceptions), so have reduced application when management priorities have to be identified. This is because assessing the conservation status of populations needs accurate estimate of population size over large areas. Indeed, population size at range scale and population trends is among the most important criteria used by IUCN for the assessment of the conservation status of species. Similarly, the assessment of the species listed in the habitat directive by the European Union specifically requires periodic evaluation of the population trends at the largest possible scale. Even using N-mixture models as surrogate of CMR methods, such a kind of target cannot be easily fulfilled. Combining these protocols, namely the first one, with niche modeling (by using the more appropriate ecological information, such as satellite images), offer a powerful tool for estimating population density over large territories and with low time effort. Indeed, we were able to achieve a reliable information on the population consistence of a target species in less than one week of field work for an island large more than 10 km^2. This approach can be easily replicated in other areas and with other species, as all the data used in our case for estimating population density of the Italian wall lizards on Montecristo can be easily obtained for other areas.

However, population estimate is not the only information that can be gathered by combining N-mixture model with ENMs, since ecological information can be also obtained. Indeed, our data showed that the Italian wall lizards on the island occur in almost all available non-rocky habitats, but not with the same density. In dense or open shrubs and stream bed habitats, lizard presence is continuous, but its density, detectability and estimated densities do greatly vary (Table 1). Lizards were denser in the most humid microhabitats, characterized by canopy shade and, more importantly, by water presence, were more than three individuals/100 m^2 were estimates. These optimal habitats cover a very small portion of the island (approximately 7%), and, therefore, represent the focal areas for the management of the species. Research effort and early and mid-day hours are also important for maximizing observations and detectability of the species. Overall, comparing estimated densities among habitats, stream bed lizards were from two to three times more abundant than in the other two habitats. Elevated rocky areas, with scarce vegetation, appeared by contrasts less suitable for the species. This information, in association with population size, can be useful for monitoring the conservation status of the species on the island and, if the case, planning managing action for improve it.

European Union imposes to Member States accurate estimates of population status and trends for the species included in Annexes II, IV and V of the Habitats Directive, but obtaining this kind of data is expensive and time consuming and often estimates are based on very restricted studies that cannot be extrapolated for the whole species areal. We showed that combining N-mixture models with ecological niche modeling is a reliable and low-cost procedure to achieve data on population changes and trends in remote and low accessible areas, such islands. We think that our approach should be adopted as a standard method for reliable population estimates, in particular for species with limited distribution. Species with a large areal could be monitored according to this procedure, but transects covering many parts of the areal and all the main habitats should be accurately planned to ensure model reliability.

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Author contributions All the authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by all the authors. The first draft of the manuscript was written by RS, and all the authors commented on previous versions of the manuscript. All the authors read and approved the final manuscript.

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Availability of data and materials Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The Ministry of Education, University and Research (MIUR) provided all the authorizations for the study (Aut. Prot. PNM-0015024, 2005-17).

Consent to participate Not applicable.

Consent for publication Not applicable.

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