

Spatial pattern and shelter distribution of the ocellated lizard (*Timon lepidus*) in two distinct Mediterranean habitats

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Abstract. The knowledge of a species' spatial ecology is essential for its conservation as it helps to implement targeted protection measures to suitable habitats. In 2011 and 2013, two French populations of ocellated lizards *Timon lepidus* were monitored through very high frequency (VHF) radio telemetry in two distinct Mediterranean habitats: a 77 ha scrubland (n = 8) and a 1590 ha semi-arid steppe (n = 11) corresponding to a heterogeneous and homogeneous habitat respectively. The variability in spatial estimates for the seasonal habitat use of the ocellated lizard was compared within the two sites using the Autocorrelated Kernel Density Estimation (AKDE). Recursive movement patterns and spatial repartition of shelters were further assessed to study the habitat influence on the species' space use. No significant differences between sexes or sites were identified in the computed AKDE ranges. This inter-site approach demonstrated higher shelter revisits in core-areas than in the rest of estimated home ranges for both sites. A higher shelter density was observed in the core areas of the lizards than in the rest of their home-ranges for the Mediterranean scrubland but not for the semi-arid steppe. Such findings might attest to the species' adaptive capabilities within two distinct Mediterranean ecosystems.

Keywords: autocorrelated kernel density estimation, habitat structure, Lacertidae, Mediterranean ecosystems, recursive movements, spatial ecology.

Introduction

Understanding the spatial ecology of a species is a crucial step for its conservation, as it helps to target and select the most suitable habitat to implement effective protection measures (Law and Dickman, 1998). A deeper insight into spatial ecology further sheds light on the numerous factors shaping a home range, which refers to the entire area within which an individual moves to find food, retreats and mates (Rose, 1982). Nevertheless, few studies focus on animal's tendency to return to previously visited locations (i.e., shelters, breeding grounds,

nesting sites, etc.; Berger-Tal and Bar-David, 2015), also called recursive movement patterns. Such behaviour is seen at different spatial scales according to the animal's behaviour (i.e., flowers for bees; large patches of vegetation for ungulate herbivores) and its knowledge allows the identification of strategic spatial units for the conservation of species (i.e., feeding area, shelters network, predator avoidance area, etc.) (Fryxell et al., 1988; Ohashi and Thomson, 2009).

Location-based tracking using embedded animal's sensors has greatly expanded in recent

years, providing high resolution data and movement trajectories for many animal species (Kays, 2015). Large animals (elephants, tigers, sharks, whales, etc.) are able of carrying relatively heavy and cumbersome equipment (e.g., Argos satellite Doppler-based positions, Global Positioning System, etc.) and benefit from the most efficient and precise technologies. In contrast, studies dealing with lighter animals with limited weight transport capacity rely heavily on very high frequency (VHF) radio telemetry, using short-range transmitters with low battery life (Kenward, 2000; Thomas, Holland and Minot, 2011). Beside an increasing focus on animal movement study and technological improvement of carried devices miniaturisation, data on smaller-sized animals with limited detection probabilities is still scarce (Crane et al., 2021). Such disparity is further explained by the challenge of attaching and maintaining tracking devices on these animals over a long period to provide high quality data with a minimal disturbance of tagged animal's biological traits.

Reptiles are the most diverse terrestrial vertebrate group and one of the most endangered clades at a global scale (Gibbons et al., 2000; Böhm et al., 2013). Yet, they suffer from deprived attention in animal movement studies. Saurian in particular represents the lesser known group within reptiles with only 5% (28/564) of genera being studied (Crane et al., 2021). The lack of knowledge on the spatial ecology of reptiles prevents smart conservation measures (e.g., protection of habitat particularly suited to the physiological needs of a species) (Imansyah et al., 2008; Böhm et al., 2013), which could benefit a whole range of biodiversity, especially when targeting umbrella species (Roberge and Angelstam, 2004).

The ocellated lizard (*Timon lepidus*) is an umbrella species typical of open Mediterranean environment, among the largest European lizard species. French populations of this species have declined considerably over the last few decades (Cheylan and Grillet, 2003, 2005),

echoing a general biodiversity loss from semi-arid Mediterranean landscapes threatened by reforestation (Preiss, Martin and Debussche, 1997; Debussche, Lepart and Dervieux, 1999; Prodon, 2000; Sirami et al., 2010). The ocellated lizard is considered as vulnerable at the national level (UICN France, MNHN and SHF, 2015) and benefits from a national action plan to halt population decline (Thirion and Doré, 2012; Thienpont, 2020). As such, the main threat for this species is identified to be the disappearance of agro-pastoralism habits, which maintain open vegetation environments and habitat connectivity (Cheylan and Grillet, 2003), while extensive urbanisation further exacerbates populations' fragmentation and habitat destruction (Doré, Cheylan and Grillet, 2015).

The studies conducted so far on this species mainly relate to trophic ecology (Hóðar, Campos and Rosales, 1996; Salvidio et al., 2006; Thirion, Grillet and Cheylan, 2009; Tatin et al., 2013), geographical range (Salvidio et al., 2004; Cheylan and Grillet, 2005; Renet et al., 2018) and microhabitat selection (Castilla and Bauwens, 1992; Díaz, Monasterio and Salvador, 2006; Grillet et al., 2010). Only two published studies attempted to estimate home ranges of the ocellated lizard (Salvador, Veiga and Esteban, 2004; Piazzon et al., 2012) but the used methods (i.e., Minimum Convex Polygon and Kernel Density Estimation) are not dealing with spatial autocorrelation and are thus not considered suitable anymore for herpetofauna (Row and Blouin Demers, 2006; Averill-Murray, Fleming and Riedle, 2020; Crane et al., 2021), in light of new spatial ecology tools (Fleming et al., 2015; Noonan et al., 2019).

In order to study the spatial ecology of the ocellated lizard, a study using VHF radio telemetry was conducted in 2011 and 2013 among two French populations of ocellated lizards in two distinct Mediterranean habitats: A scrubland (site A) displaying heterogeneous

habitats and a semi-arid steppe (site B) displaying numerous stone piles erected by man during the Second World War. The objectives were two-fold: First, to assess the variability in spatial estimates for the seasonal habitat use of the ocellated lizard within the two sites using the Autocorrelated Kernel Density Estimation (AKDE). Second, to explore the habitat influence on the spatial use of the ocellated lizard from recursive movement patterns and spatial repartition of shelters.

Material and methods

Study sites

The two ecosystems studied (site A and B) present important singularities in their landscape composition and structure.

Site A covers a 77 hectares area located on the Etoile hill in the Bouches-du-Rhône department, at the east of the Rhône valley and the Camargue delta (fig. 1). This site is characterised by scrublands (38 hectares, 48% of the total area) of various rosemary (*Salvia rosmarinus*), kermes oak (*Quercus coccifera*), shrubby hare's-ear (*Bupleurum fruticosum*) and Provence's gorse (*Ulex parviflorus*). The site is also characterised by closing scrubland from Aleppo pines (*Pinus halepensis*) recolonisation (28 hectares, 37%), while cultures (olive trees, almond, fig), open fields and plantations cover the rest (11 hectares, 14%). The climate is typically Mediterranean with a mean annual temperature of 16°C (maxima in July and August) and an annual low rainfall of 470 mm (maxima in October and November) (ONF, 2004).

Also located in the Bouches-du-Rhône department at 50 km from site A, the site B area covers 1590 hectares from the 7400 ha of the Crau plain national nature reserve (fig. 1). The natural habitat of the Crau plain represents the former delta of the Durance River which became a Mediterranean semi-arid steppe fragmented into several patches that totalize 11 000 hectares. The 7400 ha reserve are grazed each year by 40 000 sheep, which allow a very low vegetation cover to be maintained (Dutoit et al., 2011). The climate is Mediterranean with high inter-annual variability, low rainfall (400–500 mm per year, maxima in spring and autumn), long hot summers and mild winters (mean annual temperature 14°C) (Tatin et al., 2013). The landscape is scattered with thousands of stone piles built during the Second World War in order to avoid planes from landing. These stone piles now represent shelter and basking sites for the ocellated lizard (Tatin et al., 2013).

Animal captures and equipment

The analyses included a total of 19 adult ocellated lizards captured opportunistically by hand within their habitats

starting in May 2013 for site A and in April 2011 for site B. Morphometric data of the captured individuals were recorded with a measuring tape (precision ± 1 mm) for Snout-Vent Length (SVL) and a 300 g spring scale Pesola® (precision $\pm 0.3\%$) for body mass. Five males and three females were captured and monitored at site A. Four males and seven females were captured and monitored at site B. At site A, the mean mass of females ($n = 3$) was 170.0 g (\pm SD 20.0, min = 150.0, max = 190.0) and the mean SVL was 18.8 cm (\pm SD 2.0, min = 16.5, max = 20.0). The mean mass of males ($n = 5$) was 226.7 (\pm SD 58.9, min = 150.0, max = 300.0) and the mean SVL was 19.1 cm (\pm SD 2.2, min = 16.4, max = 20.9). At site B, the mean mass of females ($n = 7$) was 149.9 g (\pm SD 23.2, min = 122.0, max = 191.0) and the mean SVL was 16.6 cm (\pm SD 7.5, min = 15.8, max = 17.9). The mean mass of males ($n = 4$) was 173.0 g (\pm SD 14.9, min = 162.0, max = 194.0) and the mean SVL was 16.8 cm (\pm SD 5.4, min = 16.1, max = 17.4). Differences in SVL and mass between sexes and between sites were explored by a comparative approach with non-parametric tests (Wilcoxon tests).

The transmitters used for this study were very high frequency (VHF) radio elements (thereafter named "tags") composed of a box ($32 \times 13 \times 5$ mm) and a flexible antenna (20 cm length and 0.52 mm diameter, Biotrack Pip3). The weight of the device was 2.68 g which is less than 5% of average body mass of adult ocellated lizards (Mateo, 2011), a commonly yet arbitrary weight limit to minimise the device's impact on animal behaviour (Kingsbury and Robinson, 2016). Tags were attached by a backpack to the lizard's body following a method used previously for several species of reptiles (Warner, Thomas, and Shine, 2006; Van Winkel, 2008) and applied by Chabanier et al. (2012) to the ocellated lizard. Tensoplast bands (elastic and cohesive) were used to design a backpack functioning like a skin-tight tee-shirt allowing free movements of forelimbs and thorax (for breathing). As critically advised by several authors (Kenward, 1987; White and Garrott, 1990; Samuel and Fuller, 1996), tags were tested for signal reception range before attachment to the animals. Signal reception was accomplished by a Biotrack® Sika receiver and a Yagi antenna (3 flexible elements). When an individual lost its tag, it was either recaptured and equipped with the same tags or a new individual was captured instead then equipped with the lost tags. Individual recognition was based on the arrangement of cephalic scales and blue spots on the flanks from photos of each individual. Individuals were labelled as TIMLEP (*Timon lepidus*) followed by the site (A or B) and a digit.

Capture permits were obtained for the two sites studied by the French Government (permit numbers: 2011077-0002, 2013109-0002).

Data collection

The radio telemetry study was conducted in 2013 from May 2 to July 17 for site A (77 days) and in 2011 from April 4 to May 31 for site B (57 days). These monitoring periods correspond to the maximum activity of the ocellated lizard which extends in the Mediterranean region from April to

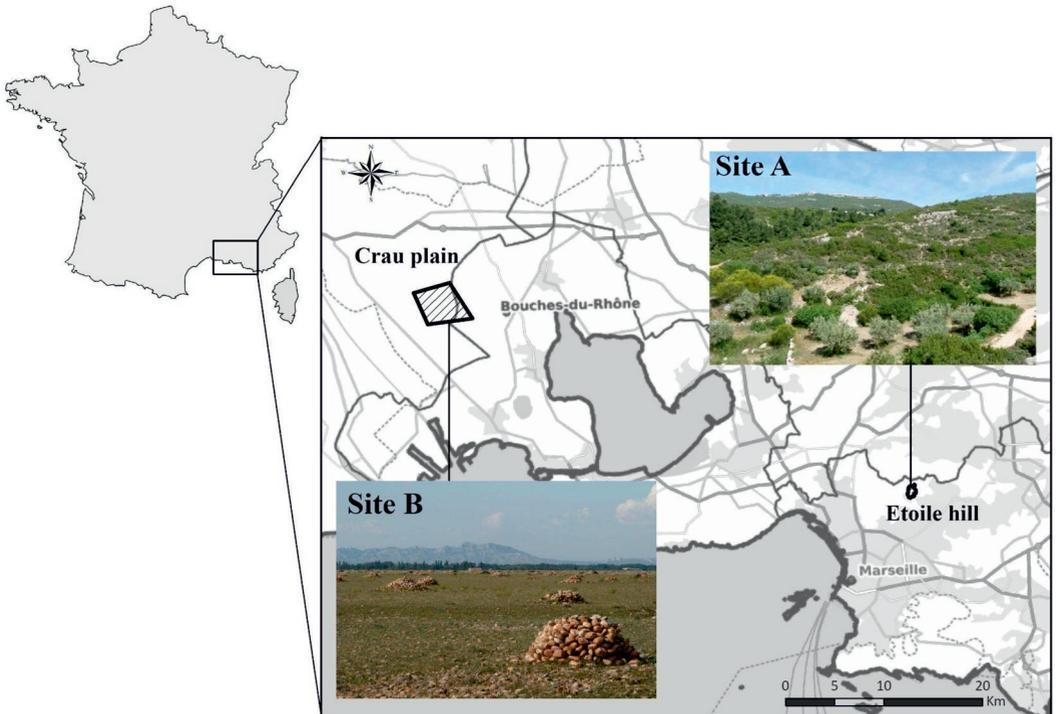


Figure 1. Location of the two study sites in south-eastern France. Site A: Etoile hill and Site B: Crau plain.

June followed by a slow-down in July and August, the most dried months (Vacher and Geniez, 2010).

Individuals were radio tracked from 8 am to 6 pm. Individuals were first detected from a distance with 10×42 binoculars and then geolocated in order to avoid any related influence on behaviour. Position was recorded in Lambert 93 coordinate system using a Garmin GPS (precision of 5 meters), as well as date and time of the day.

Seasonal home range estimation

Spatial patterns of ocellated lizards were assessed using Autocorrelated Kernel Density Estimation (AKDE) (Fleming et al., 2015). This home range estimation method based on continuous-time movement modelling represents a more reliable estimator than traditional Minimum Convex Polygon (MCP) and Kernel Density Estimation (KDE). These latter do not adequately tackle the interdependence of points (Fleming et al., 2015). AKDEs are robust in the face of data gaps (Fleming et al., 2019; Averill-Murray, Fleming and Riedle, 2020) therefore a well-adapted method for manual radio-tracking datasets that often present data gaps due to irregular sampling. AKDE is now widely used for the monitoring of several animal species (e.g., mammals: Wilson-Aggarwal et al., 2020; Meyer et al., 2021, reptiles: Hibbitts et al., 2021, birds: Mitchell, White and Arnold, 2019; Maphalala et al., 2020). It suits well for estimating the home ranges of reptiles because of their sedentary behaviour (Averill-Murray, Fleming and Riedle, 2020; Crane et al., 2021).

Both the seasonal home range area at 95% AKDE and the core area of the animal at 50% AKDE were computed. The core area represents the most frequently occupied part of the home range (i.e., a clustered point pattern) (Powell, Zimmerman and Seaman, 1997). Corrections for irregular sampling design and small sampling size in the data were performed using the pHREML (perturbative Hybrid Residual Maximum Likelihood estimation) and wAKDEc (weighted AKDE) methods following the guidelines proposed by Silva et al. (2021). The pHREML method was intended to mitigate small sample size biases. The wAKDEc method was used to correct irregularities in the sampling design (i.e., missing data or irregularity in the frequency of sampling) (Fleming et al., 2019; Silva et al., 2021). In order to substantially reduce the above-mentioned biases, parametric bootstrap method was applied in addition to pHREML wAKDEc method on each individual with extremely small effective sampling size (i.e., degree of freedom area < 5). (Fleming et al., 2019; Silva et al., 2021). Effective sampling size is characterised by the tracking duration divided by the number of home range crossings the animal undertook. To visually inspect the autocorrelation structure of the location data, estimated semi-variances as a function of time lag were plotted for each lizard. Variograms of individuals exhibiting home-range behaviour (i.e., meeting the range residency assumption for AKDEs use), and thus presenting a so-called stable home range, show an asymptote on the timescale corresponding to the home-range crossing time. On the other hand, non-range

resident individual variograms do not approach any asymptote and are therefore described as displaying an unstable home range. Analyses were carried out in R version 3.5.2 (R Core Team, 2019) using the *ctmm* package (Fleming and Calabrese, 2019) excluding individuals with an unstable home range (i.e., the range residency assumption necessary for home range estimation was not met). AICc was used to select the best fitting continuous-time movement model for each individual.

Density and spatial organisation of the shelters

In site A, the shelters for the ocellated lizard were accounted for and geolocated through field investigation over the 77 hectares of the studied area. The 400 shelters identified as such were categorized as either rocks, low walls, thickets, stumps or burrows, preferably known to be used by the ocellated lizard (Grillet et al., 2010). The number of shelters at site B were investigated through QGIS (version 3.8.3) (QGIS Development Team, 2021) by visualization of high resolution satellite pictures (Orthophotography, 2009, Bouches-du-Rhône; http://geoservices.crigepaca.org/geoserver/crige_ortho/wms) of the studied area, as stone piles are highly visible from the air. Shelter density at both sites for each home range deemed stable was then estimated by making the ratio between the number of shelters and the corresponding AKDE range for the three surfaces considered (i.e., 50% AKDE, 95% AKDE and 50% to 95% AKDE) (supplementary table S1). In the same way, mean distances between shelters were further investigated through QGIS by averaging all distances measured between closest shelters within AKDE ranges (supplementary table S1).

Auto-correlated kernel estimated ranges and habitat structure analyses

Although SVL and mass were collected from tracked individuals, the small amount of data did not allow an explanatory approach using linear models to assess which variables influenced home range size (Jenkins and Quintana-Ascencio, 2020). Even if both study sites are strongly asymmetric in surface area, they were investigated through a descriptive and comparative approach using non-parametric tests (Wilcoxon tests) looking for intra and inter-sites statistical differences between core-areas and home-range areas. Since some differences in home range size between sexes for Lacertidae were shown in the literature, with males having larger ranges (Brown, Gist and Taylor, 1995; Salvador, Veiga and Esteban, 2004), the effect of sex on home-range (95% AKDE) and core area (50% AKDE) ranges was also explored. Shelter density and distance between shelters were compared between the two sites with Wilcoxon tests. Shelter density and distance between shelters within sites were further compared between the 50% AKDE and the rest of the home range (i.e., the home range interval from the 50% AKDE band to the 95% AKDE band) in order to investigate the difference in habitat structure.

Recursive movement patterns

The analysis of recursive movement patterns was based on revisits (i.e., the number of successive visits of a shelter by the same individual) for individuals with a sample size large enough to highlight the regular use of a shelter with the considered behaviour of interest (Bracis, Bildstein and Mueller, 2018a). In this case, individuals with above 30 observation points (three females and two males at site A and three females and one male at site B) were retained for this analysis. A five meters circle radius corresponding to the precision error of the GPS device was delimited around each sighting of an individual provided with accurate coordinates, date and time recordings. The segments of an animal's trajectory from a localisation to another were determined by connecting the closest dates and time while each segment crossing a radius added a revisit to the corresponding point. Recursive movement patterns were investigated through the package *Recurse* version 1.1.2 (Bracis, Bildstein and Mueller, 2018b) in R. The number of shelters contained within the 50% AKDE range and the number of shelters contained within the 50% to 95% AKDE range, averaged among individuals within a site, were compared for each N level of revisits through a Pearson- χ^2 test.

Results

Tracking summary

A total of 8 individuals were tracked at site A (5 males, 3 females) and 11 at site B (4 males, 7 females) with a mean of $44.13 \pm \text{SD } 1.59$ (range 15-93) and $24.45 \pm \text{SD } 0.48$ (range 14-37) points collected, respectively (supplementary table S2). The mean tracking duration was $47.63 \pm \text{SD } 1.33$ days at site A (range 10-76) and $30.09 \pm \text{SD } 0.63$ days at site B (range 14-50) (supplementary table S2). The mean time lag between each point was $26.05 \pm \text{SD } 3.30$ hours at site A (range 0.02-600.67) and $31.67 \pm \text{SD } 1.10$ hours at site B (range 24-144) (supplementary table S2 and fig. S1).

Morphological differences

No significant differences in SVL and body mass were observed between males and females at site A (SVL: $W = 5$, $P = 0.858$; body mass: $W = 2$, $P = 0.212$) and site B (SVL: $W = 7$, $P = 0.857$; body mass: $W = 5.5$, $P = 0.984$). No significant differences were detected between the SVL and body mass of

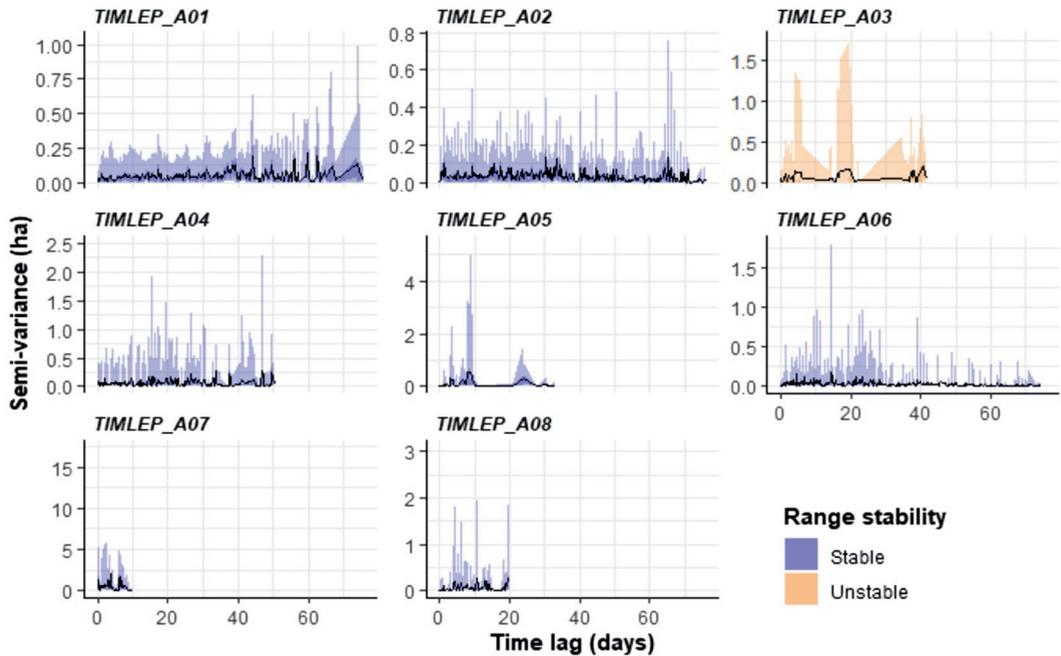


Figure 2. Variograms of 8 individuals from site A displaying semi-variance of home range area estimates with x axis starting at the beginning of each individual's tracking period. Shaded areas display the 50% and 95% confidence intervals.

males at site A and males at site B (SVL: $W = 10$, $P = 0.229$; body mass: $W = 9$, $P = 0.373$). Similarly, there were no significant differences in SVL and body mass between females from site A and site B (SVL: $W = 9$, $P = 0.373$; body mass: $W = 7$, $P = 0.857$).

Seasonal home range estimation

Despite the small sampling size and irregularities in the sampling schedule, 7 out of 8 individuals at site A and 7 out of 11 at site B showed a stable range and thus a tendency to reach the range residency assumption required to compute the AKDE ranges (figs 2 and 3). The presence of peaks in the semi-variogram of all individuals showed variation in movement and space-use pattern. As the home range size was not determined with certainty for five individuals classified as unstable (i.e., the range residency assumption necessary for home range estimation was not met), they were excluded from the following analyses.

Effective sample size for home range estimation was on average $31.86 \pm \text{SD } 1.65$ at site A (range 8.22-74.11) and $9.51 \pm \text{SD } 0.74$ at site B (0.79-20.41) (supplementary table S2), which justifies the use of the pHREML wAKDEc method (Silva et al., 2021). Site B displayed 4 individuals with a very low effective sampling size (<5 ; supplementary table S2) on which bootstrapped pHREML wAKDEc method was used (see Material and Methods).

At site A, the mean core area (50% AKDE) was $3309 \text{ m}^2 \pm \text{SD } 3078 \text{ m}^2$ for males ($n = 4$) and $1246 \text{ m}^2 \pm \text{SD } 450 \text{ m}^2$ for females ($n = 3$) (table 1). Home range estimates (95% AKDE) were on average $15382 \text{ m}^2 \pm \text{SD } 10164 \text{ m}^2$ for males ($n = 4$) and $6755 \text{ m}^2 \pm \text{SD } 2735 \text{ m}^2$ for females ($n = 3$) (table 1, supplementary fig. S2). The mean core area at site B (50% AKDE) was 15050 m^2 , $\pm \text{SD } 6860 \text{ m}^2$ for males ($n = 3$) and 1636 m^2 , $\pm \text{SD } 1459 \text{ m}^2$ for females ($n = 4$), while the mean home range estimates (95% AKDE) were 60755 m^2 , $\pm \text{SD } 28319 \text{ m}^2$ ($n = 3$) for males against 7809 m^2 , $\pm \text{SD } 6908 \text{ m}^2$

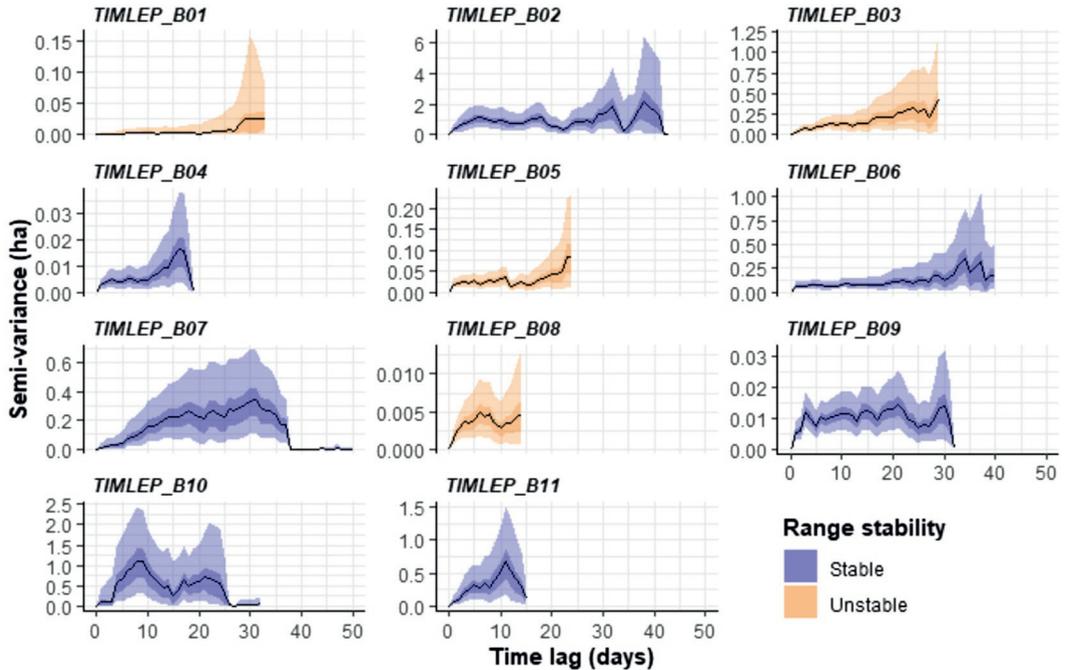


Figure 3. Variograms of 11 individuals from site B displaying semi-variance of home range area estimates with x axis starting at the beginning of each individual's tracking period. Shaded areas display the 50% and 95% confidence intervals.

($n = 4$) for females (table 1, supplementary fig. S3).

Site comparison

Home range (95% AKDE) and core area (50% AKDE) estimated size showed no significant differences between sites for both sexes combined, nor for males and females studied separately (supplementary table S3). Home range and core areas further showed no significant differences within the same site between males and females (supplementary table S3).

No significant differences in shelter density for home-range or core-areas within site A nor within site B were seen between males and females (supplementary table S4). No significant differences in average distance between shelters for home-range or core-areas within site A or site B were further seen between males and females (supplementary table S5).

Since no effect of sex was observed on the explored variables, both sexes were combined in the following analyses in order to increase

the sample size. The core areas of site A had a higher shelter density (Wilcoxon test: $W = 42.50$, $P < 0.05$, $df = 13$) and a smaller distance between shelters than site B ($W = 0.00$, $P < 0.01$) (supplementary tables S4 and S5). No significant differences were observed within the total home range estimates for shelter density ($W = 26.00$, $P = 0.902$) or average distance between shelters ($W = 14$, $P = 0.209$) (supplementary tables S4 and S5). In site A core areas, compared to the rest of the home range, shelter density was higher and distance between shelters was lower respectively ($W = 0.00$, $P < 0.01$) and ($W = 49.00$, $P < 0.01$) (supplementary tables S4 and S5). The analyses showed no such difference at site B for shelter density ($W = 26.00$, $P = 0.897$) nor average distance between shelters ($W = 19.00$, $P = 0.535$) (supplementary tables S4 and S5).

Recursive movement's patterns

All individuals from both sites revisited at least one shelter from their AKDE range while

Table 1. Summary of Autocorrelated Kernel Density Estimation (AKDE) results and movement model used per individual. Abbreviations for sex are M = male, F = female. 95% AKDE correspond to the home range estimates while 50% AKDE represent the core area estimates. 50% and 95% lowers and uppers AKDE's confidence intervals are also included. Bold rows correspond to individuals with a non-stable variogram, which were not considered in the following analyses.

Lizard ID	Site	Sex	95% AKDE	CI (95%) AKDE	50% AKDE	CI (50%) AKDE
TIMLEP_A01	A	M	7955.16	6247.73-9865.73	922.45	848.09-994.72
TIMLEP_A02	A	F	4413.63	3426.84- 5523.39	769.43	704.57- 832.39
TIMLEP_A03	A	M	7411.91	3244.08-13 272.08	2149.37	1607.98-2655.00
TIMLEP_A04	A	M	11 785.77	7873.90-16 474.03	2357.68	2047.75-2654.61
TIMLEP_A05	A	M	11 378.72	6398.21-17 769.35	2127.54	1738.75-2495.47
TIMLEP_A06	A	F	5209.24	3693.17-6981.97	1304.94	1157.36-1447.02
TIMLEP_A07	A	M	30 409.37	15 090.38-51 005.10	7828.68	6121.86-9432.34
TIMLEP_A08	A	F	9499.51	4826.17-15 728.72	1664.19	1312.20-1995.31
TIMLEP_B01	B	F	5115.78	1865.22-9977.33	1222.85	857.95-1561.32
TIMLEP_B02	B	M	92 049.48	54 338.74-139 536.80	22 499.87	18 706.86-26 100.78
TIMLEP_B03	B	F	28 769.70	12 899.75-50 895.74	5164.79	3896.85-6350.22
TIMLEP_B04	B	F	2113.21	742.18-4188.84	411.41	281.98-531.23
TIMLEP_B05	B	F	2910.11	1787.55-4301.78	570.96	481.42-656.21
TIMLEP_B06	B	F	12 256.19	7146.03-18 722.23	2678.25	2217.04-3115.75
TIMLEP_B07	B	F	15 146.29	5324.48-30 011.36	3103.36	2149.67-3986.99
TIMLEP_B08	B	M	669.59	219.12-1367.17	171.36	115.76-222.77
TIMLEP_B09	B	F	1718.67	1035.64-2571.88	352.95	295.58-407.48
TIMLEP_B10	B	M	53 321.81	20 352.20-101 891.40	13 657.87	9737.49-17 299.84
TIMLEP_B11	B	M	36 893.19	10 031.57-80 923.79	8992.41	5695.61-12 028.68

some individuals revisited preferred shelters in greater numbers (table 2). Significant differences were seen in the number of revisits between the 50% and 50% to 95% AKDE ranges at site A (Pearson's Chi-squared test: $X^2 = 37.92$, $df = 11$, $P < 0.001$) and at site B ($X^2 = 14.22$, $df = 6$, $P < 0.05$). In both cases, the core area of the lizards held the most revisited micro-habitats while the 50 to 95% area contained less revisited ones.

Discussion

The spatial patterns of the ocellated lizard were described here in two distinct Mediterranean ecosystems using the latest space use estimation method. Of the total number of tracked lizards ($n = 19$), 7 out of 8 individuals in the Mediterranean scrubland (site A) and 7 out of 11 in the semi-arid steppe (site B) showed range residency based on their variograms. The variograms for all individuals also revealed peaks of activity in space use coinciding with the breeding period. Indeed, lizards from site A and B were respectively monitored from May to July

and from April to May while the breeding season for ocellated lizards ranges from late April to early June (Thirion and Doré, 2012). However, as space use may differ throughout the year in Lacertidae (Pérez-Mellado et al., 2015), additional tracking studies over longer periods are needed to characterise space use of the ocellated lizard more accurately.

Although several lizard species show differences in home range size between males and females (males often displaying larger home ranges than females) (Griffiths, 1999; Wone and Beauchamp, 2003; Germano and Rathbun, 2016), our results show no significant effect of sex. In ocellated lizards from central Spain, Salvador, Veiga and Esteban (2004), found by using the MCP method that males significantly exhibited larger home ranges than females for 100% and 75% core area. This trend was not found for 50% core areas. Therefore, the authors concluded that the 50% core area was primarily used to fulfil energetic requirements rather than providing mating opportunities. Except a small sample size effect, the differences in results found by Salvador, Veiga and Esteban (2004)

Table 2. Number of shelters with N revisits contained within the core area (50% AKDE) and within the rest of the home range area (50% to 95% AKDE) per individual. Results are displayed as: Number of shelters within the core area| Number of shelters in the rest of the home range area. Table 2 is read as followed with TIMLEP_A01 as an example: it had 2 shelters displaying only one revisit within its core area (50% AKDE) and 15 shelters with one revisit in the rest of its home-range (50 to 95% AKDE) (line 1, column 1). TIMLEP_A01's core area further contained 4 shelters displaying 2 revisits while the rest of its home-range contained 8 shelters with 2 revisits (line 1, column 2). From then on, TIMLEP_A01's core-area displayed shelters revisited up to 7 times (line 1, column 3 to column 7) while the rest of the home-range area contained no shelters displaying 3 or more revisits (line 1, column 3 to column 12). TIMLEP_A01 had no shelters displaying 8 revisits or more (line 1, column 8 to column 12).

Lizard ID	Number of revisits (N)											
	1	2	3	4	5	6	7	8	9	10	11	12
TIMLEP_A01	2 15	4 8	8 0	7 0	7 0	6 0	7 0	0 0	0 0	0 0	0 0	0 0
TIMLEP_A02	5 22	9 5	7 8	8 2	7 0	8 0	7 0	5 0	5 0	4 0	4 0	3 0
TIMLEP_A04	1 9	4 5	7 0	2 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
TIMLEP_A06	7 11	2 8	9 2	4 1	6 0	3 0	4 0	0 0	0 0	0 0	0 0	0 0
TIMLEP_A08	6 7	4 2	2 0	8 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
TIMLEP_B02	2 13	0 0	1 0	5 0	4 0	3 0	1 0	0 0	0 0	0 0	0 0	0 0
TIMLEP_B06	4 6	5 2	7 0	6 0	2 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
TIMLEP_B07	9 7	3 3	3 0	4 0	4 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
TIMLEP_B09	1 3	3 0	4 0	5 0	5 0	3 0	0 0	0 0	0 0	0 0	0 0	0 0

and the present study can be explained by the fact that different methods between the two studies were used to estimate the home ranges, and as such the statistical analysis might have yielded distinct results. The mean computed AKDE home range areas in the present study were also slightly higher than the one calculated by Salvador et al. (2004) (MCP 100% mean home range; males: 11 087 m², n = 8; females: 3700 m², n = 4) and the one done by Piazzon et al. (2012) (KDE 90% mean home range: 12 000 m², n = 7). It becomes apparent that standardising methods in order to estimate home ranges is critical since AKDE (95%), MCP (100%) and KDE (90%) were respectively used to determine the ocellated lizard home ranges. As such results between sites or populations must be compared with caution (Nilsen, Pedersen and Linnell, 2008; Silva et al., 2021; Crane et al., 2021).

Although the effect of morphological parameters (e.g., mass or SVL) on home range sizes could not be investigated through linear models due to a small sampling size, tracked individuals were morphologically comparable when examined with non-parametric statistics. Salvador, Veiga and Esteban (2004) found that heavier individuals indeed possessed larger territories,

while sex for core area estimates and age did not play any role in home-range determination. As in our study tagged individuals of both sexes are displaying similar body size and mass, it could explain why we did not detect any seasonal home range differences between sexes.

Complementary studies on the ocellated lizard would need a focus on parameters yet to be investigated and which could play a role in home range structure (sex, mass, SVL, absence of tail, food availability, conspecific presence, etc.), making use of the latest spatial ecology available tools.

The analysis of shelter repartition for both sites did highlight structural differences within the lizard home ranges. Shelter density within the core area was significantly higher in the Mediterranean scrubland (site A) than in the semi-arid steppe (site B), while the mean estimated distance between the shelters within the core area was also significantly lower in site A compared to site B. This can be attributed to the homogenous and anthropogenic repartition of shelters (i.e., stone piles were built along parallel lines and not at random) in the Crau plain (semi-arid steppe, site B).

Furthermore, in site A, shelter density was significantly higher in the lizard's core areas

(50% AKDE) than in the rest of the estimated home-range (50 to 95% AKDE), with the mean estimated distance between the shelters being also significantly lower in the core area than in the rest of the home-range. This observation suggests that ocellated lizards discriminate between localities when establishing the core area of their home range by selecting areas with high shelter density, allowing easier retreats from predators and reducing movements in open fields. It was notably demonstrated that predation frequency on lizards increases in open habitats (Shepard, 2007), especially by birds of prey (Martín and López, 1996). The present analyses of recursive movement patterns tend to confirm such trends since shelters with higher revisits in both sites were located more frequently within the core area of the lizards. Although these results were obtained from a small sample size (5 individuals for site A, 4 individuals for site B) and therefore must be interpreted with caution, these observations might reflect the importance of core areas in the conservation of the ocellated lizard, as the species seems to be actively discriminating between the different areas of its home range. The positive relationship between shelter density and core area could not be confirmed for site B most likely because of the homogenous artificial shelter repartition inherent to the Crau plain. Such habitat configuration might indicate that the core area selection also depends on the structural and thermal quality of the shelters. Vegetation cover in surroundings (Castilla and Bauwens, 1992; Díaz, Monasterio and Salvador, 2006), abundance of rocks and crevices (Diego-Rasilla and Pérez-Mellado, 2003) and warren shape systems (Bravo, Belliure and Rebollo, 2009; Grillet et al., 2010) are all structural properties that may influence a lizard's choice of a particular retreat. The thermal quality of a retreat is furthermore known to play a role in shelter selection (Smith and Ballinger, 2001; Beck and Jennings, 2003; Hagen and Bull, 2011), and several studies demonstrated that lizards actively select

warmer microhabitats in laboratory and field conditions (Downes and Shine, 1998; Monasterio et al., 2009; Ortega and Pérez-Mellado, 2017). More specifically in the ocellated lizard, one study suggests that individuals assess the thermal quality of their refuges in order to minimise the potential thermal consequences of hiding from predation (Sannolo, Ponti and Carretero, 2019). The dynamics of these microhabitats must be carefully monitored, as a potential degradation through time of these stone piles would have a direct impact on ocellated lizard's populations established in this national nature reserve.

The influence of visibility on habitat selection and home-range size is yet to be explored in terrestrial lizards. In the Crau plain, the presence of stone-piles towering over flat surroundings is likely to influence the way a lizard apprehends its environment and adjusts his movement patterns. Thus, visibility of ocellated lizards in the Crau plain is likely superior to those of lizards from site A (shrubland) thanks to the numerous stones piles used as thermoregulation sites combined with a steppic vegetation. Such a configuration would allow better habitat perception, which in turn could assist dispersal potential as well as intra-specific interactions. Future studies would need to better consider how visibility and habitat structure could play a part in a lizard home-range determination.

Finally, and considering all those factors, habitat selection could also be simply a consequence of a lizard's habituation to its surroundings. Most lizards are believed to orient themselves through a mix of visual (Mueller-Paul et al., 2012) and olfactory cues (Leu et al., 2016), and demonstrate spatial memory abilities (LaDage et al., 2012; Font, 2019).

Conclusion

In spite of inconsistencies in the tracking schedule and a small sampling size, 14 out of 19 individuals provided useful results using AKDEs

and bias-mitigating measures (area weighting and pHREML fitting). Combining novel techniques for home-range determination, the present study of recursive movement patterns suggests that ocellated lizards significantly discriminate in shelter revisits between their core area and home-range in both sites (Mediterranean shrubland and semi-arid steppe in Crau plain). This stresses the importance of core-areas as priority targets for conservation measures. This study highlighted significant differences for shelter density between home-range and core-area, which might indicate that shelter density influences the ocellated lizard's core-area selection in a Mediterranean scrubland. Such findings reinforced the importance for studying different environment types and populations when attempting to characterise a species home range and making use of standardised spatial ecology tools. This inter-site comparative analysis allowed confronting different results otherwise overlooked when only studying one habitat type. Hence, it orients future studies to a better understanding of habitat selection mechanisms of the ocellated lizard.

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References

- Averill-Murray, R., Fleming, C.H., Riedle, J. (2020): Reptile home ranges revisited: a case study of space use of Sonoran Desert tortoises (*Gopherus morafkai*). *Herpetol. Conserv. Biol.* **15** (2): 253-271.
- Beck, D.D., Jennings, R.D. (2003): Habitat use by Gila monsters: the importance of shelters. *Herpetol. Monogr.* **17**: 111. [https://doi.org/10.1655/0733-1347\(2003\)017\[0111:HUBGMT\]2.0.CO;2](https://doi.org/10.1655/0733-1347(2003)017[0111:HUBGMT]2.0.CO;2).
- Berger-Tal, O., Bar-David, S. (2015): Recursive movement patterns: review and synthesis across species. *Ecosphere* **6**: art149. <https://doi.org/10.1890/ES15-00106.1>.
- Böhm, M., Collen, B., Baillie, J.E.M., et al. (2013): The conservation status of the world's reptiles. *Biol. Conserv.* **157**: 372-385. <https://doi.org/10.1016/j.biocon.2012.07.015>.
- Bracis, C., Bildstein, K.L., Mueller, T. (2018a): Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography* **41**: 1801-1811. <https://doi.org/10.1111/ecog.03618>.
- Bracis, C., Bildstein, K.L., Mueller, T. (2018b): Revisitation analysis uncovers spatio-temporal patterns in animal movement data. R package version 1.1.2. <https://cran.r-project.org/package=recurse>. Accessed 5 January 2021.
- Bravo, L.G., Belliure, J., Rebollo, S. (2009): European rabbits as ecosystem engineers: warrens increase lizard density and diversity. *Biodivers Conserv* **18**: 869-885. <https://doi.org/10.1007/s10531-008-9438-9>.
- Brown, R.M., Gist, D.H., Taylor, D.H. (1995): Home range ecology of an introduced population of the European wall lizard *Podarcis muralis* (Lacertilia; Lacertidae) in Cincinnati, Ohio. *Am. Midl. Nat.* **133**: 344. <https://doi.org/10.2307/2426399>.
- Castilla, A.M., Bauwens, D. (1992): Habitat selection by the lizard *Lacerta lepida* in a Mediterranean oak forest. *Herpetol. J.* **2**: 27-30.
- Chabanier, O., Renet, J., Besnard, A., Tatin, L. (2012): Une méthode d'attache de radio-émetteurs sur le lézard ocellé *Timon lepidus* (Daudin 1802): pertinence et effet sur le comportement des animaux. *Nat. Provence* **1**: 41-47.
- Cheyland, M., Grillet, P. (2003): Le lézard ocellé en France : un déclin inquiétant. *Le courrier de la nature* **205**: 25-31.
- Cheyland, M., Grillet, P. (2005): Statut passé et actuel du lézard ocellé (*Lacerta lepida*, sauriens, lacertidés) en France. Implication en termes de conservation. *Vie et Milieu* **55**: 15-30.
- Crane, M., Silva, I., Marshall, B.M., Strine, C.T. (2021): Lots of movement, little progress: a review of reptile home range literature. *PeerJ* **9**: e11742.
- Debussche, M., Lepart, J., Dervieux, A. (1999): Mediterranean landscape changes: evidence from old postcards. *Glob. Ecol.* **8**: 3-15.

- Díaz, J., Monasterio, C., Salvador, A. (2006): Abundance, microhabitat selection and conservation of eyed lizards (*Lacerta lepida*): a radiotelemetric study. *J. Zool.* **268**: 295-301.
- Diego-Rasilla, F.J., Perez-Mellado, V. (2003): Home range and habitat selection by *Podarcis hispanica* (Squamata, Lacertidae) in western Spain. *Folia Zool.* **52**: 87-98.
- Doré, F., Cheylan, M., Grillet, P. (2015): Le lézard ocellé: Un géant sur le continent européen. *Biotope* éd.
- Downes, S., Shine, R. (1998): Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. *Anim. Behav.* **55**: 1387-1396.
- Dutoit, T., Buisson, E., Fadda, S., Henry, F., Coiffait-Gombault, C., Jaunatre, R. (2011): Ten years of research in a Mediterranean pseudo-steppe: impacts of land-use changes and ecological restoration. *Sécheresse* **22**: 75-85.
- Fleming, C.H., Calabrese, J.M. (2019): ctm: continuous-time movement modeling. R package version 0.5.5. <https://CRAN.R-project.org/package=ctm>. Accessed 16 September 2021.
- Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P., Calabrese, J.M. (2015): Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* **96**: 1182-1188.
- Fleming, C.H., Noonan, M.J., Medici, E.P., Calabrese, J.M. (2019): Overcoming the challenge of small effective sample sizes in home-range estimation. *Methods Ecol. Evol.* **10**: 1679-1689.
- Font, E. (2019): Rapid learning of a spatial memory task in a lacertid lizard (*Podarcis liolepis*). *Behav. Process* **169**: 103963.
- Fryxell, J.M., Greever, J., Sinclair, A. (1988): Why are migratory ungulates so abundant? *Am. Nat.* **131**: 781-798.
- Germano, D.J., Rathbun, G.B. (2016): Home range and habitat use by blunt-nosed leopard lizards in the southern San Joaquin Desert of California. *J. Herpetol.* **5**: 429-434.
- Gibbons, J.W., Scott, D.E., Ryan, T.J., et al. (2000): The Global Decline of Reptiles, Déjà Vu Amphibians: Reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. *BioScience* **50**: 653-666.
- Griffiths, A.D. (1999): Demography and home range of the frillneck lizard, *Chlamydosaurus kingii* (Agamidae), in northern Australia. *Copeia* **1999**: 1089-1096.
- Grillet, P., Cheylan, M., Thirion, J.M., Doré, F., Bonnet, X., Dauge, C., Chollet, S., Marchand, M.A. (2010): Rabbit burrows or artificial refuges are a critical habitat component for the threatened lizard, *Timon lepidus* (Sauria, Lacertidae). *Biodivers. Conserv.* **19**: 2039-2051.
- Hagen, I.J., Bull, C.M. (2011): Home ranges in the trees: radiotelemetry of the prehensile tailed skink, *Corucia zebata*. *J. Herpetol.* **45**: 36-39.
- Hibbitts, T.J., Walkup, D.K., LaDuc, T.J., Wolaver, B.D., Pierre, J.P., Duran, M., Neuharth, D., Frizzell, S., Adams, C.S., Johnson, T.E., Yandell, D., Ryberg, W.A. (2021): Natural history of the spot-tailed earless lizards (*Holbrookia lacerata* and *H. subcaudalis*). *J. Nat. Hist.* **55**: 495-514.
- Hódar, J.A., Campos, F., Rosales, B.A. (1996): Trophic ecology of the ocellated lizard *Lacerta lepida* in an arid zone of southern Spain: relationships with availability and daily activity of prey. *J. Arid. Environ.* **33**: 95-108.
- Imansyah, M.J., Jessop, T.S., Ciofi, C., Akbar, Z. (2008): Ontogenetic differences in the spatial ecology of immature Komodo dragons. *J. Zool.* **274**: 107-115.
- Jenkins, D.G., Quintana-Ascencio, P.F. (2020): A solution to minimum sample size for regressions. *PLoS ONE* **15**: e0229345.
- Kays, R., Crofoot, M.C., Jetz, W., Wikelski, M. (2015): Terrestrial animal tracking as an eye on life and planet. *Science* **348** (6240): aaa2478.
- Kenward, R.E. (1987): *Wildlife Radio Tagging*. Academic press.
- Kenward, R.E. (2000): *A Manual for Wildlife Radio Tagging*. Academic press.
- Kingsbury, B.A., Robinson, N.J. (2016): Movement patterns and telemetry. *Reptile Ecology and Conservation: A Handbook of Techniques* **110**.
- LaDage, L.D., Roth, T.C., Cerjanic, A.M., Sinervo, B., Pravosudov, V.V. (2012): Spatial memory: are lizards really deficient? *Biol.* **8**: 939-941.
- Law, B., Dickman, C. (1998): The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. *Biodivers. Conserv.* **7**: 323-333.
- Leu, S.T., Jackson, G., Roddick, J.F., Bull, C.M. (2016): Lizard movement tracks: variation in path re-use behaviour is consistent with a scent-marking function. *PeerJ* **4**: e1844.
- Maphalala, M.I., Monadjem, A., Bildstein, K.L., McPherson, S., Hoffman, B., Downs, C.T. (2020): Ranging behaviour of long-crested eagles *Lophaelagus occipitalis* in human-modified landscapes of KwaZulu-Natal, South Africa. *Ostrich* **91**: 221-227.
- Martín, J., López, P. (1996): Avian predation on a large lizard (*Lacerta lepida*) found at low population densities in Mediterranean habitats: an analysis of bird diets. *Copeia* **1996**: 722-726.
- Mateo, J. (2011): Lagarto ocellado—*Timon lepidus*. *Enciclopedia Virtual de los Vertebrados Españoles*.
- Meyer, N.F.V., King, J., Mahony, M., Clulow, J., Beranek, C., Reedman, C., Balkenhol, N., Hayward, M.W. (2021): Large area used by squirrel gliders in an urban area, uncovered using GPS telemetry. *Ecol. Evol.* **11**: 7147-7153. <https://doi.org/10.1002/ecc3.7644>.
- Mitchell, L.J., White, P.C.L., Arnold, K.E. (2019): The trade-off between fix rate and tracking duration on estimates of home range size and habitat selection for small vertebrates. *PLoS ONE* **14**: e0219357. <https://doi.org/10.1371/journal.pone.0219357>.
- Monasterio, C., Salvador, A., Iraeta, P., Díaz, J.A. (2009): The effects of thermal biology and refuge availability on the restricted distribution of an Alpine lizard. *J. Biogeogr.* **36**: 1673-1684. <https://doi.org/10.1111/j.1365-2699.2009.02113.x>

- Mueller-Paul, J., Wilkinson, A., Hall, G., Huber, L. (2012): Response-stereotypy in the jewelled lizard (*Timon lepidus*) in a radial-arm maze. *Herpetol. Notes* **5**: 243.
- Nilsen, E.B., Pedersen, S., Linnell, J.D.C. (2008): Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? *Ecol. Res.* **23**: 635-639. <https://doi.org/10.1007/s11284-007-0421-9>.
- Noonan, M.J., Tucker, M.A., Fleming, C.H., Akre, T.S., Alberts, S.C., Ali, A.H., Altmann, J., Antunes, P.C., Belant, J.L., Beyer, D., Blaum, N. (2019): A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecol. Monogr.* **89** (2): pe01344. <https://doi.org/10.1002/ecm.1344>.
- Ohashi, K., Thomson, J.D. (2009): Trapline foraging by pollinators: its ontogeny, economics and possible consequences for plants. *Ann. Bot.* **103**: 1365-1378. <https://doi.org/10.1093/aob/mcp088>.
- ONF (2004): Natura 2000 – Site «Châine de l’Etoile – Massif du Garlaban» DOCOB – Partie «analyse et définition des objectifs». p. 59.
- Ortega, Z., Pérez-Mellado, V. (2017): The effect of thermal requirements on microhabitat selection and activity of *Podarcis lilfordi* (Squamata: Lacertidae). *Salamandra* **53**: 351-358.
- Pérez-Mellado, V., García-Díez, T., Hernández-Estévez, J.A., Tavecchia, G. (2015): Behavioural processes, ephemeral resources and spring population dynamics of an insular lizard, *Podarcis lilfordi* (Squamata: Lacertidae). *Ital. J. Zool.* **82**: 556-564. <https://doi.org/10.1080/11250003.2015.1093035>.
- Piazzon, M., Larrinaga, A.R., Rodríguez-Pérez, J., Latorre, L., Navarro, L., Santamaría, L. (2012): Seed dispersal by lizards on a continental-shelf island: predicting interspecific variation in seed rain based on plant distribution and lizard movement patterns: seed dispersal by lizards. *J. Biogeogr.* **39**: 1984-1995. <https://doi.org/10.1111/j.1365-2699.2012.02718.x>.
- Powell, R.A., Zimmerman, J.W., Seaman, D.E. (1997): Ecology and Behaviour of North American Black Bears: Home Ranges, Habitat, and Social Organization. Springer Science & Business Media.
- Preiss, E., Martin, J.L., Debussche, M. (1997): Rural depopulation and recent landscape changes in a Mediterranean region: consequences to the breeding avifauna. *Landscape Ecol.* **12**: 51-61. <https://doi.org/10.1007/BF02698207>.
- Prodon, R. (2000): Landscape Dynamics and Bird Diversity in the North Mediterranean Basin: Conservation Issues. Life and Environment in the Mediterranean. WIT Press, Southampton, p. 261-299.
- QGIS Development Team (2021): QGIS geographic information system. Open source geospatial foundation project.
- R Core Team (2019): R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. Available from: <https://www.r-project.org/>.
- Renet, J., Deso, G., Gerriet, O., Diebolt, S., Marchand, M.A., Tatin, L. (2018): L’occurrence du Léopard ocellé *Timon lepidus* (Daudin, 1802) (Sauria, Lacertidae) en altitude est-elle sporadique? Le cas du sud-est des Alpes françaises. *Naturea* **2018**: 1-13.
- Roberge, J.M., Angelstam, P. (2004): Usefulness of the Umbrella Species Concept as a Conservation Tool. *Conserv. Biol.* **18**: 76-85. <https://doi.org/10.1111/j.1523-1739.2004.00450.x>.
- Rose, B. (1982): Lizard home ranges: methodology and functions. *J. Herpetol.* **16**: 253. <https://doi.org/10.2307/1563718>.
- Row, J.R., Blouin-Demers, G. (2006): Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia* **2006**: 797-802. [https://doi.org/10.1643/0045-8511\(2006\)6\[797:KANAE0\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2006)6[797:KANAE0]2.0.CO;2).
- Salvador, A., Veiga, J.P., Esteban, M. (2004): Preliminary data on reproductive ecology of *Lacerta lepida* at a mountain site in central Spain. *Herpetol. J.* **14**: 47-49.
- Salvidio, S., Gardini, G., Calvi, G., Lamagni, L. (2006): Primi dati sulla dieta della lucertola ocellata *Timon lepidus* (Daudin, 1802) in Italia. *Acta herpetol.* **1**: 73-76.
- Salvidio, S., Lamagni, L., Bombi, P., Bologna, M.A. (2004): Distribution, ecology and conservation status of the ocellated lizard (*Timon lepidus*) in Italy (Reptilia, Lacertidae). *Ital. J. Zool.* **71**: 125-134. <https://doi.org/10.1080/11250003.2004.952549>.
- Samuel, M.D., Fuller, M.R. (1996): Radiotelemetry. 370-418. TA Bookhout Research and Management Techniques for Wildlife and Habitats. Fifth Edition, Revised. The Wildlife Society, Bethesda, Maryland, USA.
- Sannolo, M., Ponti, R., Carretero, M.A. (2019): Waitin’ on a sunny day: factors affecting lizard body temperature while hiding from predators. *J. Therm. Biol.* **84**: 146-153.
- Shepard, D.B. (2007): Habitat but not body shape affects predator attack frequency on lizard models in the Brazilian Cerrado. *Herpetologica* **63**: 193-202. [https://doi.org/10.1655/0018-0831\(2007\)63\[193:HBNBSA\]2.0.CO;2](https://doi.org/10.1655/0018-0831(2007)63[193:HBNBSA]2.0.CO;2).
- Silva, I., Fleming, C.H., Noonan, M.J., Alston, J., Folta, C., Fagan, W.F., Calabrese, J.M. (2021): Autocorrelation-informed home range estimation: a review and practical guide. *Methods Ecol. Evol.* **13**: 534-544. <https://doi.org/10.1111/2041-210X.13786>.
- Sirami, C., Nespoulous, A., Cheylan, J.P., Marty, P., Hvenegaard, G.T., Geniez, P., Schatz, B., Martin, J.L. (2010): Long-term anthropogenic and ecological dynamics of a Mediterranean landscape: impacts on multiple taxa. *Landsc. Urban Plan* **96**: 214-223. <https://doi.org/10.1016/j.landurbplan.2010.03.007>.
- Smith, G.R., Ballinger, R.E. (2001): The ecological consequences of habitat and microhabitat use in lizards: a review. *Contemp. Herpetol.* **2001**: 1-13.
- Tatin, L., Chapelin-Viscardi, J.D., Renet, J., Becker, E., Ponel, P. (2013a): Patron and variations du régime alimentaire du léopard ocellé *Timon lepidus* en milieu steppique méditerranéen semi-aride (plaine de Crau, France). *Rev. Ecol., la Terre et la Vie* **67**: 47-58.
- Tatin, L., Wolff, A., Boutin, J., Colliot, E., Dutoit, T. (2013b): Ecologie et conservation d’une steppe méditerranéenne: La plaine de Crau. Quae eds, Versailles, France.

- Thienpont, S. (2020): Plan national d'actions 2020-2029 en faveur du lézard ocellé (*Timon lepidus*). Société Herpétologique de France. https://www.ecologie.gouv.fr/sites/default/files/PNA%20L%C3%A9zard%20Ocell%C3%A9_BAT.pdf. Accessed 5 January 2022.
- Thirion, J.M., Doré, F. (2012): Plan national d'actions Lézard ocellé *Timon lepidus* 2012-2016. Ministère de l'Écologie, du Développement durable et de l'Énergie. http://www.consultations-publiques.developpement-durable.gouv.fr/IMG/pdf/pna_t-lepidus.pdf. Accessed 5 January 2022.
- Thirion, J.M., Grillet, P., Cheylan, M. (2009): Composition et variation saisonnière du régime alimentaire du Lézard ocellé *Timon lepidus* sur l'île d'Oléron (France) à partir des fèces. *Rev. Ecol., la Terre et la Vie* **64**: 239-250.
- Thomas, B., Holland, J.D., Minot, E.O. (2011): Wildlife tracking technology options and cost considerations. *Wildl. Res.* **38**: 653. <https://doi.org/10.1071/WR10211>.
- UICN France, MNHN, SHF (2015): La Liste rouge des espèces menacées en France-Chapitre Reptiles et Amphibiens de France métropolitaine, Paris, France.
- Vacher, J.P., Geniez, M. (2010): Les reptiles de France, Belgique, Luxembourg et Suisse. Biotope, Mèze (Collection Parthénope), Muséum national d'Histoire naturelle, Paris.
- Van Winkel, D. (2008): Efficiency of techniques for post-translocation monitoring of the Duvaucel's gecko (*Hoplodactylus duvaucelii*) and evidence of native avian predation on lizards: a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Conservation Biology, Massey University, Auckland, New Zealand.
- Warner, D.A., Thomas, J., Shine, R. (2006): A simple and reliable method for attaching radio-transmitters to lizards. *Herpetol. Conserv. Biol.* **1**: 129-131.
- White, G., Garrott, R. (1990): Analysis of Wildlife Radio-Telemetry Data. Academic Press, San Diego, California.
- Wilson-Aggarwal, J.K., Goodwin, C.E.D., Swan, G.J.F., Fielding, H., Tadesse, Z., Getahun, D., Odiel, A., Adam, A., Marshall, H.H., Bryant, J., Zingeser, J.A., McDonald, R.A. (2021): Ecology of domestic dogs (*Canis familiaris*) as a host for Guinea worm (*Dracunculus medinensis*) infection in Ethiopia. *Transbound Emerg. Dis.* **68**: 531-542. <https://doi.org/10.1111/tbed.13711>.
- Wone, B., Beauchamp, B. (2003): Movement, home range, and activity patterns of the horned lizard, *Phrynosoma mcallii*. *J. Herpetol.* **37**: 679-686.