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About lizards and unmanned aerial vehicles: assessing home range and habitat selection in *Lacerta agilis*

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Abstract. Understanding animal space use and habitat needs is a vital requirement for effective conservation and management measures. Considering the multiple instances in which landscapes are anthropogenically altered, it becomes increasingly important to understand what the spatial requirements of an animal are. However, smaller animals, like lizards, require finer-scale assessments, which cannot always be easily made. Therefore, we calculated home ranges of *Lacerta agilis* using data collected by radio tracking. We then studied microhabitat preference using high-resolution maps generated from photographs taken by unmanned aerial vehicles. Overall, lizards in the selected area seem to favour home ranges that include blackberry brush while avoiding high vegetation and sand. They use other structures according to individual preferences or unstudied factors. Our study portrays an efficient method with high spatial resolution to assess small-vertebrate habitat preferences, which can in turn be used in planning population-specific habitat management or compensatory measures.

Key words. Squamata, Lacertidae, *Lacerta agilis*, home range, high spatial resolution, unmanned aerial vehicles, microhabitat selection, categorical map, Maxent algorithm.

Introduction

Understanding the habitat and microhabitat requirements of animals is a key part of conservation efforts for most species. The consideration of ecological requirements such as these is vital to proper habitat management (e.g., Castilla & Bauwens 1991, Knapp & Owens 2005, Glen & Dickman 2006, Bai et al. 2020), successful reintroductions (e.g., Pizzuto et al. 2007, Liefferinge et al. 2019), and the effectiveness of compensatory measures (e.g., Birtwell et al. 2005). Ecological requirements, however, constitute a complex network of factors that is not always easy to fully unravel. Fortunately, the concept of home range entails a defined area in which every ecological need an animal has in its day-to-day life should be fulfilled, assuming the individual is successful (Burt 1943). We can therefore, with relative certainty, assume that the overall home ranges of individuals within stable populations provide everything needed to survive and thrive (Burt 1943). Consequently, characterizing habitat and microhabitat as well as other ecological factors within an animal's home range is a great first step towards establishing a species' or population's ecological profile, which is of great importance for conservation planning.

Unmanned aerial vehicles (UAVs) can be a powerful tool to monitor the environment. UAVs already find frequent application in agriculture where they facilitate the mapping of crops (Berni et al. 2009, Kaneko & Nohara 2014, Liu et al. 2020). Lately, the use of unmanned aerial vehicles has been adopted in biological fields and expanded to answer a multitude of questions. Biological fields benefit from broad vegetation analysis via remote sensing in the case of post-fire vegetation surveys for instance (Fernández-Guisuraga et al. 2018), or studies ascertaining the influence of animals on vegetation structure and composition (Qin et al. 2020). Further applications include the observation of large- to medium-sized mammals over great distances, at night, or in hard-to-reach locations with thermal imaging (Bushaw et al. 2019, He et al. 2020) or identification of specific plant species as habitat for specialized arthropods (Habel et al. 2016). As UAV technology becomes more and more affordable, new applications will be developed and survey areas will become larger. Its ability to deliver high-resolution information on vegetation is also useful when assessing microhabitat selection in animals with small home ranges, as the high resolution allows for distinction of small-scale structural differences (see Habel et al. 2016).

One animal that is of particular interest in terms of microhabitat selection due to its proximity to humans and anthropogenically altered landscapes is the Sand Lizard (*Lacerta agilis* Linnaeus, 1758). *Lacerta agilis* is an on average 18–25 cm long insectivorous lacertid native to large parts of the southern half of the Palaearctic (Edgar & Bird

2006). It is diurnal with an annual activity period from spring to early autumn while hibernating during the remaining months of the year (van Nuland & Strijbosch 1981, Edgar & Bird 2006). *Lacerta agilis* favour open-canopy landscapes with scattered shrubs over densely vegetated areas and therefore thrive in heathlands or marginal vegetation (House & Spellerberg 1983, Dent & Spellerberg 1987, Nemes et al. 2006). On the northern edges of their distribution, they are restricted to sand dune vegetation while on the southern edges they prefer montane areas (Bischoff 1988). They have benefited from anthropogenic influences such as forest clearing and farmland creation since medieval times, as these will open new areas with suitable habitats for them (Bischoff 1988). Due to their long history as a synanthropic species, populations of *L. agilis* often live near humans and are therefore easily accessible. However, they also often fall victim to developmental expansions, and subsequently become the subjects of compensation measures. This, in combination with the declining numbers of *L. agilis* (IUCN 2020), makes it a fitting species for our study and it could be a main beneficiary.

In this study, we combine high-resolution vegetation analysis via unmanned aerial vehicle-and radio-telemetry-assisted home range assessment in order to calculate and quantify the habitat and microhabitat selection of the Sand Lizard, *L. agilis*. We use an unmanned aerial vehicle to record high-resolution images of the habitat and tag individuals within the habitat with transmitters to determine the sizes, limits and variations of their home ranges by means of frequently retrieving individuals. We then analyse habitat composition and preference within the home range in order to identify important structures at microhabitat level. This approach yields a wide range of applications for conservation planning and measures and environmental compatibility assessments. Environmental compatibility assessments are conducted to test the likely impact of a planned developmental project on the environment and to integrate appropriate compensatory measures into the project plan. As prescribed in Art. 16 of the UVPG (Gesetz für die Umweltverträglichkeitsprüfung / Law for the environmental compatibility assessment) of the Federal Republic of Germany for instance, environmental compatibility assessments require, amongst other things, a description of the potentially impacted environment (Rödder et al. 2016). This includes an inventory and the assessment of impacted species. Our method allows the inclusion of the microhabitat requirements of affected species in the description of the environment and makes it easier to provide the correct microhabitat structures in compensatory measures.

Material and methods

Data collection

Our study was conducted in a part of the Dellbrücker Heide, a protected heathland landscape to the northeast of Cologne, Germany. The study area comprises approximately 1.3 ha and is bordered by a pond in the north, a ridge with vegetation in the east and south, and a forested strip leading to a road in the west (approximate corners in WGS 84: NW: 50.981237° N, 7.054102° E; NE: 50.981262° N, 7.055604° E; SE: 50.980566° N, 7.056012° E; SW: 50.980201° N, 7.054175° E).

In order to find lizards often enough to assess their home ranges, individuals were caught and outfitted with radio transmitters to retrieve them. We used V1 tags as available from Telemetrie-Service Dessau with slight modifications. In order to extend battery life, signal intensity was reduced so that the direction of the signal was still detectable in close proximity. The sensors weighed 0.35 g and operated at 200 μW. According to another study conducted in the same area (L. M. Schmitz unpubl. data), the average adult lizard body weight within this population during August and September was 10.5 g, meaning sensors averaged 3.3% of the weight of averagely sized lizards. Small individuals were not used. The transmitters had an estimated life expectancy of 30 days. We used a 4-element Yagi antenna, likewise provided by Telemetrie-Service Dessau, optimized towards frequencies at 150 Mhz as well as a self-made 5-element Yagi antenna constructed together with Werner Dreckmann of the BAFF (Bonner Arbeitskreis für Fledermausschutz / Workgroup for bat protection Bonn) according to a published instruction plan (Praxisheft 27 für Amateurfunk und Elektronik in der Schule und Freizeit, pp. 131–133). The self-made antenna was optimized towards determining the direction of incoming signals by having a narrower cone of detection. As a receiver, we used the ICOM IC-R30 from Telemetrie-Service Dessau.

Radio-telemetry surveys were carried out between 19 and 28 August 2019, after the breeding season (Edgar & Bird 2006) so as to avoid interference with mating or male/male interactions. Adult lizards were captured by hand in order to attach radio transmitters following Warner et al. (2006) with modifications in order to accommodate the different body plan of *Lacerta agilis* compared to *Amphibolurus muricatus* studied by Warner et al. (2006); the attachment procedure is detailed in Fig. 1. Nylon mesh from a fly screen was cut in an acutely angled "V" shape and the tag was glued to the bottom tip of the "V" with the antenna pointing away from the arms. We used superglue (Pattex Sekundenkleber Flüssig, cyanoacrylate) to attach the tag to the nylon mesh and to later attach the tag to the animal. Cyanoacrylate glue is commonly used on reptile skin (Price-Rees & Shine 2011, van Winkel & Ji 2014, Hansen et al. 2020) without any adverse effects observed as the glue will be inert once hardened (Hoser 2019). The resulting harness was only attached to lizards after the glue connecting the tag and the mesh had completely cured to avoid attaching the transmitter to the skin directly. Preparatory steps were therefore taken a day before going into the field. After lizards had been caught, the harness was placed on their backs with the antenna pointing caudally (Fig. 1A). The arms of the harness were then drawn over the lizards' shoulder and crossed at the chest (Fig. 1B). The arms were then drawn through the armpits towards the transmitter and tied into a knot above the transmitter (Fig. 1C). The harness was secured with a drop of superglue anterior to the shoulders, behind the armpits, and at the cross over the chest (Fig. 1D). Additionally, the knot was secured with superglue and glued to the transmitter while the excess the mesh arms was cut off (Fig. 1D). The lizard was then held as calmly as possible with its front legs spread so it would not touch the glue behind its legs before it was completely cured, as this would have glued the legs to the flanks. During the procedure, special attention was paid to ensure the lizards' shoulder joints were not impaired in their free movement and the mesh was tight enough to prevent slipping out but not too tight either, so that the animal would not be harmed. The drops of glue in front and behind the shoulders are important as lizards would otherwise have been able to push their front limbs under the mesh, resulting in a much faster loss of the harness. The harness was deliberately fixated with glue in key points, allowing the glue to come off easily during the animal's next moult and to cover as little skin as possible. Forgoing the use of glue to secure the tag to the skin directly was also deliberate, as the tag could be removed by cutting the mesh anytime without hurting the animal in case severe mobility issues became evident. Suitability of the method was assessed by watching lizard mobility immediately after the attachment and on every consecutive retrieval. In total, 15 animals (seven females and eight males) were tagged over a period of 1.5 weeks but never more than 10 at a time due to permit restrictions. If one animal lost its tag, a new one was caught and furnished with a new tag to avoid stressing a single animal too much. Animals were visually monitored by the authors for 1.5 weeks (19–28 August 2019) daily from 9 through 16–18 h. Animals were located via radio-telemetry and their coordinates were noted. An animal was considered located when visual confirmed regardless whether the animal had moved since its last retrieval or not. Due to the animals wearing numbered tags on their backs , they were easy to identify even when amongst other tagged individuals. After the tagged animals were retrieved once, they were left undisturbed for a 30-minute interval before the retrieval procedure began anew. Since retrieving itself usually took 20–30 minutes, this effectively resulted in every animal being retrieved once every 50–60 minutes. The aim was to achieve at least 19 retrievals per individual during the study period to calculate home ranges (after Rose 1982), but if the tag remained attached, retrievals were continued. Six lizards lost their tags before 19 retrievals had been achieved. A detailed history of retrievals for every individual can be found in the electronic Supplementary Table S1.

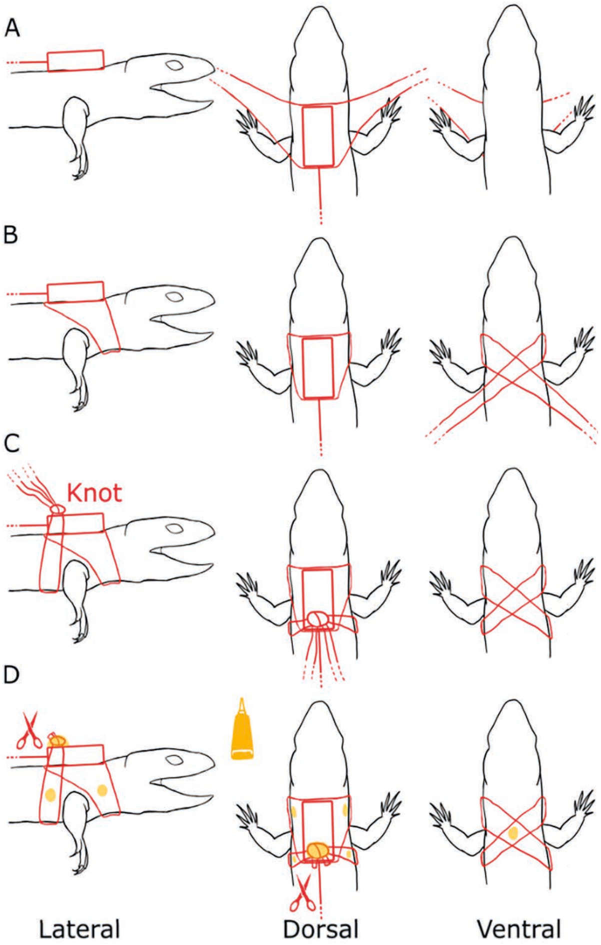

Figure 1. Attachment procedure of the radio transmitter (red rectangle) to the lizard via a mesh backpack. Read from A to D. Lateral, dorsal and ventral views of each step. Yellow spots mark glue drops.

Mapping of the area

The study area was mapped using a DJI Matrice 100 flying platform ("drone") with two cameras attached which were DJI FC350 cameras on a Zenmuse X3 gimbal, a high-definition RGB camera and a Parrot Sequoia multispectral sensor, a multispectral camera recording RGB but also red, green, red-edge and near-infrared emissions, each with a separate lens. Flights were taken during clear weather and low windspeeds on 28 August 2019 at noon. It took two 20-minute flights back-to-back to record the entire area. A flight path was programmed beforehand in the App Autopilot by Hangar Technologies Inc., running on an Apple iPad mini, to survey the area so that there was at least a 50 % overlap between neighbouring pictures. The FC350 was set to record in movie mode, and the Parrot Sequoia was set to take a picture every second and save it on a microSD card. The flight height was set to 35 m above ground.

Starting and landing periods were removed by cutting the resultant video footage and deleting pictures from these phases. We used the software Pix4DMapper 4.5 (Pix4D SA 2019) in order to mosaic the images (or video frames) and to compute the maps. Pix4DMapper was also used to calculate a normalized difference vegetation index (NDVI) and a digital surface model from the mosaiced maps and display it as additional maps. The NDVI is calculated by comparing the near-infrared channel and the red channel and provides an index of the amount of photosynthetically active vegetation.

While the images from the multispectral camera and the resulting map were georeferenced already, the high-definition RGB map had to be georeferenced in ArcMap 10.6 (ESRI 2018), using the Sequoia maps for reference. Employing R 3.6.1 (R Core Team 2020), the RGB map was resampled to the grid of the multispectral maps, divided into its red, green and blue bands, and saved as separate *.asc files along with the multispectral maps. We performed spearman rank correlation tests to test for correlation between the maps. If two maps were highly correlated (r > 0.75), one of them was excluded from further analysis. The remaining maps were stacked together with a mask to exclude large no-data areas at the edges. The channels of the RBG map were recombined by summation into a black and white image (since the channels were strongly correlated). This stack was then loaded into ArcGIS again and 10,000 randomly generated training points were plotted onto the stack. Out of these, 9,891 remained after the points that lacked data had been eliminated. The training points were then manually assigned to habitat classes based on experience from the field. The real-life habitat served as point of reference to ensure classes were distinguished properly. The classes were 'sand', 'blackberry brush', 'grass', 'trees' (and tall bushes), 'slope vegetation' (vegetation on the northern slope towards the beach), and 'low vegetation' (bushes of ≤ 1 m). The different training points for each class were saved as separate Excel files. In DIVA-GIS (Hijmans et al. 2001), points were then transformed into masks and compared with each other in case one point would have been counted towards two classes.

The Maxent algorithm (Phillips et al. 2004, 2006, 2017) was used to calculate habitat classes using the training points of the different classes as samples and the maps as environmental layers in order to examine the likelihood of each pixel belonging to a certain class based on the colour values of the pixel in the different maps. Replications for the model were set to 100 and the test percentage was 20, using a bootstrap approach. The analysis resulted in likelihood maps (cloglog format) for each class, depicting the chance of every pixel belonging to a specific land cover class. The algorithm was first trained with sand as it was the most uniformly coloured microhabitat. The resulting map of sand was then incorporated as an environmental layer for the other classes. A threshold-independent evaluation (ROC analysis) was performed. The receiver operating characteristic curve (ROC) evaluates the prediction accuracy of the model (Swets 1988, Xu et al. 2019). This analysis is a commonly used method to test the utility of a model, whereby the area under the ROC curve (AUC) provides a threshold-independent measure of model performance, since it has an intuitive interpretation that random positive instances and random negative instances are correctly ordered by the classifier (Phillips et al. 2004, 2006, Na et al. 2018, Xu et al. 2019). The accuracy of a model performance is proportional to the AUC value, thus AUC ≥ 0.9 indicates that model performance is excellent (Walden-Schreiner et al. 2017, Xu et al. 2019). Additionally, we performed a threshold-dependent analysis in DIVA-GIS, for which everything below the 10-percentile training presence cloglog threshold calculated by Maxent was reclassified as 'no data' while everything above the threshold was resampled to values between 0 and 1 based on the likelihood of each pixel corresponding to the class in question. The 10-percentile training presence cloglog threshold is one of the most commonly used thresholds in Maxent analysis (Zarzo-Arias et al. 2019). It predicts unsuitable habitat for 10% of the most extreme training points, assuming that 90% of the training points are classified correctly (Kadej et al. 2017, Zarzo-Arias et al. 2019). The results of the Maxent analysis are provided in the electronic Supplement Tables S2 for the sand analysis and S3 for the following analysis. After the Maxent analysis, 'trees' and 'slope vegetation' (which consisted mostly of tall bushes and small trees) were combined to constitute 'high vegetation'. This step became necessary after we had noted a lack of differentiation between these categories, and that 'slope vegetation' was the only class defined by its position rather than its properties. The combined class 'high vegetation', on the other hand, is defined by its properties. It has been shown for *L. agilis* that vegetation structure is the most important factor when determining habitat preference (House & Spellerberg 1983). While this could be an argument for merging 'blackberry brush' with 'low vegetation' as well, we decided against it. Blackberry is structurally distinct from average low vegetation in the area, despite also remaining below 1 m height, and could therefore be used to see if one species differs from the general low vegetation in terms of preference, potentially hinting at structural preferences of *L. agilis* within the class 'low vegetation'. The likelihood maps were then stacked to form one map with the highest likelihood value for each pixel at the top, resulting in a map displaying the most likely habitat class for every pixel and effectively showing the distribution of the aforementioned habitat classes.

Calculation of home range

Home ranges were calculated using R and the packages adehabitatHR (Calenge 2006), sp (Pebesma & Bivand 2005, Bivand et al. 2008), rgdal (Keitt 2010), and raster (Hijmans 2020). Home range was calculated for every individual with at least 19 retrievals. We calculated a 95% minimum convex polygon home range in the following abbreviated MCP (Mohr 1947) and 50% and 95% kernel density estimation home range with bivariate normal kernels in the following abbreviated K95 and K50, respectively (Worton 1989). The ad hoc method for the bivariate normal kernel for estimating the smoothing parameter h was used (see the kernelUD function in the adehabitatHR package Calenge 2006). The resulting smoothing parameters were 8.987 for ID04, 3.795 for ID05, 7.763 for ID06, 5.628 for ID11, 4.083 for ID14, 4.407 for ID22, 3.232 for ID23, 6.403 for ID24, and

4.289 for ID25. Both the kernel density estimation and minimum convex polygon methods have been shown to have limitations in the study of lizard home range despite being the most frequently used methods. Kernel density estimations have been demonstrated to require many retrievals and tend to overestimate home ranges drastically depending on the smoothing parameters chosen (Row & Blouin-Demers 2006). Lately, they have even been deemed unfit for lizard home range assessments by some authors (e.g., Row & Blouin-Demers 2006, Getz et al. 2007, Laver & Kelly 2008, Sillero et al. 2020). While minimum convex polygon estimations are more predictable, they are incapable of displaying unused areas within a home range due to their convex nature. Additionally, they display no information about the utilization distribution within the area. A solution to this was proposed by Sillero et al. (2020), in that small-scale ecological niche models (ENMs) with individual lizards were calculated within MCP home ranges to subtract unsuitable areas. We recreated this by using the variables (without the DSM map) and method used previously to calculate a categorical habitat map with the retrievals of an individual lizard to establish a distribution model. We added a mask encompassing all of the individuals' home range areas in order to facilitate modelling. We then excluded areas below the 10-percentile training cloglog threshold from the home range as unused areas. We then added the resulting home ranges to our calculated home ranges with the suffix _ENM, in the following called ENM home ranges as opposed to non-ENM home ranges, which are the home range estimations without preceding distribution modelling. We chose to keep the old home range maps despite their discussed flaws to maintain comparability with other studies. A Kruskal-Wallis test was conducted for all home range types to identify possible differences between males and females, as the data did not fulfil the assumptions for an AN(C)OVA. Additionally, the Spearman's rank correlation coefficient was calculated in order to check for a possible link between the number of retrievals and home range sizes. In both cases, p-values were adjusted with the false discovery rate (FDR) transformation to account for multiple tests.

Habitat use, preference and avoidance

Animal movements were approximated by connecting retrieval points in chronological order with straight lines. Using R, and the packages adehabitatLT (Calenge 2006), adehabitatHR (Calenge 2006), maptools (Bivand et al. 2008), raster (Hijmans 2020), SDMTools (VanDerWal et al. 2014), and splancs (Rowlingson & Diggle 2017) we simulated 100 movements according to the distances and movement angles observed in the actual home ranges, but randomized. We calculated new non-ENM home ranges from the resulting points (95% minimum convex polygon, 95% kernel density estimation, and 50% kernel density estimation), following similar movement patterns but ignoring habitat. We calculated Jakobs' electivity index for each habitat type 'sand', 'blackberry brush', 'grass', 'high vegetation' (trees and bushes of ≥ 1 m), and 'low vegetation' in the observed home ranges and the randomly generated home ranges using R. Jacobs' index (Jacobs 1974) was originally designed to study food preferences when food was available at different abundance (Jacobs 1974). This formula can also be used for other resources like habitat, however. The index is thus calculated as follows:

$$D=\frac{H-T}{(H+T)-2HT}$$

with H being the proportional use of the habitat by the animal and T being the proportional availability of the habitat in the study area. The index suggests an avoidance of the habitat if $D < 0$, a preference for the habitat if $D > 0$, and its use according to the availability if $D = 0$.

We then calculated a 95% confidence interval of the mean electivity index from the generated home ranges for one individual and checked whether the electivity index of the observed non-ENM home ranges would fall within that confidence interval. If the observed electivity index falls within the confidence interval of the electivity index of the randomly generated ones, we cannot exclude the possibility that the observed habitat preferences are a result of the distribution of habitat structures in space. If it is situated outside the confidence interval, however, we can assume that the observed electivity is not the result of random chance, but is deliberately chosen by the individual. This was only done with the non-ENM home ranges while all following calculations were done with both non-ENM and ENM home ranges. Using R, we calculated Spearman's correlation coefficient between the electivity indices for different habitats and individuals. This is to identify whether the preference or avoidance of certain habitats could be linked. We furthermore calculated Spearman's correlation coefficient between the electivity indices and home range size to potentially identify if habitat preferences change with home range size. As before, in both these cases, FDR transformation was used to account for multiple related correlation tests.

Results

Radio-telemetry

In total, 15 Sand Lizards (seven females and eight males) were tagged, of which six specimens lost their transmitters before 19 retrievals could be obtained (see electronic Supplementary Table S1). Consequently, nine specimens (five females and four males) kept their tag long enough for a sufficient number of retrievals. These animals were called ID05, ID11, ID22, ID23, and ID25 (females), ID04, ID06, ID14, and ID24 (males), respectively. Animals were mobile and could traverse dense vegetation with the tag within the first minute after their release. Only one animal was lost with the tag attached during the trial, as it left the area for very dense vegetation. Every other tag was successfully recovered. Of the observed animals, none fell to predation for the entire time the tag was attached, and only one had to be cut free from the tag after it entangled a foot in the nylon mesh after it had been observed untangled for 30 minutes prior.

Mapping of the area and Maxent analysis

In order to create a categorical map showing different habitats within the study area, the mosaic maps recorded by the multispectral camera (green, near-infrared, red and red edge channels) (Fig. 2); the maps directly calculated by Pix4D as a result of the recorded maps (NDVI and DSM) (Fig. 2); as well as the RGB map patched together from the video recorded by the 4k RGB camera (Fig. 3) were used. Before the analysis, Spearman's correlation coefficient was calculated to eliminate repetitive data (Table 1). The RGB map was split up into its three channels, but since all parts of the RGB map were highly correlated, we only used the sum of all channels in the Maxent analysis. Furthermore, the Sequoia red map correlated with both the NDVI and Sequoia green maps. Since the latter two were not strongly correlated with each other, we discarded the Sequoia red map. The Sequoia red edge map was correlated with the Sequoia NIR map so that the NIR map was kept and the red edge map discarded.

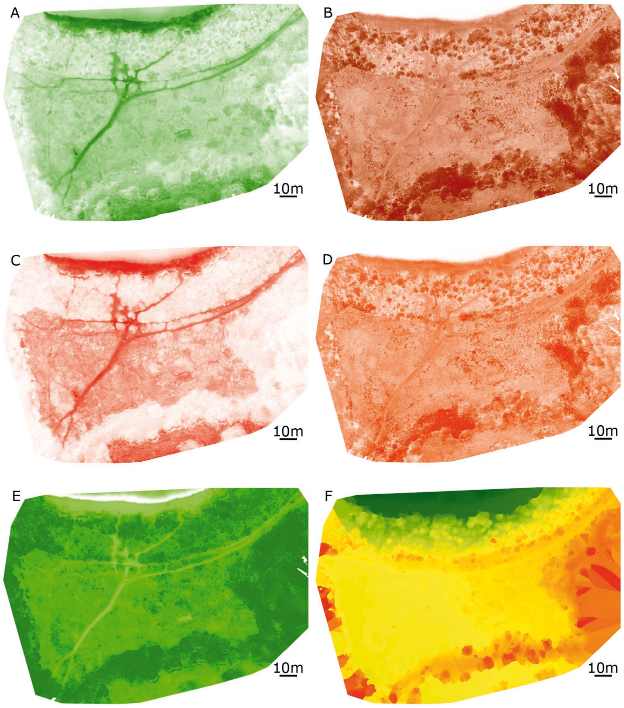

Figure 2. Mosaiced maps from the Sequoia and calculated NDVI map. Shown are the green channel (A), the near-infrared channel (B), the red channel (C), the red edge channel (D), the NDVI (E), and the DSM (F). Scales go from low reflection (white) to high reflection (colourful) except for the DSM map, which goes from low altitude (green) to high altitude (red).

The AUC values of the Maxent analysis for accuracy of the classification of training points (Table 2) show that all model performances are of high quality (Swets 1988, Walden-Schreiner et al. 2017, Xu et al. 2019). Mean Test AUC values for all classes vary between 0.804 for 'trees' and 0.886 for 'blackberry'. Furthermore, the mean value for 'sand' is 0.930. The classes 'slope' and 'trees' were com-

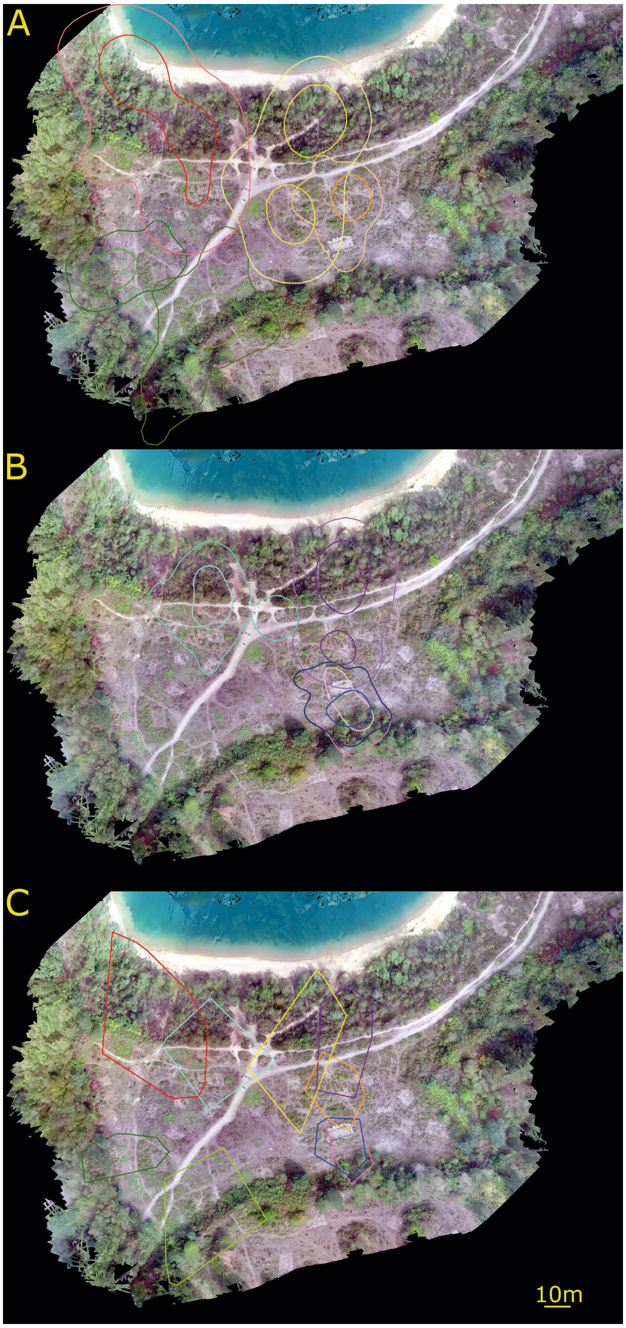

Figure 3. High-resolution RGB map with 95 and 50% kernel density estimation home ranges for all individuals (A+B) and MCP home ranges for all individuals (C). ID04 (red), ID05 (orange), ID06 (yellow), ID11 (light green), ID14 (dark green), ID22 (turquoise), ID23 (dark blue), ID24 (purple), and ID25 (pink).

Table 1. Spearman correlation coefficient between multispectral maps (Sequoia), digital surface model (DSM), NDVI, 4K RGB map (SumRGB) and its blue, green and red channels. Strongly correlated pairings are marked by *.

	4kBlue	4kGreen	4kRed	SumRGB	dsm	NDVI	SeqoiaGreen	SeqoiaNIR	SeqoiaRED	SeqoiaREG
4kBlue	1									
4kGreen	0.834*	1								
4kRed	0.884*	0.814*	1							
SumRGB	0.952*	0.924*	0.958*	1						
dsm	0.078	0.042	0.082	0.07	1					
NDVI	0.388	0.199	0.392	0.339	0.354	1				
SeqoiaGreen	0.259	0.203	0.304	0.268	0.089	0.388	1			
SeqoiaNIR	0.003	0.002	0	0	0.183	0.367	0.186	1		
SeqoiaRED	0.325	0.194	0.393	0.318	0.22	0.812*	0.766*	0.023	1	
SeqoiaREG	0.006	0.025	0.019	0.016	0.057	0.111	0.349	0.849*	0.116	1

Table 2. Training samples, test AUC and standard deviation, 10% training presence cloglog threshold, and map contributions resulting from the Maxent analyses to make the categorical map. Training samples are training points, which were assigned to each class as a means of defining it.

Class	Training samples	Test AUC ± SD	10-percentile training presence cloglog threshold	SeqoiarGreen contribution	SumRGB contribution	dsm contribution	ndvi contribution	sand_mask contribution	seqoiarNIR contribution
Blackberry	297	0.886 ± 0.014	0.317	17.130	3.702	34.387	44.015	0.000	0.765
Grass	524	0.880 ± 0.009	0.414	2.093	5.635	19.224	71.580	0.000	1.469
Low Vegetation	129	0.848 ± 0.037	0.294	15.324	2.648	21.259	32.115	0.000	28.654
Slope	1090	0.848 ± 0.008	0.378	27.940	4.532	41.039	24.496	0.000	1.992
Trees	1628	0.804 ± 0.007	0.411	1.223	0.806	27.376	69.952	0.000	0.644

bined in the class 'high vegetation' since 'slope vegetation' and 'trees' in the area were both high vegetation and it was preferable to define the categories by structure rather than position.

The categorical map (Fig. 4) has a high resolution with 1 pixel corresponding to a 3.6 × 3.6 cm area. White areas indicate the absence of data. 'High vegetation' mostly frames the area, while 'grass', 'blackberry brush' and 'low vegetation' are mostly found in the centre. Bare sand is largely limited to the beach area in the north, and the pathways. 'High vegetation' (43.19%) takes up the highest amount of landcover, whereas 'sand' (9.04%) takes up the lowest (Fig. 4). 'Blackberry brush' (15.89%), 'grass' (14.77%), and 'low vegetation' (17.12%) are distributed in similar proportions (Fig. 4).

Home ranges

Overall, there were nine specimens that had been retrieved often enough to calculate their home ranges (Figs 3, 5). In total, four males and five females were suitable for the purpose, with ID25 being the least (19) and ID11 and ID22 the mostly often retrieved ones (59). The data used for the Maxent models, as well as the contributions of the maps can be found in Table 3. The 10-percentile cloglog training thresholds, which were used to cut unused habitat out of the home range, can also be found in Table 3. Overall, test AUC was not quite as good as for the categorical map but still deemed sufficient (range: 0.592 ± 0.101 to 0.702 ± 0.084).

Overall, home ranges differ in size quite drastically (Fig. 6), with ID04 having the largest non-ENM K95 home range (4057.116 m^2), and ID23 having the smallest (781.815 m^2). While ID23 also has the smallest K95_ENM home range (523.968m^2), the largest K95_ENM home range was occupied by ID06 (2315.242 m^2). As for the core area, ID04 has the largest (non-ENM: 1126.074 m^2, ENM: 697.733 m^2) while ID23 has the smallest non-ENM (174.518 m^2) and ID05 has the smallest K50_ENM (143.324 m^2). ID04 also has the largest MCP home range (non-ENM: 1757.085 m^2,

Table 3. Training samples, test AUC and standard deviation, 10% training presence cloglog threshold, and map contributions resulting from the Maxent analyses for obtaining ecological niche models. Training samples are taken from the retrievals of individuals.

Individual	Training samples	Test AUC ± SD	10-percentile training presence cloglog threshold	SeqoiarGreen contribution	SumRGB contribution	ndvi contribution	seqoiarNIR contribution	mask contribution
ID04	35	0.702 ± 0.084	0.378	12.170	39.430	33.498	14.901	0
ID05	30	0.655 ± 0.094	0.455	26.787	23.553	38.631	11.029	0
ID06	40	0.600 ± 0.085	0.4849	25.920	17.503	33.354	23.223	0
ID11	37	0.680 ± 0.081	0.366	43.682	8.479	37.635	10.205	0
ID14	22	0.638 ± 0.096	0.501	19.996	18.342	54.627	7.034	0
ID22	40	0.648 ± 0.079	0.445	7.454	22.784	54.137	15.625	0
ID23	28	0.592 ± 0.101	0.477	30.423	14.179	34.290	21.109	0
ID24	23	0.595 ± 0.108	0.512	11.514	44.966	23.611	19.910	0
ID25	16	0.650 ± 0.123	0.467	18.568	23.366	29.889	28.177	0

ENM: 1029.755 m^2), and the smallest MCP home range was occupied by ID25 (non-ENM: 295.110 m^2, ENM: 170.430 m^2). Other home range sizes lie between these values (Fig. 6). On average, for non-ENM home ranges, K95 home ranges are 1853.263 m^2 in size. The average sizes of K50 and MCP home ranges are 457.053 m^2 and 808.084 m^2, respectively. As for ENM home ranges, average sizes were 1141.341 m^2 for K95_ENM, 326.134m^2 for K50_ENM, and 531.721 m^2 for MCP_ENM. Home range size was not significantly correlated the with the number of retrievals in any home range (Spearman rank test for K95 home range: $\rho = 0.36$, $q = 0.342$, for K95_ENM home range: $\rho = 0.377$, $q = 0.342$, for K50 home range: $\rho = 0.36$, $q = 0.342$, for K50_ENM home range: $\rho = 0.443$, $q = 0.342$, for MCP home range: $\rho = 0.72$, $q = 0.114$, for MCP_ENM home range: $\rho = 0.694$, $q = 0.114$). Similarly, home range size between males and females did not differ significantly (Kruskal-Wallis-test for K95: $\chi^2 = 2.16$, $df = 1$, $q = 0.212$, for K95_ENM: $\chi^2 = 2.16$, $df = 1$, $q = 0.212$, for K50: $\chi^2 = 2.94$, $df = 1$, $q = 0.212$, for K50_ENM: $\chi^2 = 3.84$, $df = 1$, $q = 0.212$, for MCP: $\chi^2 = 0.96$, $df = 1$, $q = 0.327$, for MCP_ENM: $\chi^2 = 1.5$, $df = 1$, $q = 0.265$).

Concerning the proportional coverage of the studied microhabitat (Table 4), 'blackberry brush' and 'high vegetation' make up the largest parts of the home ranges, with each of these covering on average roughly a quarter of the entire home range, if not more. 'Grass' and 'low vegetation' follow, each making up 13–21% of the area in different home ranges. Lastly, 'sand' covers the smallest expanse in all home ranges, ranging from 2 to 9%. 'Sand' coverage is especially low in ENM home ranges while it is highest in K95_ENM home ranges with 3.27%. This is lower than the lowest land cover in the non-ENM home ranges. Standard deviations range from ± 3 to 15%, being highest in 'blackberry brush' and 'high vegetation', and lowest in sand.

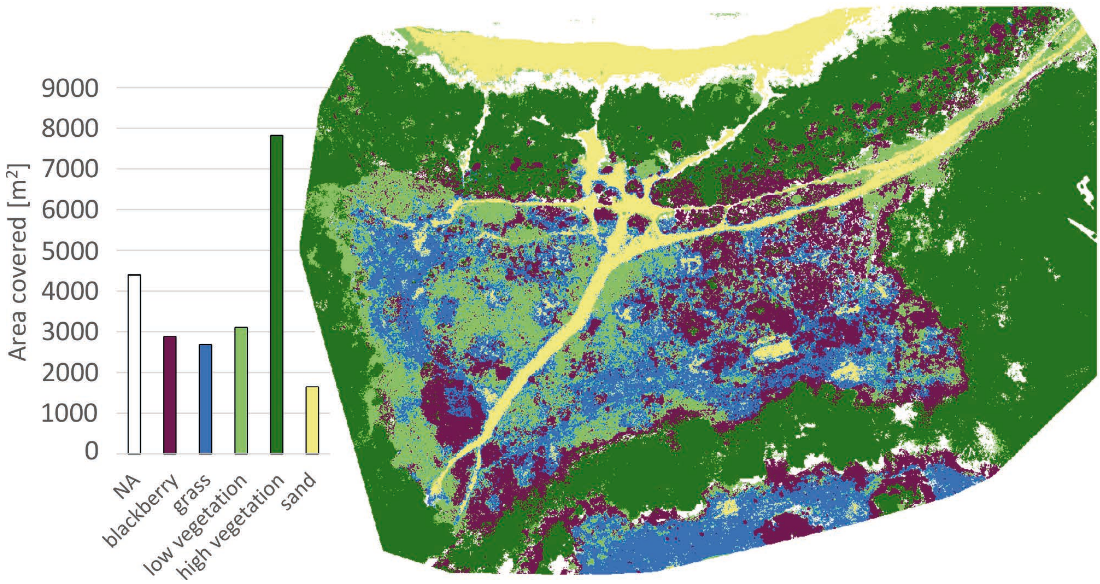

Figure 4. Microhabitat map depicting the five final microhabitat categories and the area covered by each in m^2.

Habitat use, preference, and avoidance

We calculated the electivity indices for ‘blackberry brush’, ‘grass’, ‘low vegetation’, ‘high vegetation’, and ‘sand’ for every individual inside their different home ranges (Fig. 7 for non-ENM home ranges, Fig. 8 for ENM home ranges), as well as the confidence intervals calculated from the simulated non-ENM home ranges (Fig. 7) in order to ascertain whether the electivity index falls within the confidence interval. Most electivity indices are outside the confidence interval – meaning that the electivity index of the chosen habitat structure in the home range is significantly different from that of random habitat composition, meaning it is likely that the lizards actively choose their home ranges by their composition. However, there are 13 instances where the observed electivity index lies within the confidence interval of the randomly generated home ranges. Thus, in these cases, the observed electivity is not significantly dif-

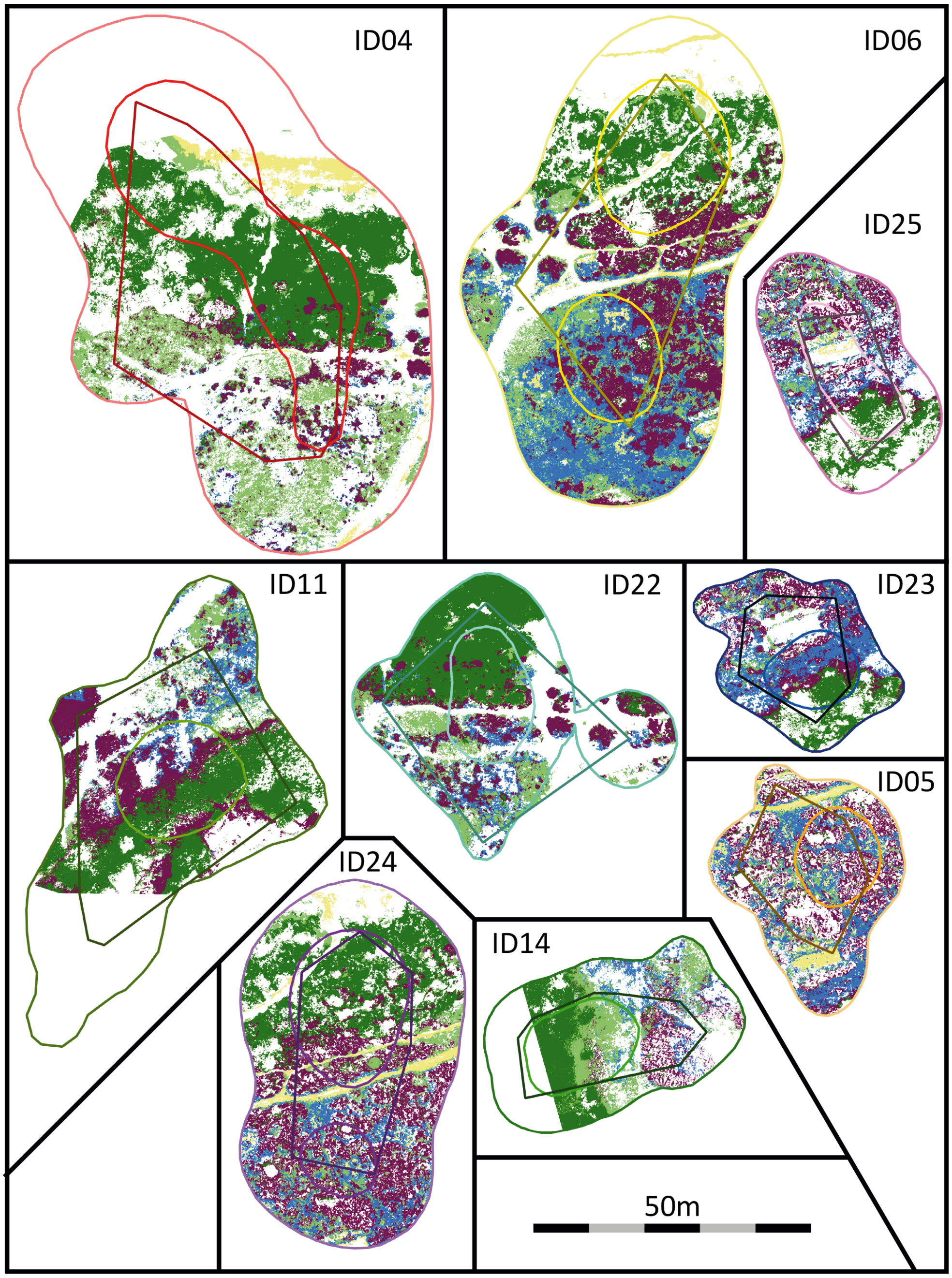

Figure 5. ENM home ranges of K95 (outer borders), K50 (inner round borders) and MCP (darker, polygon borders) home ranges. White areas are excluded from the home range either by missing data or the ENM. Habitat colourcoded as purple for ‘blackberry brush’, blue for ‘grass’, light green for ‘low vegetation’, dark green for ‘high vegetation’, and yellow for ‘sand’.

ferent from random chance. These instances are exclusively found for ‘sand’, ‘high vegetation’, and ‘grass’. The electivity index for ‘sand’ is within the confidence interval in the K95 home range and the K50 home range of individual ID05, in the K95 home range of specimen ID23, and in the MCP home range of individual ID25. The electivity index for ‘grass’ lies within the confidence interval in the K50 home range of individual ID06 and the K95 home range of individual ID23. The electivity index for ‘high vegetation’ is situated within the confidence interval in the K95 home ranges of individuals ID11, ID22, ID23 and ID24 and in the MCP home ranges of individuals ID06, ID14, and ID24. Overall, our results suggest seven cases of an electivity index being within the confidence interval in the K95 home ranges, two cases in the K50 home ranges, and four cases in the MCP home ranges. After adjusting p-values for multiple correlation tests, no electivity indices are correlated with each other within home ranges (Table 5).

Table 4. Mean and standard deviation of land cover across home range types. Home ranges with preceding species distribution model are annotated with _ENM. For habitat types, see Fig. 9.

Calculation	bb	gr	lv	tv	sa
K95 mean	26.88	19.02	18.48	26.71	8.91
K95_ENM mean	29.85	17.34	20.38	29.16	3.27
K95 standard deviation	11.88	5.48	7.21	9.29	5.36
K95_ENM standard deviation	10.47	10.04	8.34	14.11	3.81
K50 mean	26.94	14.68	15.06	38.89	4.43
K50_ENM mean	28.62	13.73	15.25	40.15	2.24
K50 standard deviation	14.68	8.57	11.18	16.39	3.77
K50_ENM standard deviation	14.55	11.33	11.19	19.72	2.25
MCP mean	28.87	16.99	17.74	28.66	7.74
MCP_ENM mean	31.69	16.78	18.89	31.53	2.76
MCP standard deviation	12.81	6.28	8.10	12.33	4.99
MCP_ENM standard deviation	11.15	9.91	9.07	15.80	2.91

In the K95 home ranges (Fig. 7), an overall preference for ‘blackberry brush’ can be observed, with only ID04 avoiding blackberry bushes and ID14 and ID22 using them according to their availability. In K95_ENM home ranges (Fig. 8), preferences for ‘blackberry brush’ increase overall compared to K95 home ranges, except in ID05 and ID14. Electivity indices of ‘grass’ are overall close to zero with most animals having a slight preference for grass, or using it as available, except ID23 and ID25 in their non-ENM home ranges and ID05 and ID23 in their K95_ENM home ranges. Here the preference is stronger. Additionally, ID24 slightly avoids grass and ID04 strongly avoids grass in its K95_ENM home range – which is a drastic difference compared to its non-ENM home range. In non-ENM home

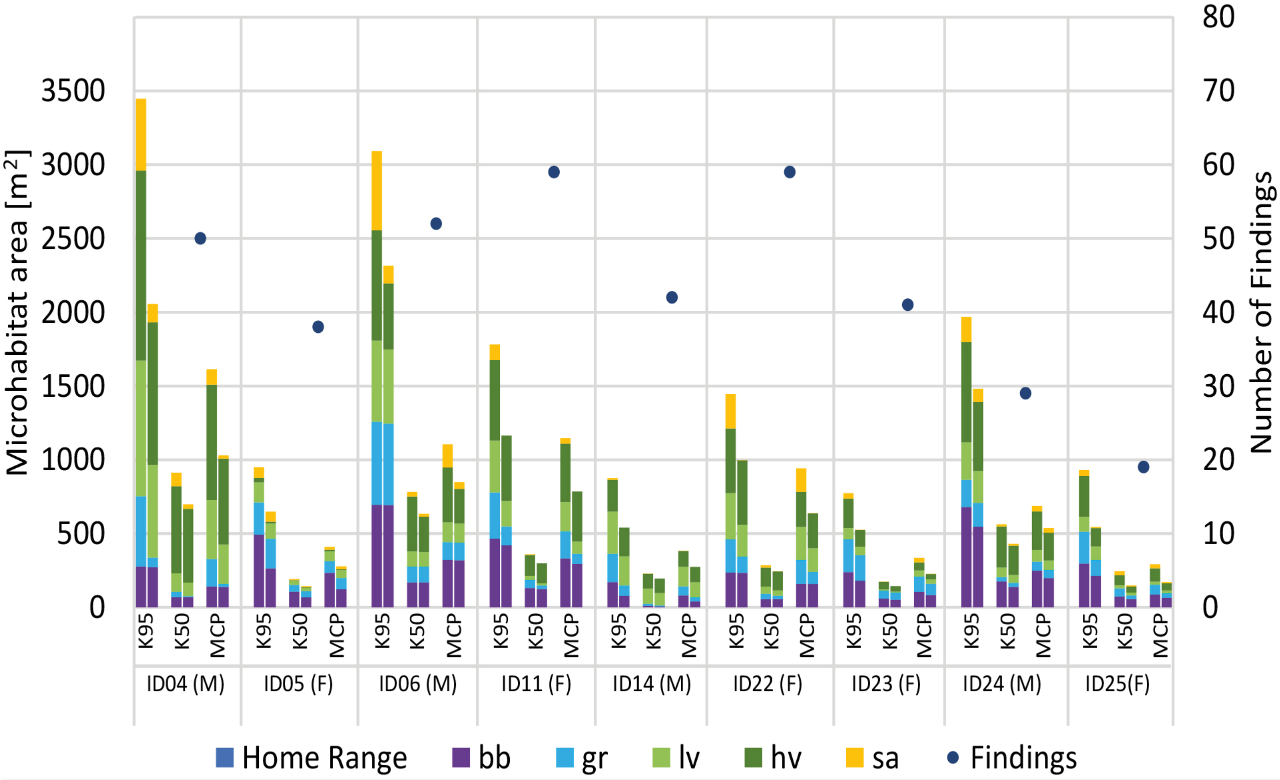

Figure 6. Microhabitat area (bars), total microhabitat area (sum of bars), and number of retrievals (points) for every individual for each of the three calculated home range types both without preceding ENM (left of the pairs) and with preceding ENM (right of the pairs) Area depicted in m^2. Sex is marked next to the IDs of the lizards as M for males and F for females.

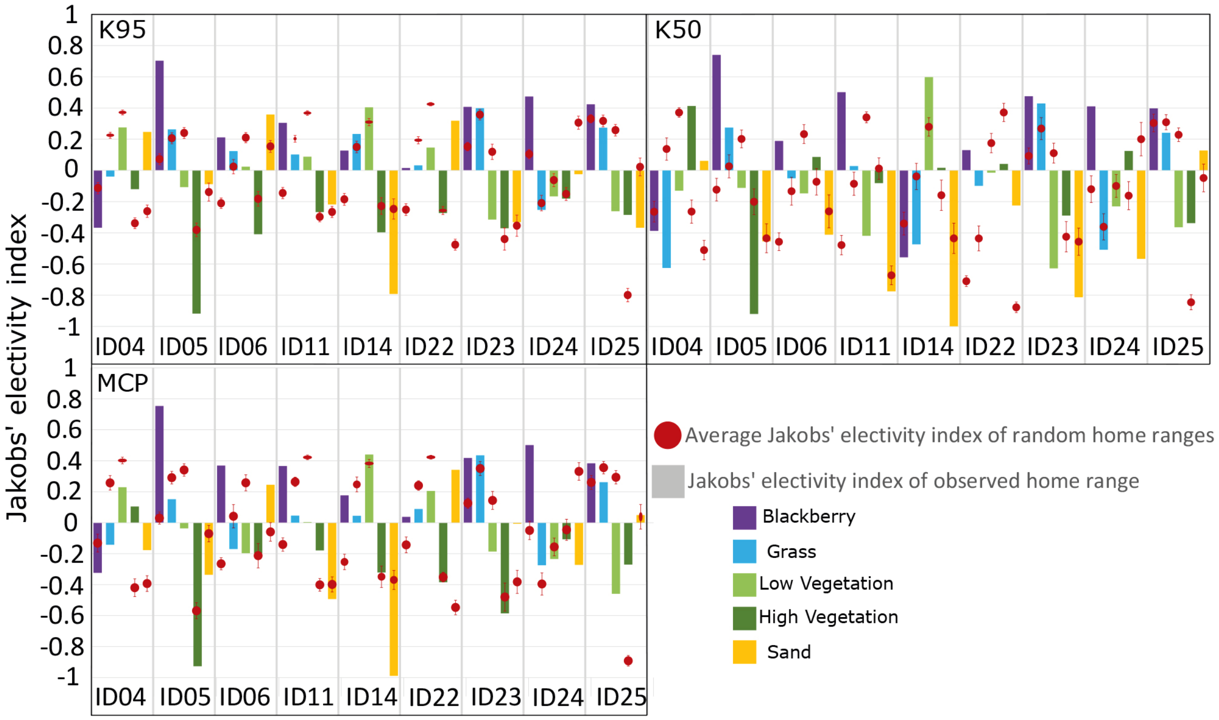

Figure 7. Jacobs' electivity index for 'blackberry brush', 'grass', 'low vegetation', 'high vegetation', and 'sand' within the K95, K50 and MCP home ranges of studied individuals. Tips of the bars represent the Jacobs' electivity indices for the observed home ranges while red dots show the averages of simulated home ranges with 95% confidence intervals. For small confidence intervals, red dots have been replaced with red ellipses in order to leave the confidence intervals visible.

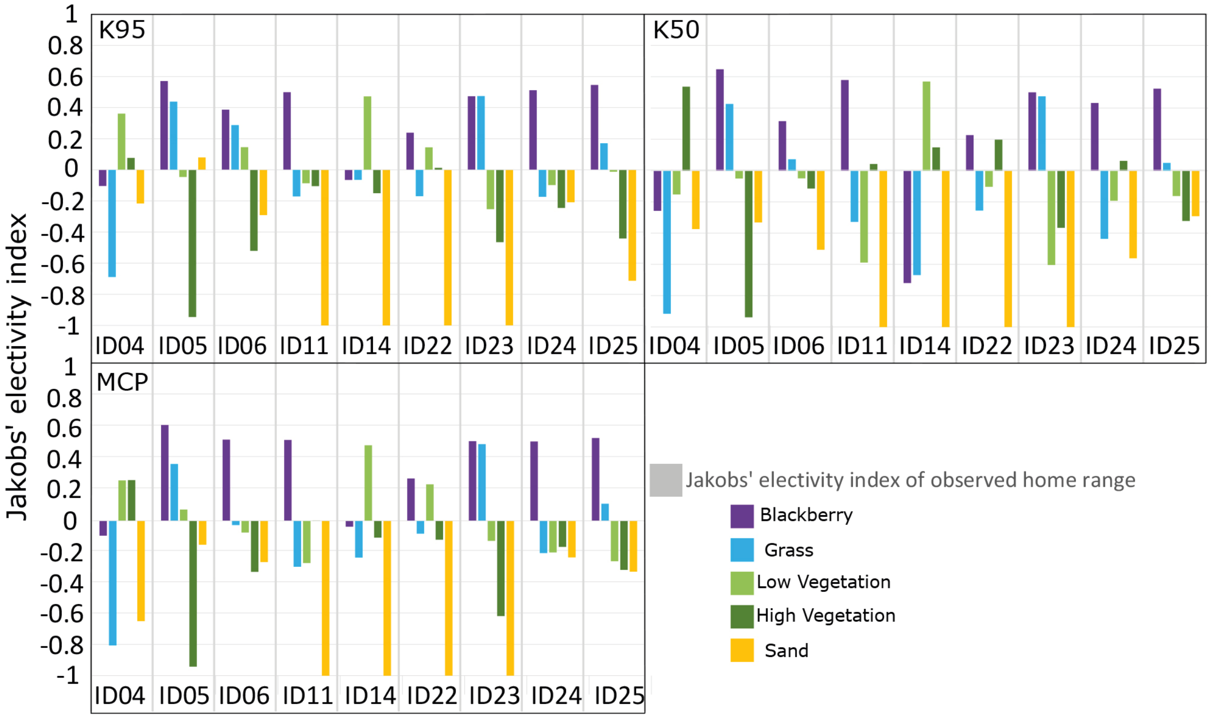

Figure 8. Jacobs' electivity index for 'blackberry brush', 'grass', 'low vegetation', 'high vegetation', and 'sand' within the K95, K50 and MCP home ranges with preceding ENM. Tips of the bars represent the Jacobs' electivity indices for the observed home ranges.

Table 5. Spearman's correlation coefficients for all pairings of Jacobs' electivity indices within the home ranges across all individuals. No pairings were significantly correlated after p-value adjustment by FDR. Home ranges with preceding species distribution model are annotated with _ENM.

Home Range	Class	Blackberry	Grass	Low Vegetation	High Vegetation
K95	Grass	0.367			
K95	Low Vegetation	-0.767	-0.483		
K95	High Vegetation	-0.333	-0.700	0.167	
K95	Sand	-0.300	-0.600	0.167	0.167
K95_ENM	Grass	0.383			
K95_ENM	Low Vegetation	-0.667	-0.250		
K95_ENM	High Vegetation	-0.650	-0.833	0.350	
K95_ENM	Sand	0.402	0.033	-0.167	-0.427
K50	Grass	0.700			
K50	Low Vegetation	-0.583	-0.483		
K50	High Vegetation	-0.600	-0.883	0.217	
K50	Sand	-0.183	-0.150	0.067	0.150
K50_ENM	Grass	0.617			
K50_ENM	Low Vegetation	-0.467	-0.167		
K50_ENM	High Vegetation	-0.800	-0.867	0.200	
K50_ENM	Sand	0.254	0.119	0.220	-0.220
MCP	Grass	0.233			
MCP	Low Vegetation	-0.700	-0.100		
MCP	High Vegetation	-0.383	-0.733	-0.033	
MCP	Sand	-0.133	0.150	-0.383	-0.083
MCP_ENM	Grass	0.667			
MCP_ENM	Low Vegetation	-0.583	-0.217		
MCP_ENM	High Vegetation	-0.733	-0.950	0.200	
MCP_ENM	Sand	0.485	0.377	-0.084	-0.561

ranges, 'low vegetation' is avoided by ID23, ID24, and ID25, but sought out by ID04, ID14 and ID22 – while ID05, ID06 and ID11 seem to neither prefer nor avoid it. Meanwhile, in their ENM home ranges, 'low vegetation' is avoided by ID23, preferred by ID05 and ID14, and used as available by the rest. 'High vegetation' is universally avoided, save for ID04, which uses it according to availability in both its K95 home ranges, as well as ID11, ID14 and ID22 which use high vegetation according to its availability in their ENM home ranges. 'Sand' is avoided by ID11, ID14, ID23, and ID25, while it is preferred by ID04, ID06, and ID22. ID05; and ID24 exhibits little in terms of avoidance or preference for 'sand' in its non-ENM home ranges, while this substrate is almost universally strongly avoided in K95_ENM home ranges, except for ID04, ID05, and ID24, which use it according to its availability. On average, 'blackberry brush' is favoured while 'sand' is avoided. 'High vegetation' is avoided in K95 and MCP home ranges. 'Grass' and 'low vegetation' are on average used according to availability. Electivity indices of 'sand' also show the highest spread of values, and this substrate is especially avoided in ENM home ranges (Fig. 9). MCP indices are very similar to their K95 counterparts in both ENM and non-ENM home range types, and show mostly similar preferences and avoidances.

In the core areas of both home range types, 'blackberry brush' is almost universally preferred except by ID04 and ID14, which avoid it in both their ENM (Fig. 8) and non-ENM (Fig. 7) home ranges. 'Grass' is avoided by ID04, ID14 and ID24 in both their K50 home ranges. ID11 and ID22 avoid 'grass' in their K50_ENM home ranges, but use it according to availability in their K50 home ranges. Additionally, 'grass' is used according to its availability by ID06 in both home range types and by ID25 in its non-ENM home range. 'Grass' is even sought out by ID05 and ID23 in both home ranges and by ID25 in its non-ENM home range. 'Low vegetation' is preferred or avoided similarly between non-ENM and ENM home ranges in the core area with only ID14 showing a strong preference. ID11 and ID23, on the other hand, avoid it whereas the other individuals use 'grass' as per its availability. ID25 avoids 'grass' a little more in its K50 home range compared to its K50_ENM home range, where it is used more as per its availability. Similarly, 'high vegetation' use is more or less constant between non-ENM and ENM home ranges in any individuals. ID04 prefers 'high vegetation', while ID04 and ID25 avoid it. The remaining individuals use 'high vegetation' more or less according to availability. 'Sand' is universally avoided in ENM home ranges, while it is almost universally avoided in non-ENM home ranges, with ID04, ID22 and ID25 coming up with an index around zero. Overall, differences between ENM and non-ENM home ranges are less drastic and less frequent in core areas. However, in core areas, variation between individuals is higher than in K95 and MCP home ranges. On average, 'blackberry brush' is preferred within the core area, while 'sand' is avoided and the remaining categories average out to neither preference nor avoidance (Fig. 9). In the core area, the difference in indices for 'sand' between non-ENM and ENM home ranges is smaller due to the already lowered index in non-ENM home ranges.

Home range size and electivity index

The electivity index of 'grass' shows a strongly negative correlation with home range size while the electivity index for 'sand' is strongly positively correlated with home range size in the K95 home range. Neither correlation is found in the K95_ENM home range (Table 6). In the non-ENM

Table 6. Spearman's correlation coefficients for all electivity indices with the size of their home ranges. Significantly correlated pairings are marked with *.

Class	K95	K95_ ENM	K50	K50_ ENM	MCP	MCP_ ENM
bb	-0.317	-0.2	-0.367	-0.517	-0.533	-0.333
gr	-0.8*	-0.55	-0.733	-0.633	-0.617	-0.633
lv	0.333	0.233	0.05	0.067	0.4	0.2
tv	0.483	0.217	0.833*	0.7	0.617	0.5
sa	0.783*	0.385	0.45	0	0	0.05

K50 home range, the electivity index of 'high vegetation' is strongly positively correlated with home range size but not in the ENM K50 home range (Table 6).

Discussion

In summary, it can be observed that the tagging of the individuals and map generation by UAV have both proven successful. Lizards could be located reliably and overall no adverse consequences were observed from the attached transmitters in all but one case, which was swiftly resolved. The resulting maps were of high resolution and they accurately depicted the environment when compared directly to the area. Within home ranges, the preferences and avoidances for low vegetation and blackberry brush are reliably nonrandom, while for some individuals, preference or avoidance for sand, grass and high vegetation is not always significantly different from random chance. Overall, blackberry bushes are strongly preferred, while sand is avoided and high vegetation is avoided in K95 and MCP home ranges. Other microhabitats average around zero preference or avoidance across all individuals. In core areas, variability in electivity is overall higher between individuals than in K95 and MCP home ranges. Core Areas show less variation between ENM and non-ENM home ranges. K95 size correlates negatively with the electivity index of grass and positively with the electivity of sand in non-ENM home ranges. Core area size correlates positively with the electivity for both high vegetation and sand. ENM home range size does not correlate significantly with any electivity index.

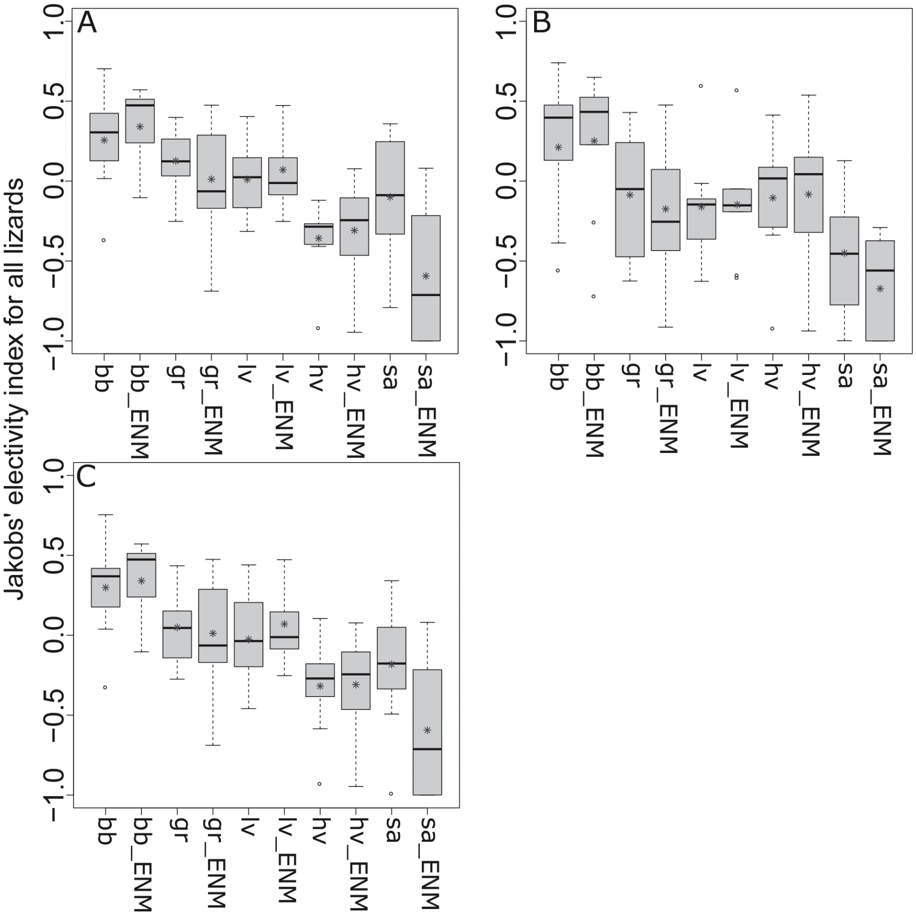

Figure 9. Boxplots showing the average (blue) and median electivity indices for 'blackberry brush' (bb), 'grass' (gr), 'low vegetation' (lv), 'high vegetation' (tv), and 'sand' (sa) for all individuals across their 95% kernel density estimation home ranges (A), their 50% kernel density estimation home ranges (B), and their minimum convex polygon home ranges (C) with and without preceding ENM.

Radio-telemetry

The number of tagged individuals is comparable to similar studies (Warrick et al. 1998, Refsnider et al. 2015, Wieczorek et al. 2020, Clement & Rödder 2021). The observed unimpeded mobility and near-complete absence of entanglement and predation suggest that the method, originally described by Warner et al. (2006), can also be used for *Lacerta agilis* with the modifications described herein. Although formal testing has yet to be conducted, as of now, suitability is based on observations. As Warner et al. (2006) have described, frequent observations are beneficial to reducing accidental mortality, as entangled lizards can become easy targets for predators and are at an increased risk of overheating. The one instance in which a lizard's foot became entangled was promptly resolved, since the lizard had been observed unentangled 30 minutes prior. Yet, the possibility of entanglement is certainly there, and we strongly advise to not only check regularly on individuals when using this method, but to also check for entangled vegetation or body parts whenever a lizard is located, in order to avoid any form of impairment, stress or mortality. The method portrayed here can be improved and adjusted to suit other setups. For example, Refsnider et al. (2015) proposed to paint the transmitters with acrylic paint to match the lizard's dorsal coloration and thus reduce detectability by predators. The same method has also been adjusted for the more cylindrical body shape of Scincidae (Price-Rees & Shine 2011). Different materials for the harnesses have been tried out, like Co-Flex® (Andover Healthcare Inc.), or the rubber of bicycle tubes (van Winkel & Ji 2014). However, van Winkel & Ji (2014) observed abrasions and skin lesions after a few weeks when using rubber harnesses on geckos, hence discouraging their use in transmitter attachment. Co-Flex® did not have the same adverse effects according to this study.

Mapping of the area and Maxent analysis

The generated maps shown in Figures 2 and 3 are all accurate representations of the study area when compared to reality on site. There are some small merging problems, occurring mainly on the edges of the map, outside of the actual study area. It is therefore important to include wide margins all around during the recording phase. Recording of images via UAV proved to be a successful way of capturing detailed maps of small areas. UAVs can hence be a powerful tool to adapt large-scale, satellite-based ecological procedures to smaller scales and finer resolutions. Satellite-based maps often fail the intended purpose due to insufficient resolution or varying temporal resolution (Habel et al. 2016). The ability to generate maps of exactly the required area at exactly the required time will be a major contributor towards more accurate ecological assessments. It also facilitates novel methods in the assessment of space use, like using ecological niche models to assess home ranges (Sillero et al. 2020). This method is limited by the size of monitorable area. However, additional battery packs, an on-site charging station, or more advanced UAVs can drastically increase the size the of coverable area, should the means for purchasing these be available. In conclusion, UAV-assisted habitat recording is a fast and efficient way to obtain high-resolution habitat maps. It can be limited by flight time, which is dependent on the budget. Although first-time costs can be comparatively high, once acquired, UAV-assisted habitat recording becomes a very time- and cost-effective method when used regularly.

Maps were tested for correlation to reduce data size and eliminate redundant data. This resulted in the channels of the RGB map, the Sequoia red, and the Sequoia red edge maps being discarded as it led to the highest variety of non-redundant maps. The AUC values for all classes of the Maxent analysis indicate good model performance (Walden-Schreiner et al. 2017, Xu et al. 2019). The map resulting from the Maxent analysis (Fig. 4) has a resolution of 1 pixel corresponding to a 3.6 × 3.6 cm area. This level of detail is quite impossible to achieve by satellite images at present (Purnamasayangsukasih et al. 2016, Liu et al. 2020). The distribution of habitat structures shows that high vegetation covers roughly three times the area that blackberry brush, grass and low vegetation do. Sand covers even less ground. Aside from the fact that, from above, taller structures obscure lower structures beneath, the large amount of high vegetation is also explained by the growth surrounding the study area. We estimate that all chosen habitat classes cover enough land to be viewed as relevant to *L. agilis*. The high amount of missing data has several reasons. First, the water of the pond area has not been classified due to its being irrelevant for the non-aquatic *L. agilis*. Second, mistakes in stitching the images together at the edges of the map create areas of 'no data' within the high vegetation outside the study area. Third, it is possible that uniquely coloured patches of vegetation have not been recognised by the model. Inspection of the categorical map (Fig. 4) shows that those spots are mostly restricted to the high vegetation surrounding the area. Most relevant is the observation that the transition zone from high vegetation to sand in the northern parts of the study area and at the beach came out poorly mapped. This flaw is probably due to the model not recognising shaded sand as such. It could be improved by adjusting the time of UAV overpasses to when that area is not shaded, or by including more shaded areas into the training points for sand in the Maxent analysis. We therefore strongly advise a conscious effort to include shaded areas in training points.

Home ranges

The observed home ranges are larger than most home ranges of sand lizards reported in the literature. *Lacerta agilis* home ranges have been calculated all over Europe. Even when looking only at a small subset of studies, results vary greatly and range from as small as 13.6 m² (Heym et al. 2013) to more than 1000 m² (Nicholson & Spellerberg

1989). In all cases, average home range size was larger for males, although significance was not always confirmed. We did not find any significant differences between males and females in our study. The lack of difference is, in our opinion, at least partially due to our small sample size of four males versus five females. It remains that the average home ranges in our study are much larger than in other recordings. This is partially mitigated by adding an ecological niche model to our home range calculation, and cutting out unused habitat from the home ranges. ENM home ranges are closer to traditional estimates and more accurately portray the habitat actually used (Sillero et al. 2020). Furthermore, Turner et al. (1969) tested the relationship between lizard weight and home range size across many lizard species and came to the conclusion that $A = 171.4W^{0.95}$ (A = home range area in m^2 and W = lizard body weight in g) is the best-fitting equation for a rough home range size estimation in lizards. Assuming a weight of 10 g for *L. agilis*, we come to a predicted home range size of 1527.604 m^2. Most K95 home range sizes are around that prediction, while MCP home ranges fall short of it, and are therefore closer to older predictions. It is noteworthy that with a K95 home range size < 3000 m^2, ID04 and ID06 have home ranges twice as large as Turner at al. (1969) predict. In general, we assume the calculated home ranges to be plausible, but we acknowledge the differences between our recordings and past publications. Many older calculations applied the MCP method or an offshoot of this method, which, as is evidenced here as well, result in smaller home range estimates even with the same data sets (see also, e.g., Hansteen et al. 1997, Barg et al. 2005, Börger et al. 2006). Additionally, habitat quality/abundance of key resources can have an inverse effect on home range size, as lower densities of food and other necessities like oviposition sites, shelters or basking areas potentially require lizards to move larger distances to satisfy their needs (Rose 1982). Finally, the number of records has shown to be a strong influence on estimations (Nicholson & Spellerberg 1989) although no such connection has been found in this case – possibly due to the small sample size. Disturbances by humans, such as the ones observed in our study area, could also lead to larger home ranges, as lizards would need access to resources even whilst evading human passers-by. Moreover, the intensity of human traffic could also affect microhabitat structure. It is possible that disturbances during retrievals would lead individuals to move across greater distances in order to evade the scientists. The effect of increased activity after handling and observation has been demonstrated in the lizard *Tiliqua rugosa* (Kerr et al. 2004). However, in this study, the risk was deemed unavoidable and if this had an effect, some lizards were clearly more affected than others. In future studies, stationary telemetry receivers (e.g., Gottwald et al. 2019) could be installed, using triangulation to locate tagged lizards within the area without the need for interference as long as the method of attachment was proven safe enough to not risk entanglement and a need for regular check-ups.

Average land cover and low standard deviations for 'sand' show a fairly constant portion of 2–8% sand within home ranges. This is in accordance with previous studies showing the necessity for a certain amount of open substrate in a *L. agilis* home range (Wouters et al. 2012). This makes sense, since open substrate – and especially sand – can be beneficial to thermoregulation due to its higher heat capacity. Generally, populations of *L. agilis* across Europe need a certain amount of open space despite their requirements for brush (Nemes et al. 2006, Wouters et al. 2012, Heltai et al. 2015, Mizsei et al. 2020). This might also be the case here, since the low standard deviation in land cover and the high variability in electivity indices for 'sand' suggests that lizards want to have a certain portion of their home range (here 2–8% on average) to be open sand and avoid or prefer sand accordingly. However, it is worth noting that within ENM home ranges, 'sand' is reduced to comprise only 2–4% of the home ranges. This shows that niche models cut out a lot of the sand present in home ranges as unused habitat, marking 'sand' as a habitat structure to be mostly avoided, as is supported by the low electivity indices discussed below. Meanwhile, other classes experience higher amounts of proportional variability within home ranges. Previous studies have shown high intraspecific variability in grass and bush cover between sexes and ontogenetic stages (Grozdanov et al. 2014). The higher individual variability found in this study could hint towards these findings, but cannot be verified due to sample constraints.

Significance of Jacobs' electivity index

In most cases, Jacobs' Electivity Indices of habitat classes within lizard home ranges are significantly different from Electivity Indices of randomly generated home ranges. Since Jacobs' electivity index calculates the use of resources relative to their availability (Jacobs 1974), this means the individual in question elects to use its surroundings differently from the average of 1000 simulated individuals that have similar mobility but no regard for habitat structure. Therefore, it can be assumed that in most cases, lizard habitat use is non-random. This is to be expected since habitat composition within the home range is specific to the animal's needs (Burt 1943). On the other hand, in cases where the observed electivity index lies within the confidence intervals of the randomly generated indices, random use of a microhabitat cannot be ruled out. In cases of smaller home ranges, like with ID05, ID14, ID23 and ID25, or fewer retrievals like ID25, the method of generating random home ranges could lead to home ranges closer to the observed ones, as less options of recombination are available.

Structural preferences and avoidances

On average, 'blackberry brush' is preferred while 'sand' is often avoided as evidenced by their average electivity indices. 'Grass' and 'low vegetation' usually average around an electivity index of zero while 'high vegetation' shows an average slightly below zero in K95 and MCP home ranges. However, the spread of values signifies major individual differences in most cases and is especially widely spread in core areas. On the other hand, differences between ENM and non-ENM home ranges are overall smaller and less frequent in core areas than in K95 and MCP home ranges.

Preference for 'blackberry brush' is unsurprising, as *L. agilis* is known to respond positively to the presence of low, shrubby vegetation (Amat et al. 2003, Edgar & Bird 2006, Nemes et al. 2006, Heltai et al. 2015, Mizsei et al. 2020). Since 'blackberry brush' is clearly favoured in almost all home ranges, while preference for other low vegetation fluctuates, we can assume that *L. agilis* actively seeks out the properties of blackberry bushes over other vegetation if the costs of doing so are not too high. Mizsei et al. (2020) cited vegetation openness as one desirable factor for *L. agilis*. Blackberry bushes in the area were generally more open than most other bushes, letting through more sunlight while also being spiky enough to discourage predators and humans from entering. These factors may place 'blackberry brush' higher on the shrub preference scale than the average low vegetation found in the area. An extensive analysis of preferred bush species, to draw out favoured structural properties as was conducted by Mizsei et al. (2020), might provide the necessary insights to further sub-classify the class of 'low vegetation' based on structural properties The overall wider spreads of electivity indices across most structures in core areas suggest that core areas differ more strongly on an individual basis. Core areas do not contain as much unused habitat either, as shows in the lack of large differences between non-ENM and ENM core areas. Habitat structure could be a secondary criterion in determining core areas for the lizard, overshadowed by other, unstudied factors. One idea would be that a core area could be defined by the presence of foraging, thermoregulation and hiding spots in close proximity to each other, which can occur in a multitude of ways. The overall preference for either 'high vegetation' (ID04), 'low vegetation' (ID14), or 'blackberry brush' (all other individuals) as structures often associated with favoured burrows (Grozdanov et al. 2014), seems to favour that hypothesis. Similarly, the more frequent avoidance of 'grass' and open 'sand' compared to K95 and MCP home ranges in the core area also favours the hypothesis, as these structures do not conceal burrows well and expose their entrances. To prove this hypothesis, a closer examination of core areas, including shelter placements, would be needed. While 'sand' is almost universally avoided, ENM home ranges show an even stronger avoidance of 'sand'. As discussed previously, lizards seem to seek out a certain small percentage of 'sand' within their habitats (Nemes et al. 2006, Wouters et al. 2012, Heltai et al. 2015, Mizsei et al. 2020). However, the thermoregulatory benefits of sand can already be exploited in small patches, while large open areas are more dangerous, exposing the animal to predators. It is likely that electivity indices are low because there are far more sandy patches available than are needed. It is worth keeping in mind that the niche model cut out habitat based on lizard locations and lizards may be less likely to be found on open sand when disturbed regularly, as in this study setup.

'High vegetation' is usually avoided or used according to availability with one exception (ID04). This finding is in accordance with the results of most previous studies (House & Spellerberg 1983, Nemes et al. 2006, Mizsei et al. 2020). Due to their small size and non-arboreal lifestyle (Edgar & Bird 2006), vegetation that spreads out higher above the ground, like trees, is very different for *L. agilis* than bushes that spread closer to ground level. The former does not offer a lot of protection to *L. agilis* but casts large shadows. This leads to the lizard being exposed to ground predators while also often having to cover larger distances between potential basking spots and appropriate shelters. Since 'high vegetation' is not excluded from ENM home ranges in the manner 'sand' is, it is possible that 'high vegetation' is used as cover to an extent, despite being overall avoided if there are better alternatives. While some individuals do show preference or avoidance for 'grass', there is no clear trend visible. Usage of 'grass' could just be based on its structure and whether it can serve as cover or for basking.

Home range size and electivity index

Correlations in non-ENM home ranges suggest that with larger K95 home ranges, electivity for 'grass' decreases, while electivity for 'sand' increases. Within core areas, electivity of 'high vegetation' is higher in larger core areas. As discussed previously, large home ranges can be a sign of lower structural quality within the home range, as individuals would need to travel greater distances to find all necessary resources (Rose 1982). This could potentially lead to areas that are rarely used and mostly just traversed, or circumvented, within the home range. While large quantities of open microhabitat are undesired due to higher exposure to predators and longer distances between resources (House & Spellerberg 1983), 'sand' could be more favourable to lizards than 'grass' in cases where these areas are unavoidable. On the one hand, 'sand' could be more favourable to frequent travelling as it may offer less resistance than 'grass' does and thus, can be traversed much quicker. Larger-scale studies on dispersal movements in Natterjack Toads (*Epidalea calamita*) have shown that sand is physically easier to traverse than grassy terrain for the toads (Stevens et al. 2004). To our knowledge, there have not been any similar studies for lizards, nor for *L. agilis* in particular, but we assume that vertical structures in a habitat may physically hinder to some extent most species of similar size in traversing it. On the other hand, unlike grass, sand brings about unique advantages for thermoregulation, digging, and oviposition due to its high heat capacity and looseness (Rose 1982). Given that high vegetation also generally proves unsuitable, the same reasoning can be applied to the larger amount of high vegetation in core areas. As habitat quality decreases, the core area needs to be larger to encompass all necessities leading to a larger amount of less suitable habitat lying between core necessities. We see our argumentation supported by the fact that these relationships are not mirrored in ENM home ranges. We theorize that the niche model has excluded a good part of these habitats due to lack of usage.

Conclusion

Radio-telemetry and unmanned aerial vehicle-assisted habitat recording have both proven to be successful in acquiring high-resolution habitat and home range information on *L. agilis*. Tagging of *Lacerta agilis* with radio transmitters was successful, as these remained attached and allowed the reliable retrieval of individuals. However, these methods still required frequent revisits, as the risk of entanglement was not fully eliminated. UAV recordings of multiple colour channels resulted in maps that distinguish between selected habitat structures. The greatest benefit has proven to be the control of spatial and temporal resolution while the main limitation of the method is flight time. Improvements can be made by avoiding shaded areas as much as possible while recording and incorporating shaded areas in the training points to help the model to recognise them.

Overall, *L. agilis* in this population tend to actively incorporate blackberry brush in their home ranges while on average avoid high vegetation and sand; grass and low vegetation differ from individual to individual but average out around no preference. Most preferences show high individual variation, which is most likely based on unexplored characteristics. Overall, we hypothesise that high vegetation and sand are largely unsuitable and incorporated mainly as travel routes between resources with two exceptions: one being that some grassy and sandy patches are needed for basking, but never anywhere near in the quantities present in our study area, and the second exception being that high vegetation does not seem to be avoided in core areas. Overall, preferences in core areas show higher individual variance then in K95 or MCP home ranges, suggesting that habitat composition might play a secondary role when determining core activity areas.

Overall, our study reveals interesting preferences and connections between habitats occupied by *L. agilis*. One has to be careful not to overinterpret the results, though, and keep in mind that some results may stem from habitat arrangement within the area and other, unstudied factors. Proportions and preferences of individuals can however be of great help to conservation planning and measures and serve as guides on how to detect, manage or create habitats suitable for *L. agilis*.

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Supplementary data

The following data are available online:

Supplementary Table S1. Retrievals of all individuals with coordinates and time of retrieval.

Supplementary Table S2. Maxent results of the first analysis containing the habitat class ‘sand’.

Supplementary Table S3. Maxent results of the second analysis containing all other habitat classes.