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Spatiotemporal patterns of habitat use by the Sand Lizard, *Lacerta agilis*: effects of climatic seasonality?

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Abstract. The distribution and occurrence of a species in its habitat are inevitably linked to its ecology. To successfully monitor and protect species, it is important to investigate which species-specific factors influence its interactions with the environment. In this study, we focus on patterns in habitat use of the Sand Lizard (*Lacerta agilis*). Differences in seasonal as well as sex and size class-dependent habitat use have been reported from the edges of this species' range. To verify such trends in the core area of its distribution, we analyzed the habitat factors weather, microclimate, microhabitat structures, and time dependence, which may have an impact on the use of space of the Sand Lizard. Using generalized linear models, hypervolumes, density estimations, and Chi-squared tests, we found that the movement patterns of individuals can neither be described by time differences, climatic conditions, or habitat composition, nor do they show habitat- or weather-related differences of movement between sexes or size. Here we demonstrate that in the case of a population from the core of this species' distribution area in the Dellbrücker Heide (Germany), habitat use is solely influenced to a low degree by differences related to the ontogeny of Sand Lizards and does not depend on any of the other evaluated factors. These results are in enormous contrast to findings in populations from the periphery of their distribution, i.e., the United Kingdom, Latvia, Romania, Bulgaria, and the Pyrenees. This implies that seasonal habitat shifts are more extreme at the edges of the range of *L. agilis*, serving to compensate deteriorating habitat conditions in the periphery.

Key words. Squamata, Lacertidae, range edges, core area, habitat factors, Dellbrücker Heide.

Introduction

Geographic distributions of species are determined by the ecological niches they occupy, which in turn are based on abiotic factors, biotic interactions, geographic accessibility, and characteristics of the individuals themselves (Soberón & Peterson 2005). The fundamental niche of a species comprises all parameters and resources, which are necessary for an indefinite maintenance of viable and reproducing populations and so determine their potential distribution. The realized niche of a species is shaped by the intersection of biological interactions (e.g., predation pressure, competition, resource availability), environmental factors such as geographic accessibility, and the physiological potential of the species itself (Hutchinson 1957, Grinnell 1917, Elton 2001).

Kühnelt suggested in 1943 that habitat choice parameters of species with a particularly wide distributional range can vary enormously depending on the geographic location. The diversity of habitat types that can be colonized by the species should be larger in the core area, where conditions are optimal, and the species here becomes eurybiontic, which suggests that individuals can tolerate a broad range of a given habitat factor (Schaefer 2012). At the edges (periphery) of large distribution ranges, conditions typically become more compromised due to a reduced availability of suitable microhabitats and hence force the lizards to be more selective. This is the reason why the species regionally becomes stenobiontic, suggesting that it can tolerate only a narrow range of a given habitat factor (Kühnelt 1943, Böhme 1978, Schaefer 2012, Böhme & Rödder 2014). Next to overall habitat choice across a species' range, seasonal habitat shifts within single populations can be linked to the same principle.

The Sand Lizard, *Lacerta agilis* Linnaeus, 1758, has one of the most extensive distribution ranges of all the world's reptile species, but has, in some areas, suffered heavy declines especially in the northwestern portions of its distribution (Edgar & Bird 2006). Main threats to this species are habitat fragmentation and destruction of microhabitat structures due to human activities (Edgar & Bird 2006, Aghasyan et al. 2021). Additionally, some populations at the edges of its distribution are quite fragmented and isolated, like in the north and northwest of the United Kingdom where populations have declined due to habitat loss (House & Spellerberg 1983, Woodfine et al. 2017). Some isolated populations occur in the mountains of Greece, Bulgaria, and in the Pyrenees at altitudes of up to at least 2500 m a.s.l. (Bulgaria). They can be found in these regions only in highly specific habitats with suitable (micro-) climatic conditions (Böhme 1978, Edgar & Bird 2006, Aghasyan et al. 2021).

At its northern range limits, the Sand Lizard is restricted to habitats with warm and dry climates suitable for thermoregulation, wherein this species tends to use colder and more humid conditions than it does on average at its southern range limits. Therefore, we expected these lizards to choose their habitats accordingly, based on available habitat types. In Latvia, *L. agilis* prefers vegetation composed of sparse low pines (*Pinus sylvestris*) with a high degree of herbal ground cover dominated by grasses and heath. The lizards generally prefer dry areas and avoid herbal growth with tall broad leaves (Ceirâns 2007). In Romania, researchers found age differences in habitat selection, with adult and yearling lizards tending to use the compact vegetation at the bases of bushes whereas hatchlings were found using lower vegetation and open patches (Nemes et al. 2006). Sexual and ontogenetic differences in microhabitat use and phenology have previously been reported and are related to reproductive cycles (Saint-Girons 1976, Nuland & Strijbosch 1981). In the Pyrenees, it was found that Sand Lizards exhibited differences in habitat use and activity, depending on sex and time of the season, with meadows being most commonly used, except during breeding season, when these lizards preferred bushes over meadows. The authors also found that juveniles rarely used bushes and preferred meadows that had been cropped short (Amat et al. 2003). In Bulgaria, researchers suggested that the height and density of grass seems to be a key microhabitat feature that spaces the sand lizard's distribution in the subspecies *L. a. bosnica* (Prieto-Ramirez et al. 2018). Furthermore, differences in microhabitat selection were detected between males and females of the subspecies *L. a. chersonensis* (Grozdanov et al. 2014). In the United Kingdom, which is part of the northwestern edge of the Sand Lizards' range, this species inhabits exclusively sandy and dry environments like coastal dunes or heathlands and prefers more open habitats (House & Spellerberg 1983, Woodfine et al. 2017). Jackson (1978) already hypothesized that climate may have an influence on Sand Lizard distribution in Britain. It was suggested that a low level of sunshine in May was one of the reasons for the decline of the Sand Lizard population on the Merseyside coast in northwestern England in the 1960's (Jackson 1978). These findings from the edges of the Sand Lizard's range show up extreme variations in habitat choice, making peripheral populations seem to compensate for overall poorer conditions by responding more extremely to different parameters of their habitat. Studies performed in these peripheral situations already provide important information on habitat selection and habitat use by this species, including that they can vary drastically between individual locations. However, to our knowledge, no study examining factors influencing spatio-temporal habitat selection in the core distribution area of the Sand Lizard has as yet been conducted. Thus, based on the available data from the periphery we hypothesize: As imposed by the principle of Kühnelt (1943), we expect spatio-temporal habitat use in the core distribution area of the species to be less pronounced compared to the range edges. To test this hypothesis, we monitored conditions in the distributional core area of *L. agilis*, focusing on the nature reserve Dellbrücker Heide, North Rhine-Westphalia, Germany. We here test if distances to habitat structures and the microhabitat use of Sand Lizards are subject to seasonal or daily differences due to changes in weather conditions. Furthermore, we assess if these parameters as well as microclimatic conditions differ depending on the sex and/or size of individuals. Our results from the core area are compared to data from the Sand Lizard's range edges.

Materials and methods

Study area

The nature reserve Dellbrücker Heide (geographic location in WGS 84: 50.98187° N; 7.05805° E, altitude: 37–59 m a.s.l) with an area of only 40 ha, is a very small part of the Bergische Heideterrasse (KuLaDig 2016). The Bergische Heideterrasse has a total length of 80 km, ranging from Duisburg to Siegburg, and was formed from the mountain fuselage of the Rhenish Slate Mountains by the erosion of older rock layers and a deposition of loose more recent layers. Despite its small extent, the Dellbrücker Heide has a remarkably high diversity in flora and fauna composed of sandy grass- and heathland areas framed by small forests, which provide a perfect mosaic of transition structures. These attributes are known to be very important for the viability of many species (Brachet et al. 1999) and constitute a highly suitable habitat for *L. agilis* (Blanke 2021).

Study design

To assess the spatial positioning of Sand Lizards in their habitat in a standardized and constant manner, visual encounter surveys were conducted using predefined transects and random points, covering all available habitat types (Fig. 1). Detectability of lizards was not only depending on habitat composition, but also on weather conditions during our fieldwork, for which reason data collection was extremely difficult on days with heavy rain or extreme heat. Days with overall poor sampling conditions therefore were subsequently avoided by checking the weather forecast every day prior to a survey (for baseline conditions for surveys see Supplementary Fig. S1). Nonetheless we tested whether sampling days represented the overall weather conditions in an appropriate manner by using the function sm.density.compare from the R package sm (Bowman & Azzalini 2018). We created density estimation plots showing the density of all days for weather variables, maximum temperature (°C), relative humidity (%), mean wind speed (m/s), sunshine, and precipitation duration (hours) at ten-minute intervals. Additionally, permutation tests of equality were computed to assess their statistical significance (Wilcox 2010), and p-values were analyzed to check if sampling days represented random samples.

Field data were recorded at least 40 times a year (52 times in 148 days with 66 h of data acquisition in total from 2 May to 26 September 2018, 40 times in 133 days with 60 h of data acquisition in total from 24 April to 3 September 2019, and 42 times in 97 days with 118 h of data acquisition in total from 7 June to 11 September 2020). Due to natural changes of the environment, such as vegetation becoming impenetrable, landslides, or other barriers, some small adjustments to the borders of transects and numbers of random points were necessary.

All transects and random points were visited equally alternating at different time intervals, at least once in the morning from approximately 9:00 to 12:00 h, at midday from approximately 12:00 to 15:00 h, and in the afternoon from approximately 15:00 h to 18:00 h, to cover possible daily variations in spatial habitat use. Assessments were conducted systematically by following a predefined and memorized path based on prominent landmarks like individual shrubs and trees to avoid pseudo-replications. Random points were searched within a radius of about 20 m depending on accessibility. The following data were collected for every Sand Lizard observation:

First, the GPS coordinates of the sampling spot was taken in decimal degrees (WGS 84) with a maximum of 5 m uncertainty in radius. Furthermore, the date and exact sampling time were noted. Microclimate data included air temperature (in °C to the nearest 0.1°C ± 3.0%) and relative humidity (in % rH to the nearest 0.1% ± 5.0%) (multimeter ELV VA19), approximately 70 cm above the sampling spot (for summary statistics of the measurements see also Supplementary Table S2), cloud cover in three categories, 0 =

Figure 1. Aerial imagery of the study area Dellbrücker Heide. Red lines indicate transect locations. Red abbreviations identify the different transects after compass directions. White dots indicate random point locations with abbreviations as individual identifiers of each point.

no clouds, 1 = some clouds, 2 = partially cloudy, 3 = closed cloud cover, substrate temperature at the sampling spot (measured with a laser infrared thermometer ennoLogic eT1050D Dual Laser), and brightness of light at the sampling spot (categorized as sunny [spot fully exposed to the sun], half-shaded [shaded with insolated patches or sunny with shaded patches], or shaded). Microhabitat structure data were assessed within a 5-m radius, including the vegetation and predominant substrate type (sand, soil, gravel, or a combination of these). Sex and size classes (male, female, subadult) were visually assigned, by rough size estimations and evaluations of the colour pattern. The category 'subadult' comprises immature juveniles and yearlings that still had smaller sizes than adults and had not yet developed their typical distinct dorsal pattern and slim head shape of females or the green flanks and broader head of males, either of which are visible already from a distance (Bischoff 1984, Olsson 1988, Edgar & Bird 2006).

Weather data

Data on the weather conditions within the sampling periods were obtained via the German Meteorological Service (DWD) from the meteorological station with the ID 2667 situated at 50°51' N, 7°09' E. These included the current air temperature (in °C) at 5 cm and 2 m above the ground, relative humidity (in %), amount (in mm) and duration of precipitation (in hours), solar irradiance (in joule), hours of sunshine, maximum, minimum, and mean wind speed (in m/s) given for every ten minutes. Here, only the data consistent with encounter times of data assessments from 2 May to 26 September 2018, 24 April to 3 September 2019, and 7 June to 11 September 2020, were used for statistical analyses. Summary statistics of these weather conditions can be found in the Supplementary Table S3, characterizing the baseline conditions applied to this study.

Distance data

To assess habitat composition, seven classes of land cover were defined based on local conditions and our experience from the field from the years 2018 and 2019: Water, sand, grass (vegetation up to 50 cm in height), scrub (vegetation from 50 cm to 5 m in height), trees (vegetation > 5 m in height), heath and blackberry. The latter two are treated as separate categories due to their being structurally different from other scrub and because they must be regarded as important structures in Sand Lizard habitats (Edgar & Bird 2006, Clement et al. 2022).

To create a categorical habitat map, the methods established by Clement et al. (2022) were applied in a modified manner. A supervised land cover classification was created based on the latest UTM tiles (2019), available from the geoportal of North Rhine-Westphalia (RGB images, 10 cm pixel resolution). A habitat map was created using MaxEnt version 3.4.1. software (Phillips et al. 2017; for details, see below), as well as the geographic information system QGIS version 3.14.16 (https://qgis.org/de/site/; last accessed 15 November 2021), and the statistics program R version 4.0.5 (R Core Team 2021). The three spectral bands (red, green, blue) of the UTM tile were extracted and used as environmental variables. As training records, 100,000 randomly generated training points were created of which as many points as possible were manually assigned to the seven habitat classes (water, sand, grass, heath, blackberry, scrub, trees). In total, 100 models were computed using a bootstrap approach with an 80:20 split for model training and testing with standard settings. The resulting probability maps represented the likelihood of each grid cell to represent one of the habitat types. Performance of the models was evaluated using the Area Under the receiver operating characteristic Curve (AUC_{Test}), which evaluates the prediction accuracy of the model (Xu et al. 2019). AUC_{Test}-values above 0.7 indicate a useful discrimination ability of the model (Phillips et al. 2017, Walden-Schreiner et al. 2017, Xu et al. 2019). In a next step, using R (R Core Team 2021), the maps generated by MaxEnt were reclassified using the 10-percentile training presence cloglog threshold, assuming an error rate of 10% in the training records, and rescaled between 0 and 1. Finally, all probability maps for the different habitat classes were combined by assigning each grid cell to the class with the highest probability. To remove some mottling for a smooth result, in R, the resolution of the map was resampled to a coarser resolution of 50 × 50 cm per pixel using the nearest-neighbour approach with the function resample() from the raster package (Hijmans 2020). Based on the land cover mosaic map, distance maps quantifying the distance of every grid cell to all seven habitat categories were created (Hijmans 2020).

Principal Component Analysis and further statistical analysis

In total, information on 32 habitat factors was collected for 947 encounters from 2018 to 2020. Dimensionality was reduced by performing a Principal Component Analysis (PCA). For this purpose, the data was sorted into four groups, including different habitat features comprised of functionally similar variables (weather, distance, microclimate, and microhabitat structure). Weather data is comprised of the thirteen variables, current air temperature (in °C) 5 cm and 2 m above the ground, relative humidity (in %), amount (in mm) and duration of precipitation (in hours), solar irradiance (in joule), hours of sunshine, and maximum, minimum, and mean wind speed (in m/s) given for every ten minutes. Distances to habitat structures are comprised of six variables, including shortest distances to sand, grass, heath, scrub, blackberry bushes, and trees. Microclimate is comprised of the five variables, cloud cover (in eighths), substrate temperature (in °C), air temperature (in °C), humidity (in %), and brightness of light at the encounter spot (sun = 1, half-shade = 2, shade = 3). Microhabitat structure contains eight variables, sloping (present = 1, not present = 0), open patches of sand, soil and/or gravel (present = 1, not present = 0), grass (present = 1, not present = 0), leaf litter (present =1, not present = 0), low vegetation of grass and scrub (from 50 to 500 cm in height (present = 1, not present = 0), trees taller than 500 cm (present = 1, not present = 0), substrate type (sand, gravel, soil and combinations), and the type of location (substrate = 1, grass = 2, leaf litter = 3, wood = 4, moss = 5, heath = 6, blackberry = 7, or scrub = 8). The PCAs were conducted for all four groups separately and only Principal Components (PCs) with eigenvalues > 1 were used for further analysis. The PCAs of the first two groups were performed with the function princomp() of the R package stats (R Core Team, 2021). The second two groups included also categorical variables and therefore, the function dudi.mix() of the package ade4 (Dray & Dufour 2007) was used.

Generalized Linear Models (GLMs), computed with the function glm() in R's stats package (R Core Team 2021), were applied to test if the distance to habitat structures depended on time, weather, microhabitat structures, or microclimatic conditions. The three different time variables, time in minutes since first encounter in 2018, Julian day, and calendar week were included to cover potential seasonal shifts. When a significant p-value was found ($p < 0.05$), the test was repeated with only the significant terms and then the R^2 was calculated to examine how well the regression model fitted the observed data. The same approach was applied to all microhabitat structure PCs, to investigate if microhabitat choice depended on sampling time or/and microclimatic conditions.

To detect diel fluctuations in habitat use, density estimation plots using the function sm.density.compare() from the R package sm (Bowman & Azzalini 2018) were conducted to show up the density of all distance PCs, microclimate PCs, and microhabitat structure PCs for the three time-intervals, 8:00–11:00 h, 11:00–14:00 h, and 14:00–20:00 h. Additionally, pairwise permutation tests of equality of the time intervals (morning/midday, morning/afternoon, midday/afternoon) were computed with 1,000 bootstraps to assess statistical significances (Wilcox 2010), and p-values were analyzed to assess if time intervals differed significantly from each other.

Multidimensional hypervolumes (HVs) of the niche spaces were created using the function hypervolume_svm() of the R package hypervolume version 2.0.12 (Blonder 2019) to estimate niche differentiation between sexes (female, male, subadult). This algorithm uses one-class support vector machines (SVM) and is implemented with a radial basis function (RBF). The two parameters of the RBF were left at the default setting ($\gamma = 0.5$ and $\nu = 0.01$), which is considered sufficient for such calculations (Blonder 2019). γ determines an upper bound on the fraction of training errors and a lower bound of the fraction of support vectors (lower values result in tighter wrapping of the shape to the data), and ν defines the inverse radius of influence of a single point (low values yield large influences and smooth, less complex wraps around the data, and high values yield small influences, make tighter but potentially noisier wraps around the data). The function hypervolume_set() was used to visualize the niche of each sex class. Afterwards, the function hypervolume_overlap_statistics() was used to compute pairwise overlap statistics for every comparison (females with males, females with subadults, and males with subadults). The function hypervolume_overlap_statistics() computes a set of four metrics: the Jaccard similarity that calculates the index of volume of intersection of 1 and 2 divided by the volume of union of 1 and 2, the Sorensen similarity that calculates twice the volume of intersection of 1 and 2 divided by volume of 1 plus the volume of 2, the unique fraction 1 that is the volume of unique component of 1 divided by volume of 1, and the unique fraction 2 that is the volume of unique component of 2 divided by volume of 2. To describe the influence of the PC axis on the HVs, the function hypervolume_variable_importance() was used across 100 replicates for each comparison, and the mean variable importance as well as the standard deviation were calculated. To investigate if sampling time (morning, midday, afternoon) influenced the encounter probability of a specific sex class, a Chi-squared test with the function chisq.test() available in the R package stats (R Core Team 2021) was conducted.

From 2018 to 2020, we obtained a total of 1095 Sand Lizard observations of which 947 had complete sets of metadata and were used in the analysis. These were 429 adult females, 295 adult males, and 223 subadults, i.e., immature juveniles and yearlings. We expected a low degree of pseudoreplication as initial population size estimates based on photographic identification revealed very low re-encounter rates (V. F. Clement unpubl. data).

Results

Creating a categorical habitat map using MaxEnt

Average AUC_{Test}-values (Table 1) ranged from 0.655 for trees to 0.949 for heath. The AUC_{Test} of trees is comparatively low, but still acceptable, as trees (predominantly *Betulus pendula*, *Fagus sylvatica*, *Prunus serotina*) cover a huge proportion of the study area and all other model performances exhibit good results, matching our experiences from the study site.

The UTM tiles from 2019 turned out to be a very accurate representation of the overall habitat composition of the Dellbrücker Heide, compared to our on-site experience in 2020. The categorical map of the Dellbrücker Heide covers an area of 36.8 ha, which represents almost the whole study area (40 ha) (Bündnis Heideterrasse e. V. 2021). Trees account for the most prominent vegetation class with over 140,000 m^2 (Fig. 2). This is not surprising, because woodlands frame all areas of lower vegetation, which mainly consist of grass and scrub while blackberry and heath are vegetation classes occurring at lower frequencies. Heath, the least frequent form of land cover, is only patchily distributed, and blackberry occurs in a more scattered fashion across the entire area. Sandy patches are predominant

Table 1. Results of habitat classification calculated with MaxEnt.

Class	Training samples	Averaged AUC_{Test} ± sd	Threshold	Band 1 contribution	Band 2 contribution	Band 3 contribution
Sand	1323	0.925 ± 0.004	0.485	35.519	3.730	60.751
Grass	4521	0.761 ± 0.005	0.419	85.449	5.226	9.325
Heath	214	0.949 ± 0.010	0.375	53.174	44.620	2.206
Scrub	1836	0.729 ± 0.010	0.416	71.724	26.604	1.673
Blackberry	157	0.810 ± 0.026	0.451	64.356	24.133	11.511
Trees	5944	0.655 ± 0.006	0.490	71.336	12.174	16.490
Water	8238	0.738 ± 0.004	0.443	77.596	0.981	21.423

in the Dellbrücker Heide where trails pass through and on the beach of the pond. Smaller artefacts are present in the transition area between sand and water. Shallow water, where the ground is visible, is wrongly classified as trees and grass. White areas in the map, which are mainly limited to the canopy of trees, indicate that land cover classification was unsuccessful here. These areas were not included in the coverage calculation of the classes and therefore are neglected in the graphic of the mosaic map (Fig. 2).

Principal Component Analysis (PCA), Generalized Linear Models (GLMs) and density estimations

The PCA based on weather conditions produced six PCs with eigenvalues > 1 (Table 2). The PCA based on distances to habitat features produced five PCs with eigenvalues > 1 (Table 3). The distances to water, as is represented by a large lake, was neglected because it had a very coarse gra-

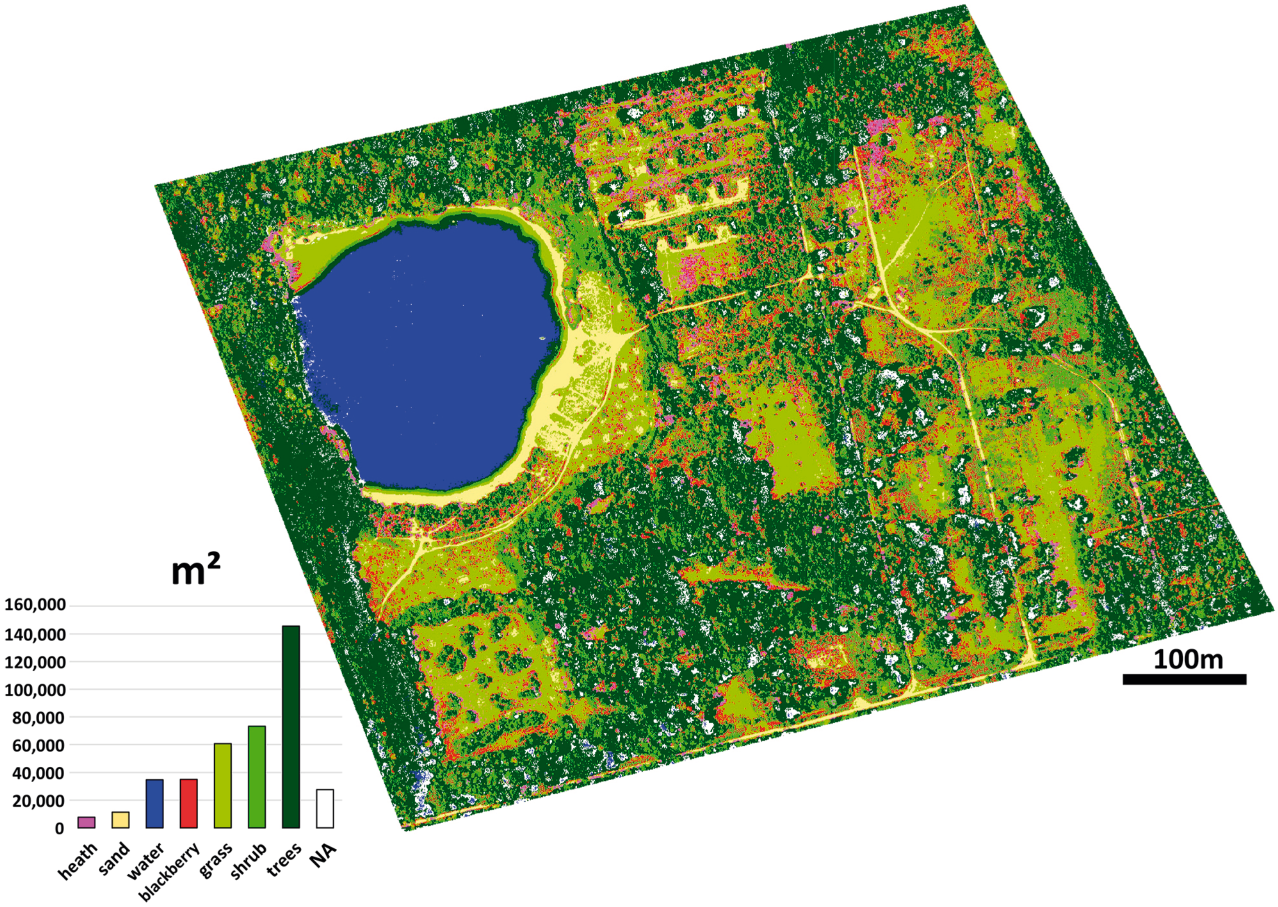

Figure 2. Land cover mosaic map depicting the seven habitat categories and the area covered by each in square metres (m²) with a resolution of 1 pixel = 50 × 50 cm.

Table 2. Summary of the Principal Component Analyses of weather conditions, showing factor loadings for each predictor, eigenvalues, explained variance, and the cumulative sums of the explained variance. The abbreviation a. g. stands for above ground.

Variable	PC1	PC2	PC3	PC4	PC5	PC6
Current temperature 200 cm a. g. (°C)	0.35	0.70	0.53	0.20	0.21	0.03
Current temperature 5 cm a. g. (°C)	0.55	0.63	0.39	0.31	0.19	0.01
Humidity 200 cm a. g. (%)	-0.49	-0.70	0.51	0.03	0.03	0.00
Maximum temperature (°C)	0.53	0.49	0.66	-0.21	-0.09	-0.04
Minimum temperature (°C)	0.50	0.51	0.66	-0.20	-0.10	-0.04
Minimum temperature 5 cm a. g. (°C)	0.73	0.36	0.54	-0.11	-0.12	0.00
Solar irradiance (joule)	0.96	-0.27	-0.04	0.01	0.01	0.00
Hours of sunshine	0.83	-0.08	-0.01	-0.15	-0.06	0.01
Hours of precipitation	-0.37	-0.05	-0.12	0.33	-0.03	-0.86
Amount of precipitation (mm)	-0.14	0.04	-0.08	0.10	0.04	-0.37
Maximum wind speed (m/s)	-0.08	-0.05	-0.12	-0.70	0.67	-0.08
Minimum wind speed (m/s)	-0.38	0.04	-0.12	-0.56	0.58	-0.06
Mean wind speed (m/s)	-0.21	0.01	-0.15	-0.67	0.65	-0.07
Eigenvalues	294.69	100.75	62.10	9.51	6.16	2.69
Explained variance	61.68	21.09	13.00	1.99	1.29	0.56
Cumulative sum of exp. var.	61.68	82.77	95.76	97.75	99.04	99.61

Table 3. Summary of the Principal Component Analyses of distance, showing factor loadings for each predictor, eigenvalues, explained variance, and the cumulative sums of the explained variance.

Variable	PC1	PC2	PC3	PC4	PC5
Distance to sand	0.99	0.02	0.14	0.03	0.01
Distance to grass	0.59	-0.09	-0.32	-0.63	-0.37
Distance to scrub	-0.13	-0.70	0.35	-0.44	0.37
Distance to trees	-0.32	-0.80	0.46	0.13	-0.16
Distance to blackberry	0.24	-0.52	-0.06	-0.71	0.16
Distance to heath	0.46	-0.63	-0.60	0.17	0.04
Eigenvalues	38.16	11.86	6.94	3.49	1.24
Explained variance	61.42	19.10	11.17	5.61	2.00
Cumulative sum of exp. var.	61.42	80.51	91.69	97.30	99.30

Table 4. Summary of the Principal Component Analysis of microclimate, showing factor loadings for each predictor, eigenvalues, explained variance, and the cumulative sum of the explained variance. “ifr” = measured with an infrared thermometer

Variable	PC1	PC2
Clouds	0.48	0.58
Substrate temperature (ifr)	-0.79	0.00
Air temperature	-0.71	0.51
Rel. humidity	0.76	-0.26
Light condition at spot	0.37	0.77
Eigenvalues	2.07	1.25
Explained variance	41.49	25.08
Cumulative sum of exp. var.	41.49	66.57

Table 5. Summary of the Principal Component Analysis of microhabitat structure, showing factor loadings for each predictor, eigenvalues, explained variance, and the cumulative sums of the explained variance.

Variable	PC1	PC2	PC3
Slope	0.21	0.36	-0.08
Open patches	-0.09	0.56	0.59
Grass	0.56	0.05	-0.51
Leaf litter	0.06	-0.45	0.33
Low vegetation	-0.79	0.06	-0.25
Trees	-0.06	-0.55	0.45
Substrate	-0.16	0.49	0.25
Location of observation	-0.82	-0.07	-0.25
Eigenvalues	1.70	1.21	1.12
Explained variance	21.21	15.11	13.95
Cumulative sum of exp. var.	21.21	36.32	50.27

dient and was not directly present in our recording areas and therefore would have distorted the PCA results. Small, temporary water bodies were not mapped. The PCA based on microclimatic conditions produced two PCs with eigenvalues > 1 (Table 4), and the PCA based on microhabitat structures produced three PCs with eigenvalues > 1 (Table 5).

GLMs for some of the combinations produced significant p-values ($p < 0.05$) (Supplementary Tables S3, S4), but when repeating the models with only the significant R^2 values were always lower than 0.07 (Supplementary Tables S5, S6), suggesting very low performances of the regressions.

Density estimation plots for all distance-related PCs depending on the time intervals morning, midday, and afternoon display a slightly lower density in the afternoon for PC1 (Fig. 3). Distance PC1 is mainly composed of positive correlations with the distances to sand and grass. The pairwise permutation tests of time groups also produced highly significant results for the comparisons of morning with afternoon ($p = 0.004$) and midday with afternoon ($p < 0.001$) (Fig. 3).

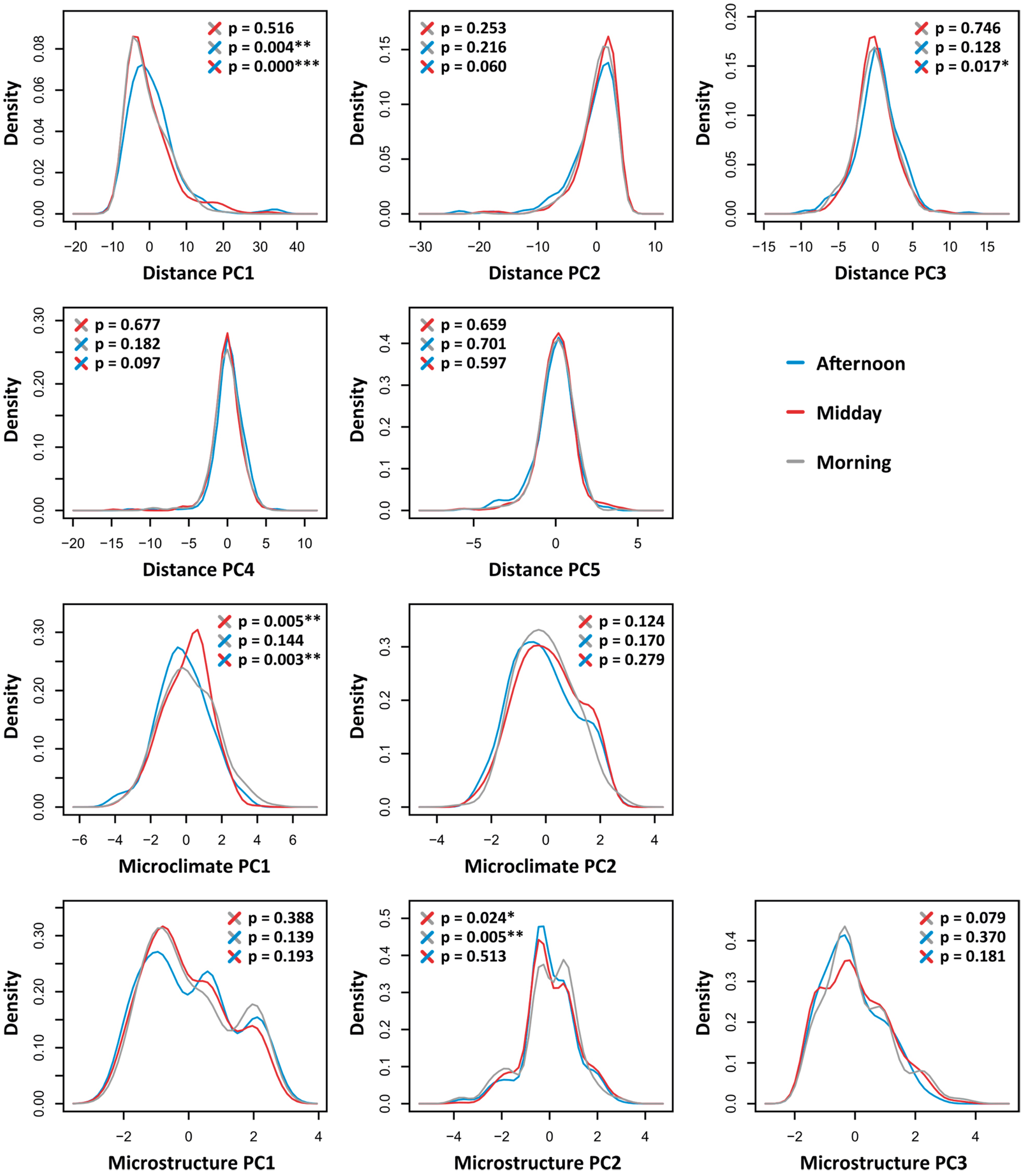

Figure 3. Density estimation plots for microclimate, distance, and microhabitat structure per time interval (morning/midday/afternoon), with p-values of pairwise permutation tests of equality. * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.005$.

Table 6. Results of overlap statistics of the hypervolumes for pairwise comparisons of females, males and subadults.

Group	Pairwise comparison	Jaccard similarity	Sörensen similarity	Unique fraction 1	Unique fraction 2
Distance	Female/male	0.538	0.700	0.318	0.281
	Female/ subadult	0.482	0.651	0.264	0.417
	Male/ subadult	0.467	0.636	0.258	0.443
Weather	Female/male	0.619	0.764	0.275	0.192
	Female/subadult	0.249	0.398	0.738	0.171
	Male/ subadult	0.245	0.394	0.734	0.243
Microclimate	Female/male	0.765	0.867	0.168	0.095
	Female/subadult	0.810	0.895	0.146	0.060
	Male/subadult	0.738	0.849	0.156	0.145
Microhabitat structure	Female/male	0.769	0.869	0.147	0.114
	Female/subadult	0.687	0.814	0.272	0.077
	Male/subadult	0.627	0.770	0.299	0.144

As for microclimate, the density plot of PC1 shows slight differences between the time groups morning and midday and midday and afternoon, respectively (Fig. 3). Microclimate PC1 is mainly correlated with decreases of the substrate and air temperatures at the exact spot of an encounter and an increase in humidity. The corresponding permutation tests with p-values of 0.005 and 0.003 also show highly significant results (Fig. 3), proving that densities at midday differ from those in the morning and in the afternoon.

As for microhabitat structure, we only found differences depending on the time interval for PC2, showing a lower density in the morning, whereas the density is slightly higher at midday and in the afternoon (Fig. 3). Microhabitat structure PC2 contains mainly a positive correlation to open patches and a negative correlation to trees. Permutation tests reflect this (morning vs. midday, $p = 0.024$; morning vs. afternoon ($p = 0.005$; Fig. 3). Pairwise permutation tests of all other PCs were not significant.

Hypervolumes and density estimation

The overlap statistics of the hypervolumes (HVs) for pairwise comparisons of females, males and subadults are provided in Table 6. For distances, both similarity indices of all pairwise comparisons are highly similar. Additionally, both unique fractions of all pairwise comparisons of the HVs are low (< 32.0%), with only subadults showing unique fractions > 40.0% as compared to females and males.

For weather, both similarity indices for pairwise comparisons of HVs of females and males are very high, with a similarity of > 60.0%. The comparisons between the HVs of females or males and those of subadults reveal values < 40.0% for both similarity indices. The unique fractions of the HVs of females and males compared to those of subadults are also very high at values of 73.8% for females and 73.4% for males. The unique fractions of HV of males compared to those of females are quite low in contrast, reaching not more than 27.5% for females and 19.2% for males.

For microclimate, both similarity indices for all pairwise comparisons are very high, with a similarity of > 70%. Furthermore, unique fractions of the HVs of all sexes are very low, reaching not more than 16.8%.

For microhabitat structures, both similarity indices for all pairwise comparisons are quite high with a similarity of > 68.5%. Furthermore, the niche of subadults does not differ much from that of females (unique fraction of the HV of subadults only 7.0%).

Density estimation plots for the sexes reveal an extremely high density of data points within a very small range especially for distance, which differ not differ between specific sex classes (Fig. 4). Permutation tests reflect this by showing only two significant differences for distance PC2 ($p = 0.02$) and PC5 ($p = 0.002$) between males and females. Distance PC2 mainly contains negative correlations with distances to scrub, trees and heath.

As for the factor weather, the density is quite broad. Permutation tests produced significant p-values for pairwise comparisons of males with subadults and females with subadults for weather PC1 and PC2. Weather PC1 contains mainly positive correlations with solar irradiance and hours of sunshine and minimum temperature 5 cm above the ground (Table 2). Weather PC2 includes a negative correlation with humidity and a positive correlation with temperature. Since both PCs share positive correlations with temperature, subadults appear to prefer different climatic conditions than do males and females. Apart from that, density estimation plots of weather PC1 suggest a bimodal distribution of subadults. At weather PC4, which contains mainly minimum and maximum wind speeds (Table 2), the density plot shows small differences between sex classes (Fig. 4). Permutation tests are significant for the comparison of males with subadults ($p = 0.01$) and suggest that females share densities at the intersection of both other groups. Since weather PC6 only represents 0.5% of

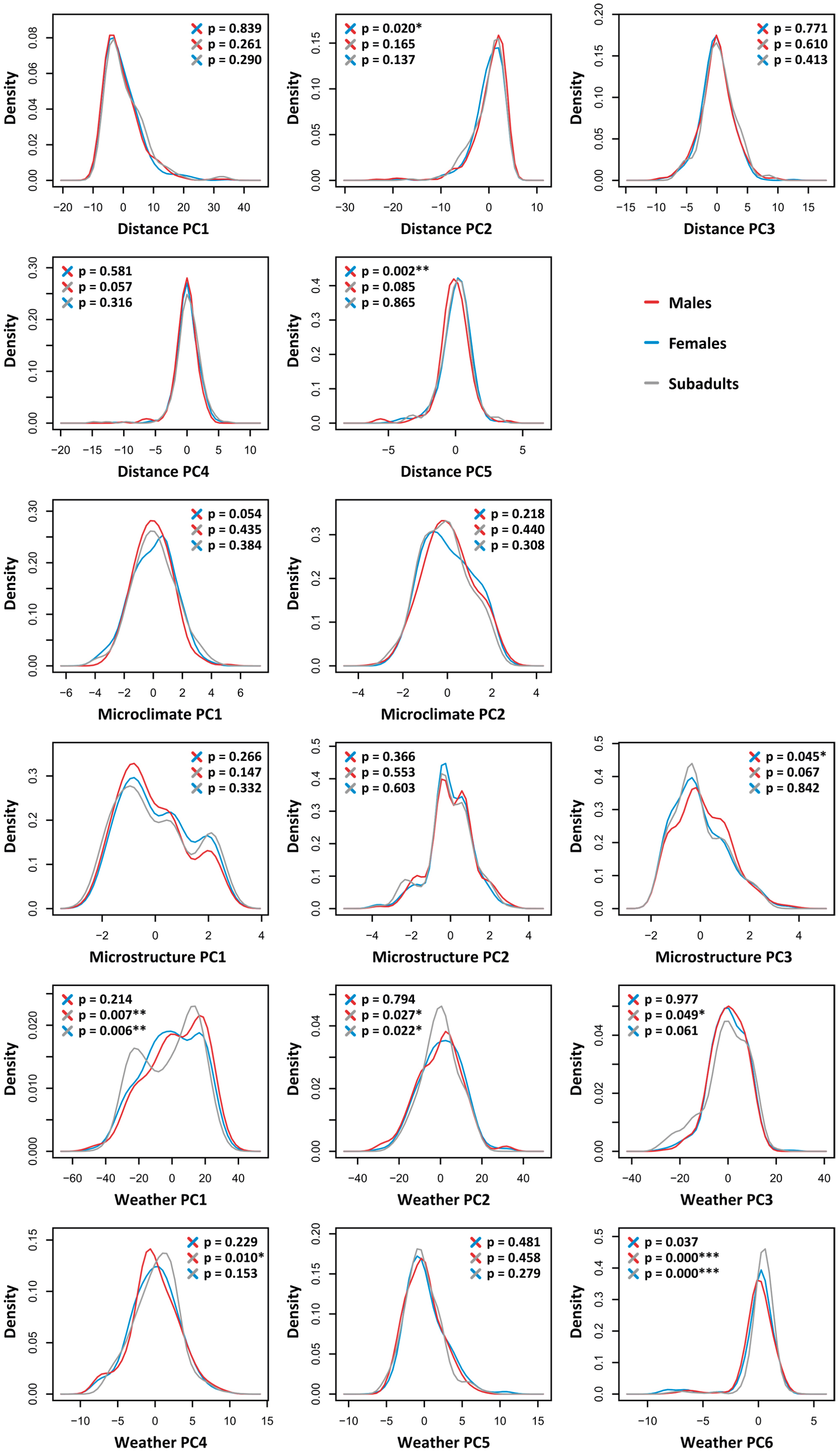

Figure 4. Density estimation plots for weather, microclimate, distance, and microhabitat structure per sex group with p-values of pairwise permutation tests of equality. * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.005$.

the total variance of the weather variables the significant p-values were neglected.

For microclimate PC1, mainly including the variable light conditions at spots, and microclimate PC2, mainly containing light conditions at the collection spots, cloud cover, and air temperatures, density estimation plots indicate that females have a lower density than males and subadults (Fig. 4). Permutation tests for microclimate do not result in any significant difference in densities between the sex groups at all.

For microhabitat structure, density estimation plots show high similarities between all sexes for all PCs (Fig. 4). Permutation tests reveal only significant differences in microstructure PC3 ($p = 0.045$) for males vs. females. Microstructure PC3 mainly contains a positive correlation with open patches and trees and a negative correlation with grass coverage.

Density estimation plots for the weather conditions on the sampling days (Fig. 5) illustrate that a broad range of different values are represented for every weather variable. Permutation tests reflect this in the shape of significant differences for all weather variables (maximum temperature $p = 0.000$, relative humidity $p = 0.000$, mean wind speed $= 0.03$, hours of sunshine $p = 0.000$, hours of precipitation $p = 0.000$).

The Chi-squared test for distribution, applied to detect if sampling time had influenced the encounter probability of a specific sex group, was not significant ($p = 0.432$, df = 4, Chi-squared = 3.810). Therefore, sex groups and time intervals are statistically independent.

Discussion

Our results of potential seasonal habitat shifts of *L. agilis* in the Dellbrücker Heide, which is part of the distributional core area of the Sand Lizard, were compared with studies assessing populations from the species' distributional range edges (Jackson 1978, House & Spellerberg 1983, Amat et al. 2003, Nemes et al. 2006, Ceirâns 2007, Grozdanov

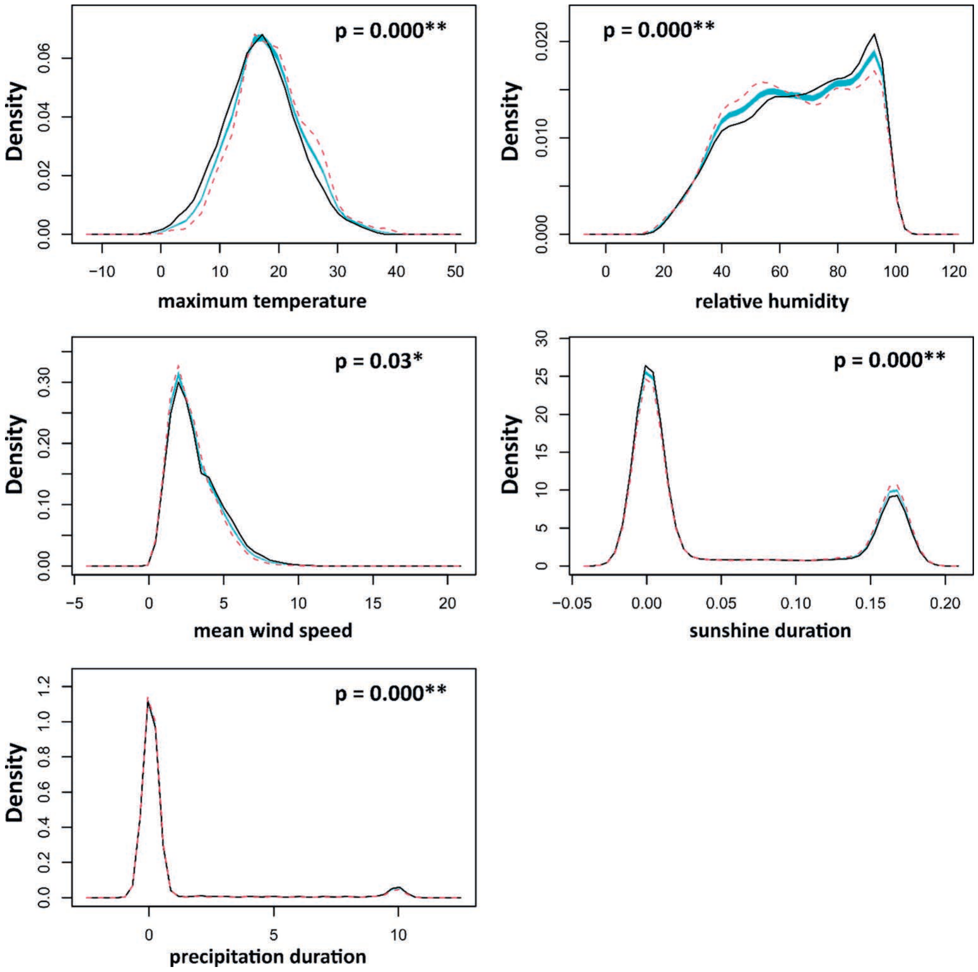

Figure 5. Density estimation plots for maximum temperature (°C), relative humidity (%), mean wind speed (m/s), hours of sunshine and precipitation (taken for every ten minutes), compared for all sampling days with p-values of permutation tests of equality. * $p < 0.05$ and ** $p < 0.01$.

et al. 2014, Woodfine et al. 2017, Prieto-Ramirez et al. 2018). These studies suggest stenopotency for the assessed populations, likely depending on geographic scale and habitat type/availability. In contrast, we have proved here the eurypotency of *L. agilis* in a part of its distributional core by investigating habitat composition and factors with potential influence on habitat use. Despite our large sample size and broad temporal coverage we found no support for the hypothesis that distances and microhabitat choice of Sand Lizards in the Dellbrücker Heide shift spatio-temporally according to daytime or season, which means that time had no influence on the movement of lizards in their habitat at all. Weather as well as microclimatic conditions apparently did not influence distances to habitat structures or the choice for structures in their microhabitat either. This indicates that the baseline conditions of the weather at the time of data acquisition (see Supplementary Fig. S1) in the Dellbrücker Heide did not induce lizards to engage in a specific behavioural pattern. We even found that the baseline conditions of the weather on sampling days were very representative and did not differ from random sampling. A high similarity in niche expression and niche sizes of lizards of all sex groups (male, female, subadult) exists for all categories (distance, weather, microclimate, microhabitat structure), which suggests that lizards do not significantly differ as to their habitat use and we did not find significant differences in weather or microclimatic preferences according to sex or size class, contrary to the results reported from distribution edges. Furthermore, sampling time did not affect our encountering of specific ontogenetic stages or sex groups.

Influence of habitat factors on habitat use

Our GLMs suggest that the Sand Lizards' movement within their habitats is independent of the time, weather, structures in their microhabitat, or microclimatic conditions. Density estimation plots and pairwise permutation tests showed that these lizards maintain a higher distance to sand and grass in the morning and midday, which is when they stay in the proximity of their hiding places in higher and denser vegetation. We also found slight differences in the microclimate when comparing midday with morning and afternoon. Temperatures in the morning are still low and lizards first must warm up in the morning and midday to stimulate their metabolism (House et al. 1980, Amat et al. 2003, Yang et al. 2015). In the afternoon, when temperatures decrease, these lizards are already warmed up and more mobile, for which reason they will then be more often found in open areas composed of grass and sand. Saint Girons (1976), who delved into activity periods of *L. agilis* in France, demonstrated that individuals left their hiding places early in the morning and became inactive already in the early afternoon, which matches our results. Although ecophysiological tests are required to prove this hypothesis, we expect that this might be caused by biotic factors. For instance, the lizards are more likely to have full stomachs in the afternoon due to successful foraging earlier in the day and hence have fewer reasons to be active. What also needs to be considered is that humidity also will decrease over time on a sunny day. Hence, habitats in the afternoon may warm up to similar temperatures but are dryer. When we set into relation the time intervals with the number of individuals encountered we found that in total 23.6% more individuals were spotted in the morning than in the afternoon. This is plausible when considering that lizards are still sluggish in the morning and are easier to spot while they bask at the bases of shrubs and in transition areas to higher vegetation. This also is reflected by the results of the microhabitat structure data where the density for some coefficients is lower in the morning and at midday at PC2, which mainly is composed of a positive correlation to open patches in the habitat and negative to trees. This suggests that Sand Lizards more often sit near trees in the morning and at midday, but are more often surrounded by open patches in the afternoon. Nonetheless, these results are only slightly obvious and not as pronounced as the density estimation plots suggest.

Sex- and size-specific niche segregation

Habitat niche utilization of the sex groups exhibit high similarities with only slight deviations in subadults. This might be due to the overall habitat composition of the Dellbrücker Heide. The whole area of 40 ha in total is quite small and contains several open areas that are framed by small pieces of woodland. Sand Lizards prefer to stay in the transition areas between lower vegetation and bare spots to higher vegetation (Schiemenz & Günther 1994, Blanke 2010, Grosse & Seyring 2015) and the Dellbrücker Heide has many of those transition areas, enabling these lizards to use them more extensively. Our results indicate that subadults use to a large extent the habitats occupied also by adult males and females, which is not surprising due to their being young males and females, but they also partly use other habitats to a smaller extent. This deviation could possibly be due to cannibalistic pressures on hatchlings when they still are very small. The latter is known to happen in Sand Lizards, and yearlings may experience competitive pressure from adults. Juveniles and small subadults could be potential prey (Böhme 1984, Corbett & Tamarind 1979, Prieto-Ramirez et al. 2018), and would be inferior opponents in interference competition (e.g., aggression towards smaller individuals) as long as they are not large enough to assert themselves (Delaney & Warner 2017, Prieto-Ramirez et al. 2018). Another reason could be that juveniles, due to their smaller body sizes, are able to also use less expansive vegetation for hiding. Permutation tests also show small differences in distances between males and females, which could be due to the breeding season, when males are known to move around more to find mating partners. This phase starts after hibernation in early spring and continues until July (Glandt & Bischoff 1988, Blanke & Fearnley 2015). Female home ranges are cited as often being much smaller than those of males, because they might tend to stay nearer to possible nesting sites (Olsson 1988, Edgar & Bird 2006). This is also represented in permutation tests for microhabitat structure that reveal a broader variation in many habitat structures in males than in females. Such a pattern can be expected, as mate guarding and home range defence is well known from the males of this species (Olson 1993, Olson et al. 1996).

According to the weather HVs, males and females are highly similar in niches with small unique fractions, showing that weather-dependent niches of males and females do not differ whereas subadults differ slightly in their weather preferences from those of males and females. This is also reflected in the density estimation plot of weather relative to sex group, according to which subadults do not only deviate partly from adults but also show a bimodal distribution for PC1 and PC2 containing solar irradiance, hours of sunshine, temperature, and humidity. These parameters are very important for thermoregulation in Sand Lizards (Jackson 1978, Dent & Spellerberg 1987, Amat et al. 2003). Younger individuals have smaller volumes and therefore heat up faster, which means that they face a higher risk of overheating, but cannot on the other hand keep body temperatures constant for longer periods, forcing them to alternate between basking and shaded spots more frequently than adults, which heat up more slowly, but due to their larger volumes can keep temperatures within the preferred range for longer periods, therefore have to bask less often, and can exploit colder areas for longer periods of time (Sagonas et al. 2013). Böhme (1984) stated that the preferred body temperature of subadults was slightly lower than that of adults. The bimodal distribution in subadults might be an artefact due to the category subadults not only comprising small juveniles but also yearlings, which are already quite large and share more similarities with the adult males and females. The deviation in subadults in density estimation plots is consistent with the HVs of weather and distance. Overall, Sand Lizards appear to occupy large climatic niches for specific habitat factors independent of their sex. This is evident from the broader spread of the densities for weather in PC1 in the respective estimation plots. The slight differences in size and sex in PC1 in the weather density plot can be explained by the fact that juveniles due to their smaller sizes thermoregulate more frequently. Sand Lizards in the Dellbrücker Heide are active not only in similar weather conditions, but also do not show any specializations for specific microclimatic conditions, as is suggested not only by the respective HVs but also permutation tests for equality.

Furthermore, when considering the choice of microhabitat structures by these lizards, HVs of sexes again come up with high similarities in all groups, and the fact that subadults have nearly no unique fractions compared to females shows that subadults use the same but fewer microhabitat structures and thus have a smaller niche size compared with both males or females, proving that they avoid certain areas in which they are out-competed by adults or are at risk of filial cannibalism (Corbett & Tamarind 1979, Böhme 1984, Prieto-Ramirez et al. 2018). Density estimation plots of microhabitat structure are consistent with the results of the HVs in that they indicate no significant differences in densities for subadults. Density plots overall illustrate a wide range in densities, evidencing that these lizards make use of a high diversity of microhabitat structures. Our study results also prove that the lack of differences in habitat use in the Dellbrücker Heide could not be caused by a differentiation between sex groups along diel timelines by showing that encounter times had no influence on the spotting of a specific sex group.

Core versus periphery of distribution

All statistic evaluations from the Dellbrücker Heide population of the Sand Lizard, which is part of the distributional core area of this species, provide completely different results to those reported from the edges/periphery of its distributional range, from which differences were reported to be very pronounced and influenced by various habitat characteristics (Jackson 1978, House & Spellerberg 1983, Amat et al. 2003, Nemes et al. 2006, Ceirâns 2007, Grozdanov et al. 2014, Woodfine et al. 2017, Prieto-Ramirez et al. 2018). Our results show only slight differences in habitat use by the Sand Lizards, which are attributed only to sexes and ontogenetic stage, meaning that these differences are shaped by characteristics of the lizards themselves but not by external circumstances. Henle et al. (2017) suggested that populations at the range edges of the Sand Lizard expressed a higher degree of specialization, had a lower diversity, and were more sensitive to habitat fragmentation compared to those at the core. This is reasonable when assuming that in the core region, living conditions for these lizards are optimal due to the combination of a wider range of suitable microhabitats (Henle et al. 2017, Prieto-Ramirez et al. 2020). This in turn makes the lizards become habitat generalists in their distributional core area, compared to the periphery where they have to adopt a higher degree of specialization to compensate for altogether poorer habitat conditions (Böhme 1978, Schaefer 2012, Böhme & Rödder 2014, Prieto-Ramirez et al. 2018). Our results prove a high range of tolerance towards many of the evaluated habitat factors of *L. agilis* in this population. Compared to populations studied in peripheral distribution ranges where lizards tended to be bound to specific habitats to an extreme extent, this constitutes an enormous contrast and shows this species' great capacity of behavioral adjustment to environmental conditions. In the absence of evidence for local adaptation or pronounced acclimatization the more parsimonious hypothesis of more limiting factors at the range edges compared to the core should be preferred. The latter is known as the Kühnelt (1943) principle, which operates at population level and is well applicable to *L. agilis*. The habitat mosaic of the Dellbrücker Heide is a perfect representation of the distributional core area of the Sand Lizard, providing optimal living conditions and a very pronounced landscape heterogeneity, which is proven by none of the evaluated habitat factor having an influence on habitat use. Therefore, proper management of those core areas with the aim of preserving habitat variability, as well as re-establishing connectivity of fragmented habitats especially in the distribution edges, are very important aspects for the conservation of the entire Sand Lizard population.

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Supplementary data

The following data are available online:

Supplementary Figure S1. Baseline weather conditions.

Supplementary Table S2. Summary statistics of the three climatic variables.

Supplementary Table S3. Summary statistics of weather data used for statistical analysis.

Supplementary Table S4. Generalized linear Model (GLM) summary statistics performed for distance Principal components.

Supplementary Table S5. Generalized linear Model (GLM) summary statistics performed for microhabitat structure Principal components (PCs).

Supplementary Table S6. Generalized linear Model (GLM) summary statistics performed for significant outcomes of the distance GLMs and computed R-squared.

Supplementary Table S7. Generalized linear Model (GLM) summary statistics performed again for significant outcomes of the microhabitat structure GLMs and computed R-squared.