




Ecological niche models improve home range estimations

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Abstract

Home ranges in animals can be estimated by different methods like minimum convex polygons, characteristic hulls or kernels while correlative ecological niche models (ENMs) are commonly employed for forecasting species' ranges. However, ENMs can also model the distribution of individuals if environmental very high spatial resolution data are available. Indeed, remote sensing (RS) can provide images with pixel sizes of few centimetres. Here, we modelled the distribution of individual lizards (*Podarcis bocagei*) combining aerial-like photographs recorded with a compact camera and a matrix of temperature/humidity data-loggers to obtain several environmental layers with very high spatial resolution. We recorded lizards' positions in a 20 × 20 m mesocosm with a high precision GPS device (~10 cm of error), multiple times per day throughout the whole period of daily activity. We built an orthophoto map (pixels of 20 cm²) from camera pictures, a digital surface model, and a land-cover supervised classification map. We recreated climate-like variables by combining data-logger data. For each individual, we calculated the distance to males and females, excluding the focal lizard. We computed individual realized niche models with Bioclim, GAM, GLM, Maxent and random forest. Models attained a very high evaluation score in most cases. The most contributing variables were related to microclimate (isothermality, minimum temperature and humidity) and distance to conspecifics. Our very high spatial resolution models provided robust information on how space is used by each lizard. Correlative models can identify the most suitable areas inside the home range, similar to core areas estimated from kernel algorithms, but allowed better statistical inference. Overall, RS tools generated high-quality environmental data, and when combined with ENMs, improved the robustness of the predictions on spatial patterns of small terrestrial animals.

Introduction

Home range (Kie *et al.*, 2010; Powell & Mitchell, 2012) is the area where an individual organism lives, defined as 'the area over which the animal normally travels in food gathering, mating and caring for young' (Burt, 1943). Home ranges are not static but may vary in size and location among individuals, sex, age, season and species (Beest *et al.*, 2011; Sillero, Corti & Carretero, 2016). Home ranges are not used homogeneously: most individuals will present a preferred area (centres of activity or core areas), where the activity is developed with more intensity inside the home range, for example feeding, basking, reproduction and resting (Hayne, 1949). Thus, home ranges can be represented as a discrete surface (a polygon) or as a continuous one (an utilization distribution, i.e. the probability of an individual being within an area of its home range at any point in time) (Van Winkle, 1975; Anderson, 1982; Worton,

1987, 1989). Also, polygons can represent home range percentiles, and for instance, the 50 percentile can be interpreted as core area.

Over time, different methods have been developed to identify and estimate home ranges (Powell & Mitchell, 2012). The simplest one is the minimum convex polygon (MCP), which generates the smallest polygon containing all records or some proportion of them (e.g. 95%) (Rose, 1982). MCP with 50% of records can be used to estimate core areas. However, MCP results tend to overestimate home ranges, as they include areas never used by animals. More complex methods, such as local convex hull (Getz *et al.*, 2007) and characteristic hull polygons (Downs & Horner, 2009), allow concave edges, disjoint regions and holes. The utilization distribution of home ranges can be also estimated with kernel density estimators (KDE), a non-parametric estimator of the probability density function of a random variable (Fieberg, 2007). However, kernels require

some parameters like the grid size and bandwidth which are difficult to determine for some species (Row & Blouin-Demers, 2006).

All above-mentioned methods estimate the home range or its utilization distribution using exclusively a set of occurrence points. However, ecological niche models (Sillero, 2011; hereafter ENMs) statistically fit a continuous surface to a set of points and environmental variables. Instead of using individuals' locations, ENMs use species' presences (with or without absences) gathered from distribution atlases (e.g. Sillero *et al.*, 2014) or museum databases (e.g. Gaubert, Papes & Peterson, 2006). The output is an estimation of the presence probability or the habitat suitability for a given species in a certain region (Sillero, 2011). Some correlative algorithms, such as logistic regressions, need locations where the species occurs (presences), but also where it does not occur (absences). Other correlative algorithms, for example Maxent (Phillips, Anderson & Schapire, 2006), can be fed exclusively with species presences. However, ENMs can model not only species occurrences, but other point patterns such as records of individuals (Sillero & Gonçalves-Seco, 2014), road-killed individuals (Sillero, 2008), snake-bite occurrences (Yañez-Arenas *et al.*, 2014) or locations of bat casualties produced by windmills (Santos *et al.*, 2013).

To our knowledge, ENMs have never been used previously to estimate home ranges, probably due to the difficulties for obtaining environmental variables meaningful for home ranges, with a very high spatial resolution (Dos Santos *et al.*, 2016). Indeed, few works have used ENMs with very high spatial resolutions (Sillero & Gonçalves-Seco, 2014; Descombes *et al.*, 2016). Fortunately, new technologies like LiDAR (Sillero & Gonçalves-Seco, 2014) and unmanned aerial vehicles (UAV or drones) (Teodoro & Araujo, 2016) can provide aerial photographs, digital surface models (DSM) and near-infrared images with spatial resolutions ranging from one metre to few centimetres (Gonçalves & Henriques, 2015). In fact, remote sensing data and techniques are currently the most important source of environmental data (Pettorelli *et al.*, 2016). Therefore, ENMs could be used to generate not only an estimation surface of the space used by an individual organism but also to identify the main factors driving such utilization distribution. Here, we propose using ENMs (Bioclim, GAM, GLM, Maxent and random forest algorithms) and environmental variables with a very high spatial resolution (20 cm) obtained by interpolation of data-loggers' records (temperature and humidity) and remote sensing images (vegetation classes and a digital elevation model derived from aerial-like photographs). As a model example, we apply this novel methodology to estimate the utilization distribution of several lizards in an outdoor enclosure under natural conditions. Specifically, we aimed (1) to evaluate the viability of ENMs for estimating utilization distribution and (2) to determine the environmental factors limiting space use.

Materials and methods

Study area

Fieldwork was performed in a mesocosm (Fig. 1), built at the Astronomic Observatory Professor Manuel de Barros

(41°06'22.6"N, 8°35'18.9"W, 230 m; Vila Nova de Gaia, Portugal). The mesocosm was an enclosed area of 20 × 20 m with a representative sample of the lizards' natural environment (grassy and bush vegetation, tree trunks and rocks) and fenced by a plastic wall. Previous searches ensured that no lizards, other than those released in this study, were present.

Study species

Podarcis bocagei is a small insectivorous lizard of the family Lacertidae, endemic to north-west Iberian Peninsula; it is a diurnal heliothermic species which occupies a wide range of natural and anthropomorphized habitats (Pinho, Harris & Ferrand, 2008). We randomly captured 31 adult individuals (21 males and 10 females), by noose (García-Muñoz & Sillero, 2010) at Madalena coastal dunes (Vila Nova de Gaia, Portugal: 41°06'11.0"N 8°39'40.1"W) during the breeding season (May 2016). Only individuals with a snout-vent-length greater than 45 mm (adults) were considered for the study (Carretero *et al.*, 2006). We could easily assess sex based on morphometrics (Kaliontzopoulou, Carretero & Llorente, 2006) and sexual secondary characters (Galán, 2008).

Obtaining individual locations

To identify free-ranging lizards inside the enclosure we marked each individual with a unique combination of three non-toxic colour dye. Sampling in the enclosure was conducted between May and July 2016. A researcher (RdS) walked haphazardly through the mesocosm looking for lizards, several times per day, throughout the entire range of the lizards' daily activity.

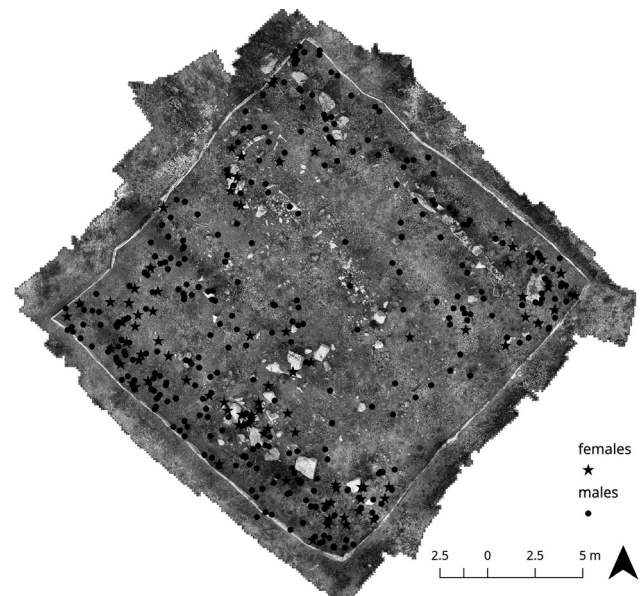


Figure 1 Study area (mesocosm, 20 × 20 m; Vila Nova de Gaia, Portugal) and all female and male presences of the Iberian lizard *Podarcis bocagei*.

In each survey, the whole extent of the mesocosm was sampled only once to avoid pseudo-replication (Hulbert, 1984). The study area was left undisturbed during 30 min between samplings, allowing lizards to recover their normal activity after any eventual disturbance; and also granting independence between observations. The time between two consecutive sightings was always higher than the minimum time a lizard could move between two consecutive locations. Consequently, a position could not be predicted from the previous one, regardless the lizard effectively moves or not. RdS recorded the position of each lizard with a Trimble GeoExplorer 2008 XM GPS receptor (around 10 cm error) for 60 s. The location error was lower than the pixel resolution of environmental variables (20 cm, see below). We created a data dictionary for the GPS receiver with Trimble GPS Pathfinder Office software v 5.0 to avoid input errors and to facilitate data input when registering lizards' colour marks.

Minimum convex polygons

We first estimated home range areas with minimum convex polygons (MCP) instead of kernel density estimations (KDE) or local convex hulls (LoCoH) because of the intrinsic difficulties of gathering a high number of locations per individual (Getz *et al.*, 2007; Laver & Kelly, 2008). Moreover, kernels may be inadequate for herpetofauna (Row & Blouin-Demers, 2006). We calculated MCPs using the package AdehabitatHR (Calenge, 2011) of the R 3.6.1 software (RCoreTeam, 2019) and 90% of the lizards' locations (Jennrich & Turner, 1969). Home ranges were determined for individuals with ten or more sightings (following Diego-Rasilla & Pérez-Mellado, 2003). We removed sporadic displacements by excluding 10% of the locations, using the corresponding parameter implemented in the function `mcp` in AdehabitatHR package. The specific percentage of locations is the farthest away from the centroid of the home range (computed by the arithmetic mean of the coordinates of the relocations for each set of locations). We selected this threshold to exclude the same proportion of presences as in the ecological niche modelling algorithms (see Ecological niche modelling section). We also estimated MCPs with 50% of the lizards' locations as a representation of core areas (Laver & Kelly, 2008). We calculated the area of the home range per individual. All analyses were performed with R 3.6.1 (R Core Team, 2019).

Environmental variables

We obtained environmental variables from several sources: aerial-like photographs, GPS device and data-loggers. The original spatial resolution of all variables was 2 cm. All variables were aggregated to a spatial resolution of 20 cm to ensure that all lizards' records were located correctly in the pixel where they were sighted. All the variables were generated using ArcGIS version 10.3.1 (ESRI, Redlands, CA, USA).

We built an orthophoto map of the mesocosm from a set of 1152 individual photographs captured by a Canon PowerShot A495 camera fastened to a stick (4 m length) and processed

using Agisoft Photoscan 1.2.0 photogrammetry software. These photographs were taken using sequential mode and covered the entire area by walking throughout the mesocosm. Agisoft Photoscan aligns and extracts matching points from the numerous photographs, creates a point cloud, generates a sparse cloud including the texture from the images, and finally creates the orthophoto generating the textures from the photographs and the relief from the matching points. The spatial resolution of the mesocosm map was 2 cm. Additionally, a DEM with a pixel resolution of 2 cm was created using 3016 accurate altitude points obtained with an RTK-GPS (Trimble TSC3 and Trimble R4 receiver) and a triangulated irregular network (TIN) with ArcGIS software.

We obtained a map of potential refuges for lizards by classifying the orthophoto with a supervised maximum likelihood classification algorithm in ArcGIS and using four different classes (refuges, vegetation, bare soil and organic soil). A refuge was here defined as a crack in a rock, a small hole or an entire rock or bush where the lizard could retreat in. The supervised classes were calculated with four training polygons for each class containing: (1) 620 000 pixels for refuges; (2) 210 000 pixels for vegetation; (3) 270 000 pixels for bare soil; and (4) 240 000 pixels for organic soil.

We monitored the temperature and humidity conditions of the mesocosm by placing a matrix of 50 data-loggers (27 Maxim's iButton DS1921G for temperature and 23 Maxim's iButton DS1923 for humidity and temperature; precision ± 0.5), programmed to record data every 15 min. We used a random point generation algorithm to assure the data-loggers would be evenly placed in all types of land-cover features present in the mesocosm (vegetation, bare soil and rocks). All data-loggers were geo-referenced using a high precision RTK-GPS (Trimble TSC3 and Trimble R4 receiver). The logs were organized by hours and interpolated with Ordinary Kriging (Hengl, 2009) to create daily maps of average temperature ($^{\circ}\text{C}$) and relative humidity (%H) which describe the spatiotemporal variation of the conditions within the mesocosm. We recreated climate-like variables mimicking Bioclim variables (Nix, 1986; Booth *et al.*, 1988, 2014), as those used in the Worldclim data series (Hijmans *et al.*, 2005), by combining the data from the data-loggers. As such, we generated 15 variables related to temperature and humidity (Table 1).

In addition, we calculated the elevation after the digital surface model as well as the distance to each land-cover class (organic soil, bare soil, vegetation, rocks) from the mesocosm supervised classification, in order to avoid categorical variables. We also calculated the distance to both males and females for each individual, excluding the lizard modelled.

Of the initial set of 21 variables, we selected five with a correlation lower than 0.6 (Table 1). After the correlation analysis, we confirmed the reduced collinearity between variables, rejecting any variable with a variance inflation factor (VIF) higher than 2, using the `usdm` R package (Naimi *et al.*, 2014).

Except for land cover, the variables of climate and distance to individuals were dynamic, as they change with time. Unfortunately, the number of points was insufficient to calculate

Table 1 List of variables created: climate-like Bioclim variables, elevation, distance to each land-cover class (organic soil, bare soil, vegetation, rocks), and distance to males and females (excluding the lizard modelled). In bold, the selected variables (with a correlation lower than 0.6 and VIF lower than 2)

Variable name	Variable description
Bio 1	Maximum temperature
Bio 2	Average daily maximum temperature
Bio 3	Minimum temperature
Bio 4	Average daily minimum temperature
Bio 5	Range of temperatures
Bio 6	Range of average temperatures
Bio 7	Maximum humidity
Bio 8	Average daily maximum humidity
Bio 9	Minimum humidity
Bio 10	Average daily minimum humidity
Bio 11	Range of humidity
Bio 12	Range of average humidity
Bio 13	Temperature seasonality
Bio 14	Humidity seasonality
Bio 15	Isothermality
MDT	Elevation
Org	Organic soil
Soil	Bare soil
Veg	Vegetation
Rock	Rocks
Dist	Distance to females or males

models over time and analysing temporal variation of the home range was beyond the scope to this study.

Ecological niche modelling

We calculated realized niche models (*sensu* Sillero, 2011) for each individual to infer habitat suitability inside the mesocosm. We used several correlative methods: Bioclim for presence-only data (Nix, 1986; Booth *et al.*, 2014); maximum entropy for presence-background data (Phillips *et al.*, 2006, 2017); and generalized additive models-GAM, generalized linear models-GLM and random forest-RFO for presence-absence data (Breiman, 1999; Guisan, Edwards & Hastie, 2002). We created pseudo-absences as surrogates of absences because we have only presences. Pseudo-absences were specific for each individual, that is pseudo-absences were the presences of all individuals except that to be modelled, separated from the individual's presences by a specific distance: the expected distance provided by the nearest neighbourhood index (Clark & Evans, 1954). We consider this as the most objective method for defining the pseudo-absences, applied similarly to all individuals, but specific to each one of them. Maximum entropy models were calculated with Maxent software 3.4.1 (Phillips *et al.*, 2017), in clog-log format with default parameters. Bioclim, GLM, GAM and RF were calculated with ENMTools R package (Warren *et al.*, 2019). All lizards' records were considered as training data because some individuals had a limited sample size (below 30 records; see Table 1). For all algorithms, we

calculated the arithmetic mean and the standard deviation of a set of 10 models per species and dataset through an iterative process, as training and pseudo-absences or background data are selected randomly (Sillero & Carretero, 2013).

We obtained binary habitat suitability maps (*sensu* Sillero, 2011; with two categories, suitable and unsuitable habitats) from all the realized niche models by applying two thresholds: the '10% of presence records', as the value of the habitat suitability index corresponding to the 10% location (ranked from low to high values); and the median, to exclude the 50% of each individual's locations. We selected these thresholds to exclude the same proportion of presences as in the MCP calculations (see Home ranges section). Then, we calculated the area size of each habitat suitability map.

We obtained the contribution of each variable from Maxent models. Contributions were determined by the average percentage of contribution of each variable to the 10 replicated Maxent models (Phillips, Anderson & Schapire, 2006) through a factor analysis: (1) a jackknife analysis of the average AUC using training and test data and (2) a calculation of the average percentage contribution of each variable to the models. For this purpose, the variables were excluded in turn and a model was created with the remaining variables. A model was then created using each variable.

Model validation

Realized niche models were tested with the area under the curve (AUC) of the receiver operating characteristics (ROC) plots as a measure of the overall fit of the models (Liu *et al.*, 2005). AUC was selected because it is independent of prevalence (VanDerWal *et al.*, 2009), although it depends on the relationship between the extent of the study area and the species range (Lobo, Jiménez-Valverde & Real, 2008). To avoid that individuals with restricted distributions might attain artificially higher AUC values (VanDerWal *et al.*, 2009), we calculated the AUC values for a set of 100 null models for each algorithm following the methodology proposed by Raes & ter Steege (2007). For that, we created 100 sets of random points per individual with the same number as the individual's presences following a Poisson distribution. Then, we calculated the realized niche models for all the algorithms and obtained the corresponding AUC values. We expect that the AUC values from the null models will be significantly lower than the AUC values from the empirical models. We used dismo R package for Maxent and ENMTools for the rest of algorithms (Warren *et al.*, 2019). We compared both sets of AUC values per individual with an ANOVA.

Overlapping MCP and habitat suitability maps

We overlapped the two sets of habitat suitability maps of each individual (corresponding to the thresholds of 10% and 50% presences) and algorithm with the corresponding MCP with 90% and 50% of locations and calculated the size of the overlapping area. Then, we compared the size of the overlapped

area between sexes with an ANOVA. In all cases, we checked for data normality and homoscedasticity, and log-transformed the variables if necessary. All statistical analyses were performed with R 3.6.1 (R Core Team, 2019).

Results

Individuals analysed

Of the 10 females and 21 males initially introduced in the mesocosm, females were re-sighted 115 times (range 4–16) and males 337 times (6–41). We excluded from all the analyses those individuals with less than nine points (three females and six males) because the sample size was insufficient for modelling purposes. Thus, we analysed six females and 15 males, with 79 point records (range 10–16) and 290 point records (range 10–41), respectively.

Minimum convex polygons

Minimum Convex Polygon from males had a larger size than MCP from females (ANOVA of log area: d.f. = 1,19, $F = 10.89$, $P = 0.0037$; females = $0.0026 \pm 0.0015 \text{ m}^2$; males = $0.0069 \pm 0.0046 \text{ m}^2$). Females occupied three different areas of the mesocosm while males used the whole mesocosm, although sightings concentrated more in the area with more females (Fig. 2).

Realized niche models

Almost all individual models had an AUC higher than 0.7: very few algorithms had low values (Table 2). All null models had AUC values significantly lower than the individual models (Table S1 and Text S1). Some individual models, either males or females, presented a restricted surface (Fig. 3). However, most of them presented either a widespread or a scattered suitable surface: see for instance female RBR or RRB in Fig S1 or male BRW or BPB in Fig. S2.

The variables contributing most to the Maxent models for females were Isothermality for three individuals, Minimum temperature for two individuals and Minimum humidity for a single individual (Table S2). The variables contributing most to the Maxent for males were Minimum humidity for four individuals, Isothermality for three individuals and Distance to females and Soil for one individual (Table S2). The other algorithms did not provide the contribution of variables.

Comparing ENMs with MCP

Minimum Convex Polygons with 90% and 50% of locations overlapped with the individual models in low percentages for females: MCP90, $16.54 \text{ m}^2 \pm 9.38$, range: 6.64–23.19; MCP 50, $2.72 \text{ m}^2 \pm 2.09$, range: 0.61–4.58 (Table 3 and Table S3; Fig. 4, Figs. S3, and Fig. S4). The percentage of overlap was higher in males: MCP90, $41.85 \text{ m}^2 \pm 28.03$, range: 6.13–57.52; MCP50, $7.38 \text{ m}^2 \pm 4.65$, range: 0.74–11.20 (Table 3 and Table S3; Figs. 4, Figs. S5 and S6). There were significant differences between overlaps and both sexes, except for RF

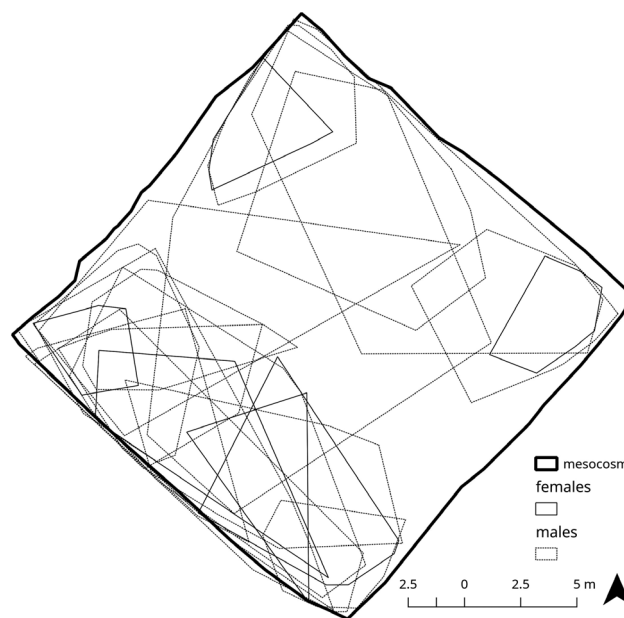


Figure 2 All minimum convex polygons (MCP) for females (6) and males (15) inside the mesocosm (20 × 20 m).

model (Table 4). However, the interaction was not significant (Table 4).

Discussion

This novel methodology for estimating home ranges through ENMs revealed statistically powerful and valuable results outperforming the estimations based on MCP alone. As such, ENMs were able to determine the intensity of space use inside the MCPs as well as their environmental and non-environmental (e.g. social) conditions responsible at the individual level. Individual models tended to present a widespread and scattered suitable surface in males, but a restricted suitable surface in females. These results are concordant with previous studies on lizards' home ranges, mostly based on MCPs, namely the main function of home ranges in male lizards is to maintain a mating area (Rose, 1981). Indeed, reproductive success in females does depend on resource distribution, while in males is limited by access to mating partners (Stamps, Losos & Andrews, 1997; Mahrt, 1998; Haenel, Smith & John-Alder, 2003). Hence, male lizards keep larger home ranges to overlap with more females (Germano, 2007; Verwajen & Van Damme, 2008; Sillero *et al.*, 2016). Some lizard species lack such differences likely due to different mating systems (Boag, 1973). Consequently, females and especially males with poor body condition need to disperse greater distances as they have more difficulties to establish stable home ranges (Olsson, Gullberg & Tegelström, 1997).

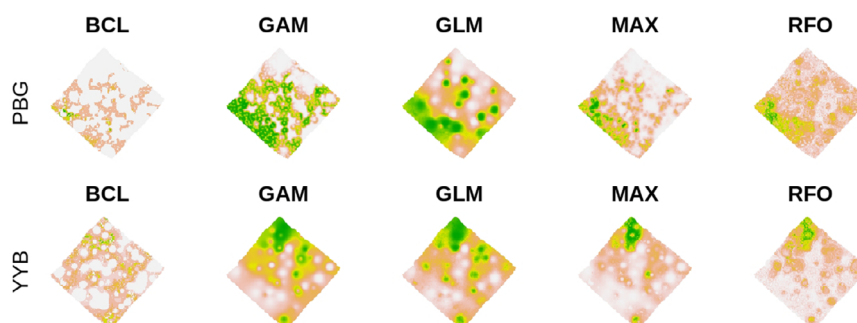
The variables contributing most to the Maxent models were related to (micro)climate (isothermality, minimum temperature and humidity). Distances to males or females and soil had a high contribution as well, but always in a secondary position.

Table 2 Area Under the Curve (AUC) and threshold (10% presence) values per individual (females and males) and modelling algorithm: individual identity code, sample size, Bioclim, generalized additive models (GAM), generalized linear models (GLM), Maxent and random forest (RFO)

	<i>n</i>	Metrics	Bioclim	GAM	GLM	Maxent	RFO
Females							
PBG	15	AUC	0.9022	0.9451	0.8346	0.9641	0.9933
		Threshold 10%	0.0666	0.3155	0.5061	0.5620	0.4233
		Threshold 50%	0.2000	0.7934	0.6997	0.6570	0.5639
PYB	19	AUC	0.8982	0.9190	0.7997	0.8749	0.9945
		Threshold 10%	0.0010	0.4855	0.3339	0.4453	0.3879
		Threshold 50%	0.1579	0.7816	0.6232	0.6710	0.5608
RBR	14	AUC	0.7946	0.8086	0.7651	0.8311	0.9978
		Threshold 10%	0.0713	0.2656	0.5398	0.4907	0.3412
		Threshold 50%	0.1786	0.6767	0.6185	0.6739	0.5918
RBW	11	AUC	0.8646	0.9418	0.8910	0.8767	0.9979
		Threshold 10%	0.0908	0.3994	0.4131	0.4818	0.3626
		Threshold 50%	0.0909	0.7980	0.7980	0.6477	0.5183
RGB	14	AUC	0.7347	0.8857	0.8696	0.8427	0.9979
		Threshold 10%	0.0666	0.5501	0.3946	0.3799	0.3550
		Threshold 50%	0.2000	0.7301	0.7395	0.6755	0.5381
RRB	13	AUC	0.8634	0.9304	0.8976	0.8499	0.9987
		Threshold 10%	0.0768	0.6257	0.3786	0.4017	0.4522
		Threshold 50%	0.2308	0.7704	0.8070	0.5955	0.5953
Males							
BPB	18	AUC	0.6508	0.5596	0.6595	0.8285	0.9965
		Threshold 10%	0.0555	0.4968	0.3677	0.4011	0.3473
		Threshold 50%	0.1667	0.4995	0.5304	0.5817	0.4652
BPP	19	AUC	0.8809	0.8356	0.8037	0.9000	0.9931
		Threshold 10%	0.0525	0.3998	0.3964	0.3759	0.3620
		Threshold 50%	0.1579	0.6973	0.6253	0.6527	0.5473
BPW	12	AUC	0.9450	0.8428	0.8778	0.8814	0.9961
		Threshold 10%	0.0832	0.3384	0.3440	0.4225	0.3730
		Threshold 50%	0.2500	0.6590	0.7896	0.6944	0.5055
BRW	14	AUC	0.7196	0.6797	0.6708	0.7448	0.9989
		Threshold 10%	0.0713	0.4999	0.3563	0.4179	0.3623
		Threshold 50%	0.1786	0.5000	0.5664	0.5627	0.4953
BWB	20	AUC	0.6824	0.8186	0.8422	0.8935	0.9886
		Threshold 10%	0.0499	0.6316	0.5383	0.2999	0.4629
		Threshold 50%	0.1500	0.6750	0.7587	0.6665	0.5126
BWP	12	AUC	0.8720	0.6887	0.7178	0.7239	0.9970
		Threshold 10%	0.0832	0.4204	0.4333	0.4330	0.3721
		Threshold 50%	0.0833	0.5048	0.5532	0.6053	0.5316
BWW	10	AUC	0.8759	0.8072	0.8428	0.8455	0.9988
		Threshold 10%	0.0999	0.3644	0.4880	0.4264	0.4015
		Threshold 50%	0.1000	0.6215	0.7048	0.6630	0.4983
RBB	43	AUC	0.7943	0.8051	0.8034	0.8720	0.9925
		Threshold 10%	0.0232	0.4814	0.4207	0.2742	0.3782
		Threshold 50%	0.2326	0.6825	0.7113	0.6900	0.6035
RBY	20	AUC	0.7023	0.6154	0.6725	0.8063	0.9955
		Threshold 10%	0.0499	0.4864	0.4439	0.4377	0.3157
		Threshold 50%	0.1500	0.5262	0.5472	0.6659	0.4961
WBR	24	AUC	0.6882	0.7762	0.7766	0.8272	0.9943
		Threshold 10%	0.0416	0.4824	0.2811	0.3192	0.3747
		Threshold 50%	0.1250	0.6037	0.6254	0.6025	0.4783
WBW	18	AUC	0.7511	0.6667	0.6594	0.7807	0.9966
		Threshold 10%	0.0050	0.5382	0.3323	0.3579	0.3427
		Threshold 50%	0.1667	0.5383	0.5279	0.6726	0.4951
WBY	20	AUC	0.8101	0.6312	0.6730	0.8254	0.9883
		Threshold	0.0499	0.3569	0.3476	0.3854	0.3304
		Threshold 50%	0.2000	0.5765	0.5882	0.6756	0.4625

Table 2 Continued.

	<i>n</i>	Metrics	Bioclim	GAM	GLM	Maxent	RFO
WRB	28	AUC	0.8161	0.7692	0.6507	0.8676	0.9865
		Threshold 10%	0.0312	0.4847	0.4208	0.4212	0.3204
		Threshold 50%	0.2188	0.6425	0.5560	0.7130	0.5959
YWB	16	AUC	0.8513	0.7852	0.7258	0.9035	0.9955
		Threshold 10%	0.0624	0.4973	0.4446	0.2899	0.3499
		Threshold 50%	0.1250	0.6345	0.6067	0.8303	0.5585
YYB	33	AUC	0.7200	0.8628	0.8447	0.9212	0.9823
		Threshold 10%	0.0302	0.3848	0.2689	0.2502	0.3756
		Threshold 50%	0.1212	0.6450	0.6668	0.5427	0.5807

**Figure 3** Examples of realized niche models (Bioclim, GAM, GLM, Maxent and random forest) for a female (PBG) and a male (YYB). Habitat suitability increases from light to dark colours.**Table 3** Area and overlap size results between habitat suitability models (of Bioclim, generalized additive models-GAM, generalized linear models-GLM, Maxent and random forest-RFO) and minimum convex polygons (MCPs) with 90% and 50% of locations for females and males

	Bioclim	GAM	GLM	Maxent	RF
Females					
MCP90	151.37 ± 44.73	189.55 ± 75.93	180.05 ± 79.77	111.02 ± 44.30	19.67 ± 7.38
26.34 ± 15.11	15.05 ± 8.67	20.47 ± 11.58	23.19 ± 12.31	17.33 ± 10.82	6.64 ± 3.54
MCP50	61.88 ± 36.60	82.53 ± 55.14	95.29 ± 55.73	41.55 ± 14.18	2.60 ± 2.03
7.16 ± 5.30	1.72 ± 0.70	3.35 ± 2.22	4.58 ± 3.99	3.35 ± 3.02	0.61 ± 0.53
Males					
MCP90	203.98 ± 72.28	200.54 ± 100.63	199.57 ± 81.40	153.76 ± 64.15	10.38 ± 8.81
69.43 ± 45.81	46.23 ± 29.95	50.40 ± 29.08	57.52 ± 44.08	48.97 ± 32.03	6.13 ± 5.04
MCP50	87.16 ± 41.82	75.41 ± 39.19	72.47 ± 33.39	43.08 ± 24.60	1.88 ± 1.59
20.37 ± 14.01	7.42 ± 5.00	10.52 ± 6.52	11.20 ± 7.97	7.03 ± 2.98	0.74 ± 0.80

The table is organized as a matrix: the first two lines of values in the semi table correspond to the sizes of the habitat suitability maps; the first column corresponds of values to the sizes of MCPs with 90% and 50% of locations.

The values inside the matrix are the size of overlaps between models and MCPs. First lines correspond to mean values; second lines are the standard deviation. See Table S3 for results per individuals.

Studies modelling the distribution of *Podarcis* species showed a strong dependence on temperature and humidity (Sá-Sousa, 2000; Román *et al.*, 2006; Kaliontzopoulou *et al.*, 2008; Sillero & Carretero, 2013).

Minimum Convex Polygons overlapped with ENMs, although with a high variation across individuals and algorithms. The home ranges of females based on MCP were small

(Rose, 1981) and provided relatively uniform ENM surfaces; thus, the overlaps were small as well. However, the MCPs of males were large, overlapping more with the realized niche models. As the core areas were smaller, the overlaps with the realized niche model were also restricted.

All realized niche models provided similar overlapping results, except RF which obtained the smallest overlaps. In

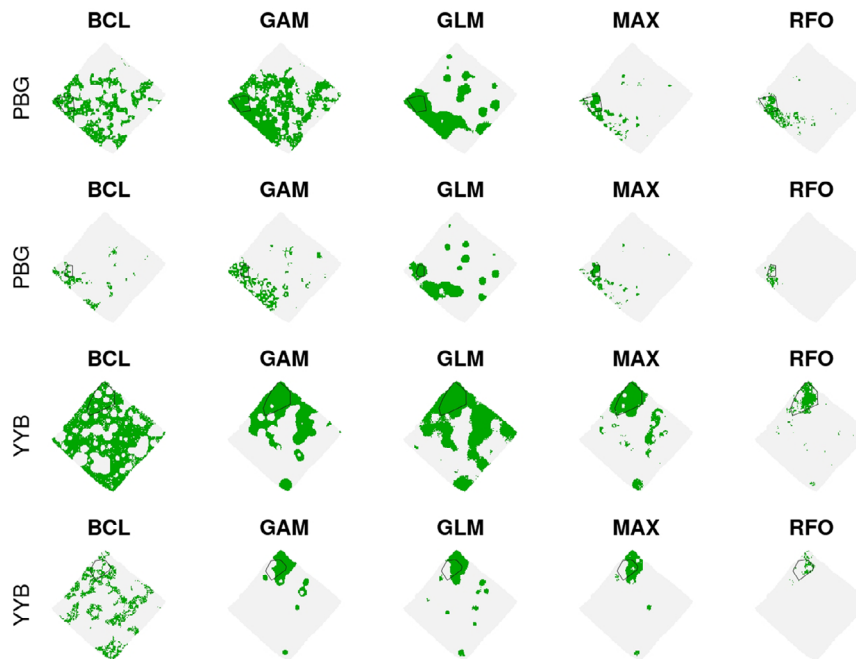


Figure 4 Examples of habitat suitability maps (Bioclim, GAM, GLM, Maxent and random forest) for a female (PBG) and a male (YYB) overlapped with their corresponding home range representation (MCP: minimum convex polygon). The external line corresponds to the MCP with 90% or 50% of locations. The first line of habitat suitability maps were calculated from the realized niche models by applying the threshold of 10% of presence records and the second one with the threshold of 50% of presence records.

Table 4 ANOVA results for comparing overlaps of minimum convex polygons (MCPs) and habitat suitability maps (of Bioclim, generalized additive models-GAM, generalized linear models-GLM, Maxent and random forest-RFO) between females and males, using Sex as co-variable. Size of overlaps and MCPs were transformed into logarithms

Algorithm	MCP90	F value	d.f.	P value	MCP50	F value	d.f.	P value
Bioclim	Sex	89.839	1	0.000	Sex	49.213	1	0.000
	MCP90	106.948	1	0.000	MCP50	26.365	1	0.000
	Sex:MCP90	0.012	1	0.914	Sex:MCP50	0.663	1	0.427
GAM	Sex	26.942	1	0.000	Sex	36.058	1	0.000
	MCP90	26.764	1	0.000	MCP50	30.433	1	0.000
	Sex:MCP90	0.083	1	0.777	Sex:MCP50	0.001	1	0.973
GLM	Sex	68.164	1	0.000	Sex	29.57	1	0.000
	MCP90	164.36	1	0.000	MCP50	56.28	1	0.000
	Sex:MCP90	0.798	1	0.384	Sex:MCP50	1.21	1	0.287
Maxent	Sex	70.295	1	0.000	Sex	22.648	1	0.000
	MCP90	79.398	1	0.000	MCP50	18.305	1	0.000
	Sex:MCP90	0.289	1	0.598	Sex:MCP50	1.606	1	0.222
RFO	Sex	0.664	1	0.426	Sex	0.002	1	0.967
	MCP90	0.018	1	0.895	MCP50	0.031	1	0.887
	Sex:MCP90	0.275	1	0.606	Sex:MCP50	0.967	1	0.339

general, for females and males, RF identified less suitable habitats and Bioclim more. There were some exceptions for some individuals where GLM or GAM identified large surfaces of suitable habitats. Maxent was very stable across all individuals. Bioclim tended to produce very fragmented surfaces of

suitability. Obviously, these results will change with the selected threshold. These results agree with other studies comparing different ecological niche modelling algorithms: Bioclim as presence-only method provide always very large models, while presence-absence algorithms can restrict more the results

to the observed point distributions (Elith *et al.*, 2006). In fact, ENM algorithms can be placed in a gradient between the potential and the realized niches (Jiménez-Valverde, Lobo & Hortal, 2008): Bioclim is close to the potential niche, while Maxent, GLM and GAM are close to the realized niche. Depending on what type of niche model is forecast (Sillero, 2011), a different type of algorithm must be selected. Thus, presence-only models may be better to identify those 'occasional sallies outside the area, perhaps exploratory in nature' that should not be considered as part of the home range, following the home range definition by Burt (1943). Presence-absence algorithms, such as RF, will not identify other suitable habitats outside the home range that can be interesting for exploratory purposes.

It is important to note that Maxent is prone to overfit the models. The most correct process to avoid this issue is to set the regularization parameter individually for each species (in our case, each individual) as showed in (Warren & Seifert, 2011). However, when calculating models for several entities, it is necessary to calculate the models with exactly the same conditions, as each entity would require a different regularization parameter.

Overall, using ENM to estimate animals' home ranges present several advantages over MCPs. Specifically:

- (1) Ecological niche models (ENMs) provide a quantification of the importance of variables determining space use and response curves for each environmental variable. This is not available from simple geographical methods like MCP or characteristic hulls, or even from more complex resource function models like kernels.
- (2) ENMs provide non-uniform surfaces of space use, like kernels. However, kernels are not recommended in cases such as lizards where home range size increases with the bandwidth, producing a wide range of values on different individuals (Row & Blouin-Demers, 2006). Thus, ENMs stand the only alternative method to produce non-uniform surfaces for space use studies.
- (3) ENMs allow an easy estimation of core areas, as in MCP. Core areas can be determined in ENMs by defining thresholds of habitat suitability, in a similar subjective way like MCPs (e.g. 50%). On the other hand, kernels can estimate objectively core areas with a time-maximizing function, which define the areas where an animal spends a maximum amount of time (VanderWal & Rodgers, 2012). ENMs therefore provide an easier solution when animals locations are not enough to calculate kernels.
- (4) ENMs are relatively easy to calculate. Obviously, some general parameters must be set, but the same is true when calculating kernels. Certainly, the obtention of environmental variables at a high spatial resolution may be time- and resource-consuming.

The major limitation for applying ENMs to the estimation of home ranges is to obtain environmental variables with very high spatial resolution. Indeed, few studies have applied ENMs with very high spatial resolutions. For example, Bogosian III *et al.* (2012) combined mechanistic and correlative models for

a lizard species using data with a spatial resolution of 1 m. Although locations were collected by telemetry, individuals were not modelled separately. Sillero & Gonçalves-Seco (2014) were the first in using LiDAR-derived data with a spatial resolution of 1 m to model with Maxent four species of lizards and analyse the spatial structure of their community. Carretero *et al.* (2010) presented Maxent models with a spatial resolution of 30 m using data derived from the ASTER Global DEM (Hirt, Filmer & Featherstone, 2010) for a species of lizard in Spain. Other studies used also LiDAR data to model the distribution of birds with generalized linear models and Maxent (Tattoni, Rizzolli & Pedrini, 2012) and with RF (Martinuzzi *et al.*, 2009). LiDAR is currently the main source of very high-resolution data for ecological studies. However, Hatten (2014) used also Landsat imagery in addition to LiDAR to map and monitor Mount Graham red squirrel habitats.

Remote sensing has started recently to be used as an important data source in ENMs (He *et al.*, 2015; Rocchini *et al.*, 2015). Few studies have evaluated the accuracy of ENMs calculated with satellite imagery in comparison with other data sources (Thuiller, Araujo & Lavorel, 2004; Sillero *et al.*, 2012). Climatic satellite imagery data improve ENMs when combined with ground-based maps (Suarez-Seoane, Osborne & Rosema, 2004). Similar ENMs were obtained with land-cover data (Venier *et al.*, 2004) and with climatic and NDVI data (Zimmermann *et al.*, 2007), but not with NDVI data only (Parra, Graham & Freile, 2004). However, Sillero *et al.* (2012) showed that ENMs calculated only with satellite imagery (e.g. Landsat) are similar to models calculated only with ground-based data.

In summary, the very high spatial resolution models proposed in this work improved the quality of the information about space use by each lizard. Correlative models were better and more objective than MCPs at identifying the most suitable areas inside the home range, similarly to the core areas estimated from kernel algorithms. Consequently, remote sensing tools provided high-quality environmental data, produced better home range estimations based on ENMs, which could be statistically compared. Overall, the approach based on correlative models improved home range estimations and, in general, interpretations of spatial patterns of animals at very small scales, which opens a promising study field in the next future.

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Author contributions

RS and NS conceived the idea and designed the methodology. RS collected the data. NS performed the analyses and led the writing. MAC and ACT help in all stages of the fieldwork and

analyses. All authors contributed critically to the drafts and gave final approval for publication.

Statement about data archive

The data will be archived in the storage facilities of the Spatial Biology Lab at the Research Centre on Geo-Spatial Science of the Faculty of Science of the University of Porto. All data will be provided upon request.

References

- Anderson, D.J. (1982). The home range : a new nonparametric estimation technique. *Ecology* **63**, 103–112.
- van Beest, F.M., Rivrud, I.M., Loe, L.E., Milner, J.M. & Mysterud, A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *J. Anim. Ecol.* **80**, 771–785.
- Boag, D.A. (1973). Spatial relationships among members of a population of wall lizards. *Oecologia* **12**, 1–13.
- Bogosian, V. III, Hellgren, E.C., Sears, M.W. & Moody, R.W. (2012). High-resolution niche models via a correlative approach: comparing and combining correlative and process-based information. *Ecol. Modell.* **237–238**, 63–73.
- Booth, T.H., Nix, H.A., Busby, J.R. & Hutchinson, M.F. (2014). BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. *Divers. Distrib.* **20**, 1–9.
- Booth, T.H., Nix, H.A., Hutchinson, M.F. & Jovanic, T. (1988). Niche analysis and tree species introduction. *For. Ecol. Manage.* **23**, 47–59.
- Breiman, L. (1999). Random forest. *Mach. Learn.* **45**, 1–35.
- Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals. *J. Mammal.* **24**, 346–352.
- Calenge, C. (2011). *Home Range Estimation in R: the adehabitatHR Package*.
- Carretero, M.A., Ceacero, F., García-Muñoz, E., Sillero, N., Olmedo, M.I., Hernández-Sastre, P.L. & Rubio, J.L. (2010). *Seguimiento de Algyroides marchi. Informe final*. Monografías SARE. Madrid.
- Carretero, M.A., Vasconcelos, R., Fonseca, M., Kaliontzopoulou, A., Brito, J.C., Harris, J.D. & Perera, A. (2006). Escape tactics of two syntopic forms of the *Lacerta perspicillata* complex with different colour patterns. *Can. J. Zool.* **84**, 1594–1603.
- Clark, P.J. & Evans, F.C. (1954). Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* **35**, 445–453.
- Descombes, P., Petitpierre, B., Morard, E., Berthoud, M., Guisan, A. & Vittoz, P. (2016). Monitoring and distribution modelling of invasive species along riverine habitats at very high resolution. *Biol. Invasions* **18**, 3665–3679.
- Diego-Rasilla, F.J. & Pérez-Mellado, V. (2003). Home range and habitat selection by *Podarcis hispanica* (Squamata, Lacertidae) in Western Spain. *Folia Zool.* **52**, 87–98.
- Dos Santos, R., Teodoro, A.C., Carretero, M., & (2016). Remote sensing as a tool to analyse lizards behaviour. In *Proceedings SPIE Remote Sensing: 9998*, 1–10. Neale, C.M.U. & Maltese, A. (Eds.). Edinburgh, United Kingdom. <https://doi.org/10.1117/12.2241093>
- Downs, J.A. & Horner, M.W. (2009). A Characteristic-hull based method for home range estimation. *Trans. GIS* **13**, 527–537.
- Elith, J., Graham, C., Anderson, R., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R., Huettmann, F., Leathwick, J., Lehmann, A., Li, J., Lohmann, L., Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R., Soberón, J., Williams, S., Wisz, M. & Zimmermann, N.E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129–151.
- Fieberg, J. (2007). Kernel density estimators of home range: Smoothing and the autocorrelation red herring. *Ecology* **88**, 1059–1066.
- Galán, P. (2008). Ontogenetic and sexual variation in the coloration of the lacertid lizards *Iberolacerta monticola* and *Podarcis bocagei*. Do the females prefer the greener males? *Anim. Biol.* **58**, 173–198.
- García-Muñoz, E. & Sillero, N. (2010). Two new types of noose for capturing herps. *Acta Herpetol.* **5**, 259–263.
- Gaubert, P., Papes, M. & Peterson, A.T. (2006). Natural history collections and the conservation of poorly known taxa: Ecological niche modeling in central African rainforest genets (*Genetta* spp.). *Biol. Conserv.* **1**, 106–117.
- Germano, J.M. (2007). Movements, home ranges, and capture effect of the endangered Otago Skink (*Oligosoma ottagense*). *J. Herpetol.* **41**, 179–186.
- Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J. & Wilmsers, C.C. (2007). LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS One* **2**, e207.
- Gonçalves, J.A. & Henriques, R. (2015). UAV photogrammetry for topographic monitoring of coastal areas. *ISPRS J. Photogramm. Remote Sens.* **104**, 101–111.
- Guisan, A., Edwards, T.C. & Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol. Modell.* **157**, 89–100.
- Haenel, G.J., Smith, L.C. & John-Alder, H.B. (2003). Home-Range Analysis in *Sceloporus undulatus*. II. A Test of Spatial Relationships and Reproductive Success. *Copeia* **2003**, 113–123.
- Hatten, J.R. (2014). Mapping and monitoring Mount Graham red squirrel habitat with Lidar and Landsat imagery. *Ecol. Modell.* **289**, 106–123.
- Hayne, D.W. (1949). Calculation of size of home range. *J. Mammal.* **1**, 1–18.
- He, K.S., Bradley, B.A., Cord, A.F., Rocchini, D., Tuanmu, M.N., Schmidlein, S., Turner, W., Wegmann, M. & Pettorelli, N. (2015). Will remote sensing shape the next generation of

- species distribution models? *Remote Sens. Ecol. Conserv.* **1**, 4–18.
- Hengl, T. (2009). *A practical guide to geostatistical mapping*. Ispira, Italy: Joint Research Centre.
- Hijmans, R.J., Cameron, E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978.
- Hirt, C., Filmer, M.S. & Featherstone, W.E. (2010). Comparison and validation of the recent freely available ASTER-GDEM ver1, SRTM ver4.1 and GEODATA DEM-9s ver3 digital elevation models over Australia. *Aust. J. Earth Sci.* **57**, 337–347.
- Hulbert, S. (1984). Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**, 187–211.
- Jennrich, R.I. & Turner, F.B. (1969). Measurement of non-circular home range. *J. Theor. Biol.* **22**, 227–237.
- Jiménez-Valverde, A., Lobo, J.M. & Hortal, J. (2008). Not as good as they seem: the importance of concepts in species distribution modelling. *Divers. Distrib.* **6**, 885–890.
- Kalioztopoulou, A., Brito, J.C., Carretero, M.A., Larbes, S. & Harris, D.J. (2008). Modelling the partially unknown distribution of wall lizards (*Podarcis*) in North Africa: ecological affinities, potential areas of occurrence, and methodological constraints. *Can. J. Zool.* **86**, 992–1001.
- Kalioztopoulou, A., Carretero, M.A. & Llorente, G.A. (2006). Patterns of shape and size sexual dimorphism in a population of *Podarcis hispanica** (Reptilia: Lacertidae) from NE Iberia. In *Mainland and insular lacertid lizards: a mediterranean perspective*: 73–89. Corti, C., Lo Cascio, P. & Biaggini, M. (Eds.). Firenze, Italy: Firenze University Press.
- Kie, J.G., Matthiopoulos, J., Fieberg, J., Powell, R.A., Cagnacci, F., Mitchell, M.S., Gaillard, J.-M. & Moorcroft, P.R. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 2221–2231.
- Laver, P.N. & Kelly, M.J. (2008). A critical review of home range studies. *J. Wildl. Manage.* **72**, 290–298.
- Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**, 385–393.
- Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008). AUC: a misleading measure of the performance of predictive distribution models. *Glob. Ecol. Biogeogr.* **17**, 145–151.
- Mahrt, L.A. (1998). Territorial establishment and maintenance by female Tree Lizards, *Urosaurus ornatus*. *J. Herpetol.* **32**, 176–182.
- Martinuzzi, S., Vierling, L.A., Gould, W.A., Falkowski, M.J., Evans, J.S., Hudak, A.T. & Vierling, K.T. (2009). Remote Sensing of Environment Mapping snags and understory shrubs for a LiDAR-based assessment of wildlife habitat suitability. *Remote Sens. Environ.* **113**, 2533–2546.
- Naimi, B., Hamm, N., Groen, T.A., Skidmore, A.K. & Toxopeus, A.G. (2014). Where is positional uncertainty a problem for species distribution modelling? *Ecography* **37**, 191–203.
- Nix, H.A. (1986). A biogeographic analysis of Australian Elapid Snakes. In *Atlas of Elapid Snakes of Australia*: 4–15.
- Longmore, R. (Ed.). Canberra: Australian Flora and Fauna Series Number 7. Australian Government Publishing Service.
- Olsson, M., Gullberg, A. & Tegelström, H. (1997). Determinants of breeding dispersal in the sand lizard, *Lacerta agilis*, (Reptilia, Squamata). *Biol. J. Linn. Soc.* **60**, 243–256.
- Parra, J.L., Graham, C.C. & Freile, J.F. (2004). Evaluating alternative data sets for ecological niche models of birds in the Andes. *Ecography* **3**, 350–360.
- Pettorelli, N., Wegmann, M., Skidmore, A., Múcher, S., Dawson, T.P., Fernandez, M., Lucas, R., *et al.* (2016). Framing the concept of satellite remote sensing essential biodiversity variables: challenges and future directions. *Remote Sens. Ecol. Conserv.* **2**, 122–131.
- Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E. & Blair, M.E. (2017). Opening the black box: an open-source release of Maxent. *Ecography* **40**, 887–893.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**, 231–259.
- Pinho, C., Harris, D.J. & Ferrand, N. (2008). Non-equilibrium estimates of gene flow inferred from nuclear genealogies suggest that Iberian and North African wall lizards (*Podarcis* spp.) are an assemblage of incipient species. *BMC Evol. Biol.* **8**, 63.
- Powell, R.A. & Mitchell, M.S. (2012). What is a home range? *J. Mammal.* **93**, 948–958.
- R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing, <https://www.R-project.org/>
- Raes, N. & ter Steege, H. (2007). A null-model for significance testing of presence-only species distribution models. *Ecography* **30**, 727–736.
- Rocchini, D., Andreo, V., Forster, M., Garzon-Lopez, C.X., Gutierrez, A.P., Gillespie, T.W., Hauffe, H.C., He, K.S., Kleinschmit, B., Mairota, P., Marcantonio, M., Metz, M., Nagendra, H., Pareeth, S., Ponti, L., Ricotta, C., Rizzoli, A., Schaab, G., Zebisch, M., Zorer, R. & Neteler, M. (2015). Potential of remote sensing to predict species invasions: a modelling perspective. *Prog. Phys. Geogr.* **39**, 283–309.
- Román, R., Ruiz, G., Delibes, M. & Revilla, E. (2006). Factores ambientales condicionantes de la presencia de la lagartija de Carbonell *Podarcis carbonelli* (Pérez-Mellado, 1981) en la comarca de Doñana. *Anim. Biodivers. Conserv.* **29**, 73–82.
- Rose, B. (1981). Factors affecting activity in *Sceloporus virgatus*. *Ecology* **62**, 706–716.
- Rose, B. (1982). Lizard home ranges: methodology and functions. *J. Herpetol.* **3**, 253–269.
- Row, J.R. & Blouin-Demers, G. (2006). Kernels are not accurate estimators of home-range size for Herpetofauna. *Copeia* **2006**, 797–802.
- Santos, H., Rodrigues, L., Jones, G. & Rebelo, H. (2013). Using species distribution modelling to predict bat fatality risk at wind farms. *Biol. Conserv.* **157**, 178–186.
- Sá-Sousa, P. (2000). A predictive distribution model for the Iberian wall lizard (*Podarcis hispanicus*) Portugal. *Herpetol. J.* **10**, 1–11.

- Sillero, N. (2008). Amphibian mortality levels on Spanish country roads: descriptive and spatial analysis. *Amphibia-Reptilia* **29**, 337–347.
- Sillero, N. (2011). What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. *Ecol. Modell.* **222**, 1343–1346.
- Sillero, N., Bonardi, A., Corti, C., Creemers, R., Crochet, P., Ficetola, G.F., Kuzmin, S., Lymberakis, P., Pous, P.De, Sindaco, R., Speybroeck, J., Toxopeus, B., Vieites, D.R. & Vences, M. (2014). Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphibia-Reptilia* **35**, 1–31.
- Sillero, N., Brito, J.C., Martín-Alfageme, S., García-Meléndez, E., Toxopeus, A.G. & Skidmore, A. (2012). The significance of using satellite imagery data only in Ecological Niche Modelling. *Acta Herpetol.* **7**, 221–237.
- Sillero, N. & Carretero, M.A. (2013). Modelling the past and future distribution of contracting species. The Iberian lizard *Podarcis carbonelli* (Squamata: Lacertidae) as a case study. *Zool. Anz.* **252**, 289–298.
- Sillero, N., Corti, C. & Carretero, M.A. (2016). Home ranges of parthenogenetic and bisexual species in a community of *Darevskia* lizards (Reptilia: Lacertidae). *Zool. Middle East* **62**, 306–318.
- Sillero, N. & Gonçalves-Seco, L. (2014). Spatial structure analysis of a reptile community with airborne LiDAR data. *Int. J. Geogr. Inf. Sci.* **28**, 1709–1722.
- Stamps, J.A., Losos, J.B. & Andrews, R.M. (1997). A comparative study of population density and sexual size dimorphism in lizards. *Am. Nat.* **149**, 64–90.
- Suarez-Seoane, S., Osborne, P.E. & Rosema, A. (2004). Can climate data from METEOSAT improve wildlife distribution models? *Ecography* **5**, 629–636.
- Tattoni, C., Rizzolli, F. & Pedrini, P. (2012). Can LiDAR data improve bird habitat suitability models? *Ecol. Modell.* **245**, 103–110.
- Teodoro, A.C. & Araujo, R. (2016). Comparison of performance of object-based image analysis techniques available in open source software (Spring and Orfeo Toolbox/Monteverdi) considering very high spatial resolution data. *J. Appl. Remote Sens.* **10**, 16011.
- Thuiller, W., Araujo, M.B. & Lavorel, S. (2004). Do we need land-cover data to model species distributions in Europe? *J. Biogeogr.* **3**, 353–361.
- Van Winkle, W. (1975). Comparison of several probabilistic home-range models. *J. Wildlife Manag.* **39**, 118–123.
- VanderWal, E. & Rodgers, A.R. (2012). An individual-based quantitative approach for delineating core areas of animal space use. *Ecol. Modell.* **224**, 48–53.
- VanDerWal, J., Shoo, L.P., Graham, C. & Williams, S.E. (2009). Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecol. Modell.* **220**, 589–594.
- Venier, L.A., Pearce, J., McKee, J.E., McKenney, D.W. & Niemi, G.J. (2004). Climate and satellite-derived land cover for predicting breeding bird distribution in the Great Lakes Basin. *J. Biogeogr.* **2**, 315–331.
- Verwajen, D. & Van Damme, R. (2008). Wide home ranges for widely foraging lizards. *Zoology* **111**, 37–47.
- Warren, D., Matzke, N., Cardillo, J., Baumgartner, R., Beaumont, L., Huron, N., Simões, M., Iglesias, T.L. & Dinnage, R. (2019). *ENMTools R Package*. <https://doi.org/10.5281/zenodo.3268814>
- Warren, D. L. & Seifert, S. N. (2011). Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* **21**, 335–342.
- Worton, B.J. (1987). A review of models of home range for animal movement. *Ecol. Modell.* **3–4**, 277–298.
- Worton, B.J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **1**, 164–168.
- Yañez-Arenas, C., Peterson, A.T., Mokondoko, P., Rojas-Soto, O. & Martínez-Meyer, E. (2014). The use of ecological niche modeling to infer potential risk areas of snakebite in the Mexican State of Veracruz. *PLoS One* **9**, e100957.
- Zimmermann, N.E., Edwards, T.C., Moisen, G.G., Frescino, T.S. & Blackard, J.A. (2007). Remote sensing-based predictors improve distribution models of rare, early successional and broadleaf tree species in Utah. *J. Appl. Ecol.* **5**, 1057–1067.

Supporting Information

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

Figure S1. Results of null models of females and males for Bioclim, GAM, GLM and random forest.

Figure S2. All realized niche models for males. Habitat suitability increases from light to dark colours.

Figure S3. All overlaps for females between habitat suitability maps and Minimum Convex Polygons with 90% of locations.

Figure S4. All overlaps for females between habitat suitability maps and Minimum Convex Polygons with 50% of locations.

Figure S5. All overlaps for males between habitat suitability maps and Minimum Convex Polygons with 90% of locations.

Figure S6. All overlaps for males between habitat suitability maps and Minimum Convex Polygons with 50% of locations.

Table S1. Comparison of null and individual Maxent models: ANOVA or Kruskal–Wallis results per individual (females and males). Average and standard deviation AUC from empirical and null models are indicated.

Table S2. Variable contribution to Maxent models (in bold the first variable contributing most; in italic the second one) per individual (females and males). See Table 1 for variable codes. In the case of females, Dist corresponds to Distance to males; and in the case of males, to Distance to females.

Table S3. Area and overlap size results between habitat suitability models and Minimum Convex Polygons per individuals (females and males). The table is organized as a matrix: the first two lines of values in the semi table corresponds to the sizes of the habitat suitability maps; the first column corresponds of values to the sizes of MCPs with 90% and 50% of

locations. The values inside the matrix are the size of overlaps between models and MCPs. First lines correspond to mean values; second lines are the standard deviation. See Table S3 for results per individuals.

Text S1. Results of null models of females and males for Bioclim, GAM, GLM and random forest.