Spring home range and spatiotemporal activity of Edward's Sand Racer (*Psammodromus edwarsianus*) in a protected natural area of southern France

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Abstract

Home range and spatiotemporal activity are often lacking for small vertebrates that are difficult to mark individually and to monitor over sufficiently long-time scales to collect reliable information. This is particularly the case for the Edward's Sand Racer Psammodromus edwarsianus*, a small Mediterranean lizard that is almost threatened with extinction in France. In order to fill these gaps, we conducted a four-year mark-recapture survey (2019-2022) carried out on a 0.5ha quadrat composed of two distinct habitats of equivalent surface area (open rocky area and Aleppo pine forest). We estimated the 95% and 50% (core area) spring home ranges for 10 adult individuals (5 males and 5 females) using the Autocorrelated Kernel Density Estimation method. We assessed daily activity patterns of* P. edwardsianus *and tested whether these differed between the two habitat types using a Generalized Linear Mixed Model. The surface of spring home range varied greatly between individuals (for females, 95% AKDE range from 733m² to 3340m² and 50% AKDE range from 158m² to 546m². For males, 95% AKDE range from 4556m² to 7434m² and 50% AKDE range from 779m² to 1658m²), and reached up to 290 times the value formerly reported in the literature with significantly larger spring home ranges for males than females. The activity of* P. edwardsianus *did not vary significantly between the two habitats, and regardless of habitat type, activity was highest in the morning and late afternoon. The data collected have enabled us to gain a better understanding of the displacement potential and the spatiotemporal activity patterns of* P. edwardsianus*. This study also provide methodological elements and advice for optimizing the monitoring of this species.*

Résumé

Les données sur la taille des domaines vitaux et l'activité spatio-temporelle des petits vertébrés sont souvent lacunaires. En effet, les animaux de petite taille sont difficiles à marquer individuellement

et à suivre sur des périodes suffisamment longues pour recueillir des informations fiables. C'est notamment le cas pour le Psammodrome d'Edwards, Psammodromus edwarsianus, *un petit lézard méditerranéen quasiment menacé d'extinction en France. Pour combler ces lacunes, une population de Psammodrome d'Edwards a été suivie par Capture-Marquage-Recapture (CMR) durant 4 ans (2019-2022) sur un quadrat de 0,5 ha composé de deux habitats distincts de surface équivalente (zone rocheuse ouverte et forêt de pins d'Alep). Nous avons estimé les domaines vitaux printaniers à 95 % et 50 % (aire centrale) pour 10 individus adultes (5 mâles et 5 femelles) à l'aide de la méthode AKDE (Autocorrelated Kernel Density Estimation). Nous avons étudié le rythme d'activité quotidien du Psammodrome d'Edwards et vérifié s'il différait entre les deux types d'habitat à partir d'un modèle linéaire mixte généralisé (GLMM). La surface du domaine vital printanier présente une forte variabilité individuelle (pour les femelles, les AKDE à 95 % vont de 733 m² à 3 340 m² et les AKDE à 50 % vont de 158 m² à 546 m². Pour les mâles, les AKDE à 95 % vont de 4 556 m² à 7 434 m² et les AKDE à 50 % vont de 779 m² à 1 658 m²) et elle est jusqu'à 290 fois supérieure à ce qui était actuellement connu pour cette espèce. En outre, les domaines vitaux printaniers sont significativement plus grands pour les mâles que pour les femelles. L'activité du Psammodrome d'Edwards n'a pas varié de manière significative entre les deux habitats et, quel que soit le type d'habitat, l'activité était la plus élevée le matin et en fin d'après-midi. Les données collectées nous ont permis de mieux comprendre l'utilisation de l'espace et l'activité spatio-temporelle des individus étudiés. Cette étude fournit également des éléments méthodologiques et des conseils pour une meilleure optimisation du suivi de cette espèce.*

Introduction

Understanding space use patterns of animals is a fundamental element for devising conservation strategies. However, individual spatial behavior is not fixed and depends on external factors, both biotic (e.g., intra- and interspecific interactions) and abiotic factors (e.g., resource availability and distribution, temperature), but also on the physiological status of the animal (Nathan *et al.* 2008). For example, the physiological need for an ectotherm to regulate its body temperature drives it to find a more suitable location according to external environmental conditions. A significant component of space utilization is the home range, defined by Burt (1943) as the area most frequently used by an animal for essential activities such as foraging and mating. Individuals tend to spend more time within the core area

of their home range where resources, such as shelter or food, are usually present in greater quantity or quality (Asensio *et al.* 2012; Fernandez-Duque & van der Heide 2013; Powell *et al.* 2016; Renet *et al.* 2022). As the home range reflects individual needs, its estimation has important implications for species conservation and management (Schofield *et al.* 2010; Zeale *et al.* 2012; Tanferna *et al.* 2013; Di Franco *et al.* 2018).

Modelling home ranges and characterizing space use require multiple spatial observations from the same individual. However, it is currently challenging to equip small species with telemetry devices, such as VHF or GPS transmitters. If saurians represent less than 5% of studies in spatial ecology based on telemetry among terrestrial reptiles, this is due in part to their smaller size to body mass ratio, as well as their frequent fossorial or arboreal habits, which complicate the attachment or implantation of telemetry devices (Crane *et al.* 2021). In this case, mark-recapture tracking, which typically involves visual markers (e.g., elastomer implants, scale incisions, hot or coloured markings, photo-identification) or smaller implants (e.g., PIT-tagging) for individual recognition, can provide sufficient location data to describe space use (Cadi *et al.* 2008; Hurme 2015; Tisell *et al.* 2019; Simpson *et al.* 2020). Some studies have shown that home range and core area estimations do not significantly differ between mark-recapture and radio-telemetry methods (Cadi *et al.* 2008; Tisell *et al.* 2019), suggesting that the mark-recapture approach is a valid alternative solution to characterize individual space use especially for small species that cannot be equipped with on-board tracking systems.

The spatiotemporal activity of an individual refers to how he distributes its activity over time and space. In reptiles, the efficiency of thermoregulation strongly depends on their ability to adjust their activity at both spatial and temporal scales in response to temperature variations (Clusella-Trullas & Chown 2014; Taylor *et al.* 2021). In temperate regions, lizards are more active during periods of moderate temperatures than during extreme thermal conditions. For instance, in a Mediterranean environment, lizards exhibit bimodal summer activity patterns characterized by a peak of activity just after sunrise, a period of reduced activity around midday, and a second slightly less pronounced peak in the late afternoon (Carrascal & Diaz 1989). This bimodal activity pattern is particularly

pronounced in small lizards weighing less than 2-3 grams, primarily due to their low thermal inertia, which exposes them to greater risks of overheating (Herczeg *et al*. 2007). Moreover, lizards can adjust their use of sunlit and shaded areas according to seasons and the time of day in response to ambient temperature fluctuations. For instance, they exhibit a strong preference for sunlit areas when the air temperature is below their optimal temperature (Carrascal & Diaz 1989). This explains the greater selection of sunlit sites in spring and a progressive preference for shaded sites as the warmer summer months arrive (Díaz & Cabezas-Díaz 2004).

The Edward's Sand Racer *Psammodromus edwarsianus* is a Lacertid of small body size (total length < 13cm) (Fitze 2012). Living in arid areas, its distribution encompasses the eastern part of the Iberian Peninsula and a large part of the French Mediterranean region (Mendès *et al*. 2017). This saurian is generally found in open habitats where the vegetation cover on the ground is low (e.g., coastal dunes, stony plains, scrublands, low maquis) (Carretero 1993; Vacher & Geniez 2010). The activity of *P. edwardsianus* varies with the seasons (Mellado & Olmedo 1984), peaking in spring (breeding period) and decreasing in summer (Seva Román 1982; Barbadillo 1987; Fitze 2012). The strongly carinated scales covering its back indicate its burrowing nature. The brownish-gray back of the species is ornated with six yellowish lateral lines crossed by rectangular black spots (Muratet 2015). When threatened, *P. edwarsianus* quickly flees and suddenly stops after reaching a shelter, where it remains immobile to avoid predator detection (Fitze 2012). Because of the difficulty of detecting this animal, catching it, marking it permanently and the considerable sampling effort involved, there are gaps in our knowledge of its home range and habitat use. In France, *P. edwarsianus* is particularly affected by the fragmentation of its natural habitats as a result of urbanization projects and reforestation following changes in agricultural practices, which sometimes leads to the total closure of its habitats. It is therefore urgent to better characterize certain aspects of its ecology and provide relevant conservation measures.

We conducted a four-year spring mark-recapture monitoring (2019-2022) in a protected natural area to describe space use of *P. edwarsianus*. Specifically, we estimated the spring home range and core area size for a part of the population. We also characterized the spatiotemporal activity patterns and tested whether these patterns varied within a habitat complex composed of an open rocky habitat and a pine forest in the process of colonization. Based on our results, we recommended specific management measures to improve species' conservation and provided guidelines on how to optimize future monitoring efforts for the species.

Material and methods

Study area

We conducted the study in the Mediterranean region of southeastern France, specifically in the protected area of the Sainte-Victoire national nature reserve (commune of Beaurecueil) in the central part named "Grands Creux" (43°31.72'N, 5°32.52'E), where public access is prohibited (Fig. 1a). We delimited a study quadrat of 5000m² (71 x 71m) in a sector consisting of two distinct adjacent habitats with equivalent surfaces. The first habitat was an open rocky area with very low ground vegetation cover and small copses of Rosemary (*Rosmarinus officinalis*)
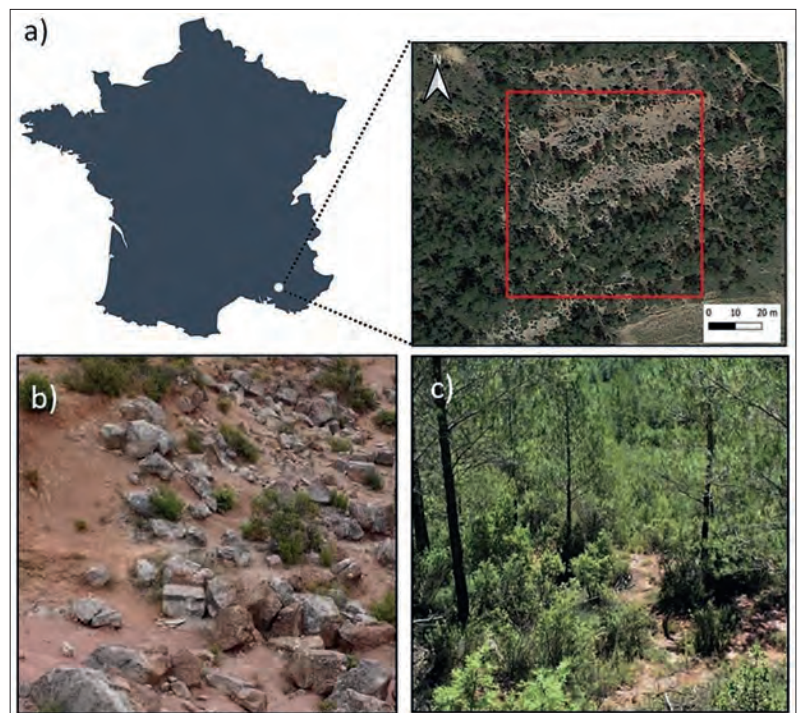

Figure 1 – a) Location of the Sainte-Victoire nature reserve in southern France (white dot) and aerial view of the study quadrat (red square); b) Open rocky habitat and c) an Aleppo pine forest within the study quadrat.

and Kermes oak (*Quercus coccifera*) scattered on red clay substrate (Fig. 1b). The other habitat on the quadrat was an Aleppo Pine Forest (*Pinus halepensis*) with an understory of shrub species: *Rosmarinus officinalis, Juniperus oxycedrus, Phillyrea angustifolia, Cytisus spinosus, Quercus coccifera* (Fig. 1c).

Data collection

From 2019 to 2022, we conducted a monitoring of a *P. edwarsianus* population during spring (late April to mid-June) when *P. edwarsianus* exhibits maximum breeding activity (Pascual-González & Pérez-Mellado 1989). Depending on the year, we combined or alternated pitfall trapping and hand catches to capture lizards. In 2019, we conducted only passive pitfall trap captures on a total of 14 capture days. In 2020, we combined pitfall trapping and manual capture on a total of 17 capture days. In 2021 and 2022, we employed only manual trapping for a total of 14 and 13 days of capture, respectively. We divided the sampling period each year into several sessions of two to three consecutive days of capture.

We used 120 buckets (22.6cm x 19cm) of 5.6-liter capacity, buried flush to the ground and evenly distributed every 5 meters across the study quadrat for pitfall trapping. This passive capture device was selected for its reported capture success in lizard ecology studies (Enge 2001; Rotger *et al.* 2016; Wilson 2016). When used, the device was monitored hourly from 9:00 a.m. to 7:00 p.m.

In years involving manual capture, two to three experienced observers were mobilized to properly execute this technique. The survey for hand-capture involved six hours of daily time split into three hours in the morning and three hours in the afternoon.

All captured individuals were sexed and marked. We determined sex by the presence of dilated femoral pores and a cloacal bulge in males. We only captured individuals that were at least eight to nine months old and considered sexually mature (Pascual-González & Pérez-Mellado 1989). To mark the individuals, we superficially cauterized the scales of their lower jaw using a ®bvi Accu-Temp cauterizing pen, following the method of Ekner *et al.* (2011) (Fig. 2). We used a headband magnifier (®Schweizer, magnification x 3) for better accuracy. This method is quick to use (10 seconds) and
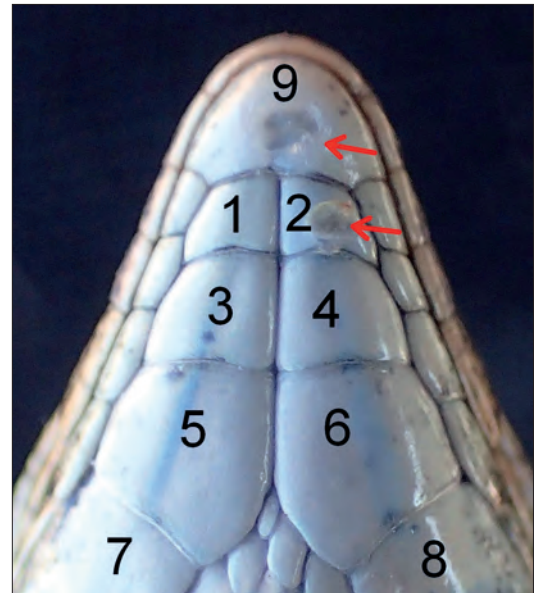

Figure 2 – *Individual identification system proposed by Ekner* et al. *(2011) and superficial cauterisation of the scales of the lower jaw (located by red arrows). Photo: Julien Renet*

Figure 3 – *Dorsal marking (red arrow) of an adult male (n°35) for remote reading with binoculars. Photo: Julien Renet*

limits the stress associated with handling because the animal is released immediately. In addition, previous studies have shown that this marking method has no obvious negative effects on reptiles (Winne *et al*. 2006; Vervust & Van Damme 2009). We also took a second photographic marking based on the patterns on the back and the arrangement of the gular scales specific to each individual to reduce the risk of inter-annual misidentification, such as an individual incorrectly considered as a new capture (Perera & Pérez-Mellado 2004). To limit intra-annual manipulations and enable remote individual recognition with binoculars (®Swarovski EL 10x42), we inscribed an identification number on the back of each individual using a paint pen (®Edding 750 no-toxic) (Fig. 3). Paint markings last for around 25 days before being erased spontaneously (by rubbing) or leaving with the moult. When reading is no longer possible from a distance, the animal is recaptured, identified by the cauterisation code and marked again on its back.

Each individual captured or remotely identified at a distance with binoculars was geolocated using a GPS (®Garmin eTrex 20X) with an accuracy of 3 meters.

Home range estimation

We utilized an Autocorrelated Kernel Density Estimation (AKDE) (Fleming *et al*. 2015) to estimate the home ranges of *P. edwarsianus* from geolocalized observations. This continuous-time model-based method has the advantage of accounting for autocorrelation in spatial data and accommodating irregular sampling intervals (Fleming *et al*. 2018) and small sample sizes (Fleming *et al*. 2019).

In order to obtain the most accurate home range estimates possible, individuals must show site fidelity with stationary movements over a defined time period (Horne *et al*. 2020). We confirmed the site fidelity for each individual by examining the semi-variograms displaying the semi-variance in positions as a function of the time lag separating observations (Fleming *et al*. 2014). We then applied two estimators to fit the AKDEs: the perturbative Hybrid Residual Maximum Likelihood estimation (pHREML), which reduces bias related to small sample sizes (Fleming *et al*. 2019), and the weighted AKDE (wAKDEc), which corrects for irregularities in the sampling design (Fleming *et al*. 2018). Finally, we selected the best individual movement

model based on the Akaike information criterion (AIC) to estimate the 95% and 50% (core area) home range size.

All analyses were conducted using the ctmm package (Calabrese *et al*. 2016) on R software (v. 1.4.1717) (R Core Team 2021).

Spatiotemporal activity patterns

During each monitoring session, we installed two ambient temperature and relative humidity loggers (®Tiny Tag TGP 4500) at about 1.50m above the ground. Both loggers recorded data every five minutes, with one device placed in the open rocky habitat and the other in the Aleppo pine forest. We used these loggers to record and compare temperature (in °C) and relative humidity (in %) between the two habitats, resulting in a dataset of 29,432 data points for each variable. To compare the means obtained for these variables between the two habitats, we used a non-parametric Wilcoxon-Mann-Whitney test.

To assess the daily spring activity of *P. edwarsianus* and examine whether habitat selection (open rocky area or Aleppo pine forest) differed during the day, we performed an analysis based on the number of passive captures (captured only with pitfall traps) to avoid bias related to visual detection, which could differ depending on the habitat. Specifically, we used the number of individuals captured in pitfall traps between April 29 and June 19, 2019 for a total of 14 days during which the traps were open. We conducted trap checks hourly and associated each individual captured in a bucket with the corresponding habitat type. Captures were grouped and classified into three time slots: 09:00 a.m. to 12:00 p.m., 01:00 p.m. to 04:00 p.m., and 04:00 p.m. to 07:00 p.m.

We used a Generalized Linear Mixed Model (GLMM) to investigate potential differences in the number of passive captures (n = 110), obtained from 41 different sexually mature individuals (25 males and 16 females), between habitat types (n = 2), time slots (n = 3), and the interaction between these two factors. No strong correlation was identified between habitat type and time slot (correlation test, |r|< 0.7), allowing them to be considered as fixed effects in the analyses (Hosmer & Lemeshow 2000). Trap sessions was treated as a random effect. Using glmmTMB (Magnusson *et al*. 2017) and MuMIn (Barton 2020) packages, we

generated models representing all combinations of explanatory variables, and fitted them with a Poisson distribution. We selected the best-fitting model to explain the number of passive captures of *P. edwarsianus* based on the AIC corrected for small numbers (AICc). We considered only models with ΔAICc < 2 as plausible (Burnham & Anderson 2002), with the model with the lowest AICc selected as the best model (Wagenmakers & Farrell 2004; Bolker 2008, 2016). To assess the goodness of fit of the various models, we calculated the marginal R^2 (Rm^2), which estimates the variance explained by the explanatory variables, using the performance package (Lüdecke *et al*. 2021). The data were analyzed using R software (v. 1.4.1717) (R Core Team 2021).

Results

Home range estimation

The four years of monitoring provided sufficient GPS locations to study the spring home range of 10 sexually mature individuals (189 geolocated observations in total), including 5 males and 5 females. One individual was recaptured over four years (2019-2022), while three individuals were observed for just one year, four for two years, and two for three years (Table 1). The minimum GPS location value was 15 and the maximum was of 33, with a mean of 18.9 and a median of 16.

Our results showed that the 95% spring home ranges ranged from 733 to 7434m², while the 50% core areas ranged from 158 to 1658m²

for both sexes combined (Table 1, Fig. 4). For females, the mean spring home range (95% AKDE) was 2131m² ± SD 1038m², and the 50% core area (50% AKDE) was 420m² ± SD 157m². In contrast, for males, the mean spring home range (95% AKDE) was 5687m² ± SD 1303m², and the 50% core area (50% AKDE) was 1162m² ± SD 322m² (Table 1, Fig. 4). We also found that male home ranges were significantly larger than female home ranges at both 95% (t-test, t = -4.7724, P < 0.01) and 50% (t-test, t = -4.6302, P < 0.01) confidence levels (Fig. 5).

Daily activity and habitat selection

The rocky open habitat exhibited significantly higher mean temperature compared to the Aleppo pine forest at the end of the four years of spring monitoring (Wilcoxon, W = 23363910, P < 0.001). Conversely, relative humidity was significantly lower in the rocky open habitat (Wilcoxon, W = 30085835, P < 0.001).

Between April and June 2019, a total of 110 passive captures of *P. edwarsianus* were recorded, representing 41 distinct individuals (25 males and 16 females). The Aleppo pine forest habitat accounted for 52 captures, while the open rocky habitat resulted in 58 captures. Additionally, significant variations in capture counts were observed across different time slots during the day. Specifically, there were 47 captures recorded between 09:00 a.m. and 12:00 p.m. and 49 captures between 04:00 p.m. and 07:00 p.m. In contrast, the time slot from 01:00 p.m. to 04:00 p.m. yielded only 14 captures, suggesting reduced lizard

Table 1 – Summary of Autocorrelated Kernel Density Estimation (AKDE) results per individual presented in m². The 95% AKDEs correspond to the spring home range estimates while the 50% AKDEs represent the core area estimates. Confidence intervals (CI) are also shown for each category (95% and 50%). Abbreviations: M: Male. F: Female., SVL: Snout-Vent Length ASS: absolute sample size (raw number of geolocated data). ESS: effective sample size (the value obtained by the tracking duration divided by the number of home range crossings made by the animal). SIM: start of individual monitoring. EIM: end of individual monitoring.

| Individual	Sex	SVL range (mm)	ASS	ESS	SIM	EIM	95% AKDE	CI (95%) AKDE	50% AKDE	CI (50%) AKDE
PSAM_16	F	40 to 44	16	16.73	2019-05-01	2020-06-17	733.25	425.02-1124.15	158.06	130.57-184.13
PSAM_26	M	40 to 42	33	26.76	2019-05-01	2022-05-17	6719.63	4418.98-9494.75	1658.33	1432.34-1874.57
PSAM_48	F	40.5 to 43	20	19.09	2019-05-21	2021-06-17	1713.86	1033.287-2563.83	463.02	387.84-534.50
PSAM_49	M	41 to 43	25	19.22	2019-05-14	2021-05-31	4555.87	2751.962-6807.07	1203.61	1008.86-1388.78
PSAM_346	M	40	16	15.82	2021-05-03	2021-06-07	4729.47	2693.46-7329.20	779.08	639.58-911.20
PSAM_368	M	41	15	14.00	2021-05-05	2021-06-17	7433.87	4064.17-11804.13	1151.30	931.61-1358.84
PSAM_234	M	39.5 to 40	17	16.00	2020-05-20	2021-05-26	4997.78	2856.67-7727.89	1019.16	837.75-1191.02
PSAM_279	F	41	16	9.96	2021-05-03	2021-06-17	2955.14	1414.65-5053.44	528.80	408.30-641.82
PSAM_347	F	44 to 45	16	15.90	2021-05-04	2022-05-10	3339.59	1905.07-5170.12	546.51	448.92-638.95
PSAM_349	F	41 to 43	15	14.73	2021-05-04	2022-04-27	1915.44	1065.56-3010.41	404.54	329.37-475.64
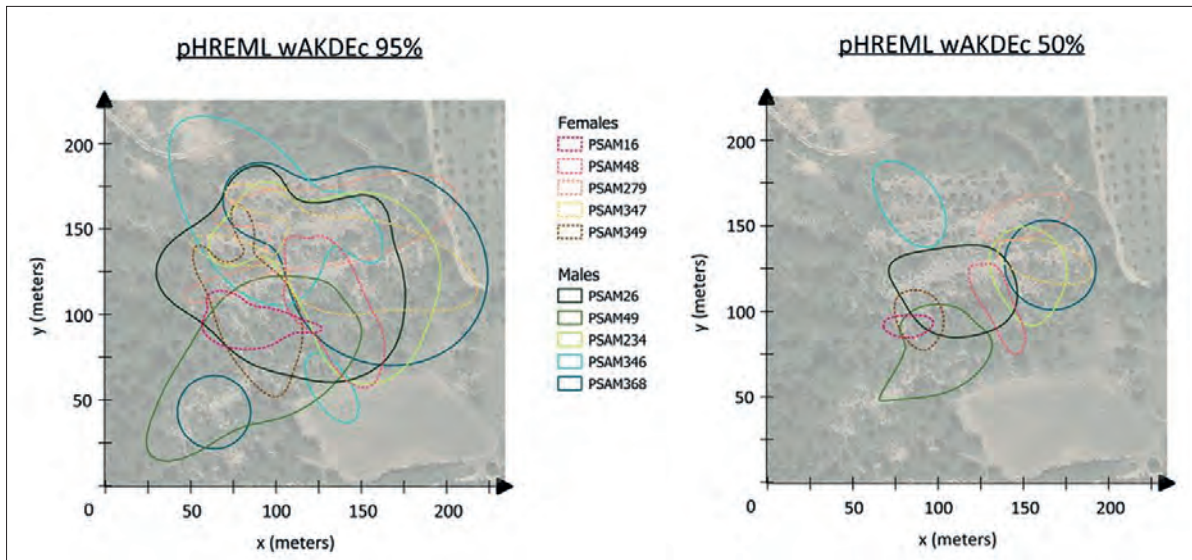
Figure 4 – Projection of estimated home ranges (pHREML wAKDEc 95% and pHREML wAKDEc 50%) for the 10 individuals (5 males and 5 females) in the study area within the Sainte-Victoire Nature Reserve. Longitude (x) and latitude (y) axis are in meters.
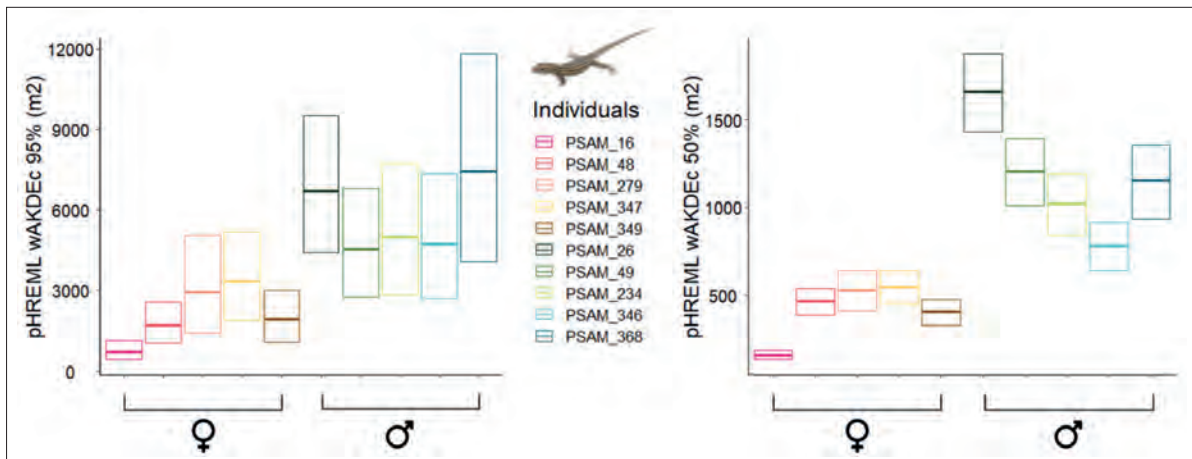

Figure 5 – Boxplots displaying the home ranges (pHREML AKDEc 95%) and core areas (pHREML AKDEc 50%) of the 10 individuals (5 males and 5 females). Middle lines represent the estimated values, while horizontal lines indicate the minimum and maximum confidence intervals.

Figure 6 – Boxplots of the number of passive captures of Psammodromus edwarsianus for the three time slots and two habitat types (Aleppo pine forest and open rocky habitat). Boxes represent the median (bold horizontal black axis), 1st and 3rd quartile (lower and upper end of the box) and interquartile (ends of axes perpendicular to the box).
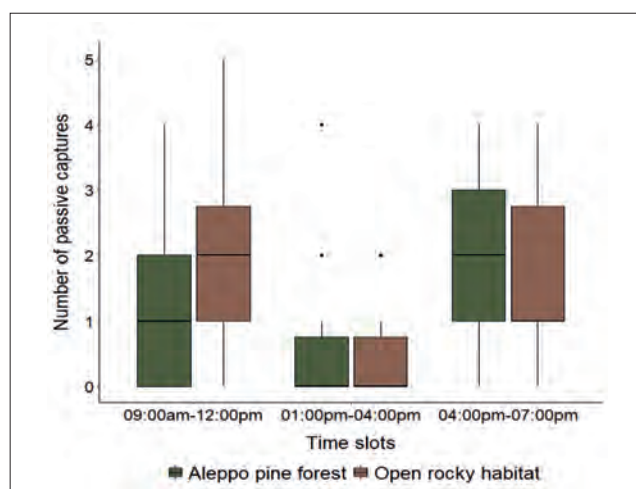
activity during this period (Fig. 6). Selection of the best model based on the AICc showed that time slots were the only significant factor influencing passive captures, while no significant effects of habitat or interaction with time slots were found (Table 2). In other words, lizards seemed to use the open and semi-enclosed area in the same way, regardless of the time slot.

Table 2 – *Construction of models to explain the number of passive captures of* P. edwarsianus. *Model 4 is the null model containing neither time slot, habitat, nor interaction as explanatory variables. For each model, degrees of freedom (df), AIC and ΔAICc scores are specified. The marginal R2 values describe the proportion of variance explained by the explanatory variables and provide information on the goodness of fit of the models. With a ΔAICc < 2 and lowest AICc, model 1 (in bold) is the best model.*

Models	Explanatory variables	df	AICc	ΔAICc	Rm²
1	**Time slot**	**5**	**253.3**	**0.00**	**0.376**
2	Habitat + Time slot	6	255.3	1.94	0.378
3	Habitat*Time slot	8	258.3	4.93	0.390
4	1	3	273.8	20.44	0.000
5	Habitat	4	275.6	22.26	0.005

Discussion

New insights on the *P. edwarsianus* home range

The analysis of spring home ranges reveals a significant vagility in *P. edwarsianus* that was not previously demonstrated. The highest estimated home range (7434m² for ID 368) is over 290 times larger than the value reported in the literature (25m²) (Seva Román 1982). Moreover, estimated home ranges for the 10 individuals studied are presumably under-estimated as the data used to obtain spatial estimates were collected from random visual observations within the study quadrat's perimeter, rather than from telemetry tracking. This can result in a truncation effect when the mark-recapture grid size is smaller than the home range (Tisell *et al*. 2019). The significantly larger spring home range of males compared to females is consistent with results observed in most lizard species (Griffiths 1999; Wone & Beauchamp 2003; Germano & Rathbun 2016). Males appear to be more vagile in the spring and less confined than females. This difference may be explained by the gestation of females, which occurs rapidly at the beginning of spring, with oviposition observed as early as April (In Den Bosch 1986). As a result, a change in thermal behaviour (i.e., modification of the time allocated to thermoregulation) associated with a reduction in locomotor capacities linked to a strong weight gain (up to 1g) during this period (In Den Bosch 1986) are likely to modify the spatial patterns of females. Gravid females of *Microlophus occipitalis* (Watkins 1997) and *Zootoca vivipara* (Le Galliard *et al*. 2003) have been shown to exhibit reduced rates of movement and decreased performance, while

gravid females of *Crotaphytus collaris* modify their spatial behaviour by staying closer to refuges (Husak 2006).

In this study, we also demonstrate that the home ranges of *P. edwarsianus* are not limited to open rocky habitats, but also include Aleppo pine forests. The individuals therefore clearly move from an open habitat to a forest habitat in the process of being closed, without the latter representing a repulsive barrier. This stage of ecological succession therefore still seems to be suitable for this species locally.

Spatiotemporal activity and influence of habitat use

We observed a significant decrease in passive captures during the time slot of 1:00 p.m. to 4:00 p.m. in spring (late April to mid-June) based on the activity analysis. As noted by Carretero and Llorente (1993), the recorded activity exhibited a bimodal distribution, with a major reduction during the hottest hours of the day. This activity pattern is typically associated with lizards inhabiting deserts or other seasonally warm environments, such as the Mediterranean region (Adolph & Porter 1993).

Our GLMM analysis based on passive captures (pitfall traps) found no difference in habitat use dynamics between the open rocky area and the Aleppo pine forest during spring. Although the species is particularly well adapted to early stages of Mediterranean vegetation (Carretero & Llorente, 1997-1998), the importance of wooded and more closed habitats should not be downplayed, especially if they are adjacent to open habitats. Climate change and degradations in the suitability of thermal conditions directly threaten ecotherms such as lizards (Sinervo *et al*. 2010; Kubisch *et al*. 2016; Flesch *et al*. 2017), and in some arid and semi-arid regions, temperature increases are so rapid that adaptation rates do not keep pace with climate change (Radchuk *et al*. 2019). Some lizard species (such as those in the genus *Sceloporus* in Mexico), when subjected to thermal stress (e.g., excessively high ambient temperature), are forced to spend more time sheltered from solar radiation (Kearney *et al*. 2009; Sinervo *et al*. 2010). This thermal behavioural shift has resulted in reduced time devoted to foraging and mating searches, and eventually population decline. In light of this context, the availability of cooler and shaded habitats (e.g.,

forests) would help alleviate thermal stress for many ectotherms (Sunday *et al*. 2014). Our results demonstrate that the wooded area recorded lower temperatures and higher relative humidity compared to the rocky area during the same periods. The habitats composed of a tree layer in the study quadrat and other reserve sectors probably already serve as thermal refuges against extreme summer temperatures. On the other hand, more in-depth studies in forest stands with different structures (and at different seasons) are needed to better understand the role of this habitat on the dynamics of *P. edwarsianus* populations and at what stage of evolution it becomes unfavourable to the species.

Indeed, it has been established that the development of excessively dense vegetation cover resulting from the ecological succession process could lead to population decline, as observed on El Prat de Llobregat beach (Barcelona, Spain) (Fitze 2012). Aerial photographs obtained from the geoportal website (https://www.geoportail.gouv.fr) of the Sainte-Victoire Nature Reserve from 1950 to 1965 clearly show an expansion of the Aleppo pine forest in the study area. Monitoring its development and characterizing the evolution of its structure, especially at the level of the understory, will be necessary in the future for the conservation of this ectothermic species. Multivariate analyses have shown that several species of Mediterranean-Iberian lizards (including *Psammodromus*) preferentially use open forest zones composed of low bushes and are more abundant in such areas (Martín & Lopez 2002).

Management implications

Robust methods for collecting and analyzing spatial data provide new insights into the home range and spatiotemporal activity patterns of *P. edwarsianus*. To better understand the ecological requirements of the species, it is essential to consider these new findings. The conservation of a mosaic habitat with sun basking spots and thermal shelters should be promoted in the nature reserve area to ensure the maintenance of populations.

Selective cutting could be considered in the densest forest areas to promote the development of the shrub layer in the lower levels. This would make it possible to study the colonisation processes of new corridors and to test the responses to different silvicultural management methods. Initially, it is recommended to follow the recommendations of Azor *et al*. (2015), who reported a positive and significant response of the reptile community in terms of diversity and abundance after a 66% reduction in pine density. Felled trees and cutting residues should be kept on the ground to increase shelter density and humidity levels during the organic matter decomposition process. An analysis of the most relevant forest units to be treated should be carried out to prioritize tree felling interventions based on the structure of the forest cover and the spatial distribution of *P. edwarsianus* population.

Passive captures and time slots indicate a decrease in activity rhythm during the hottest hours of the day in spring. To maximize the chances of observing individuals during chorological or presence-absence studies, this time slot should be avoided in spring. These findings could also provide a framework for optimizing naturalist expertise during environmental impact assessment.

Acknowledgements

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