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Home ranges of Sand Lizards, *Lacerta agilis* (Squamata: Sauria: Lacertidae), along railway tracks

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Abstract. Railway tracks are important novel habitats for Sand Lizards, *Lacerta agilis*, where they often occur in high densities. However, railways are subject to regular interventions, which might threaten local Sand Lizard populations. To assess possible threats through maintenance and construction, detailed knowledge of how Sand Lizards use habitats along railway tracks is essential. Therefore, we assessed the home ranges of Sand Lizards with radiotelemetry in 2020 and 2021 and determined if home ranges differed between seasons and sexes. We further assessed the present microhabitats including the lizards' sleeping sites. Our study took place in Brandenburg, Germany. We found that home ranges are smallest in spring and largest in summer but didn't find significant differences between male and female Sand Lizards. Home range size was best predicted by calendar week, with larger home ranges during warmer seasons. The home range core areas were located directly along the railway track. Sleeping sites were found mostly in the embankment and in the track ballast. The latter was the main sleeping habitat in summer, while in spring and late summer sleeping sites were mainly located in the embankment and at the forest edge. Our study shows that railway tracks and the adjacent embankments with high structural diversity provide all crucial elements for the occurrence of Sand Lizards throughout the year, while exact habitat use varies among seasons. We furthermore provide detailed insights into the use of different microhabitats as hiding and sleeping sites.

Key words. Autocorrelated kernel density estimation, microhabitat, sleeping sites, radiotelemetry.

Zusammenfassung: Bahnstrecken gehören zu den wichtigsten Sekundärlebensräumen der Zauneidechse (*Lacerta agilis*). Zur Aufrechterhaltung des Bahnbetriebs sind jedoch regelmäßige Eingriffe an Bahnstrecken notwendig, welche eine Gefahr für lokalen Zauneidechsenpopulationen sein können. Um mögliche Bedrohungen durch Instandhaltung und Bauarbeiten einschätzen zu können, sind detaillierte Kenntnisse darüber erforderlich, wie Zauneidechsen ihren Lebensraum entlang von Bahnstrecken nutzen. Daher haben wir in den Jahren 2020 und 2021 die Aktionsräume von Zauneidechsen mit Hilfe von Radiotelemetrie untersucht und festgestellt, ob sich diese zwischen den Jahreszeiten und den Geschlechtern unterscheiden. Zudem haben wir die an Bahnstrecken vorhandenen Mikrohabitate einschließlich der Schlafplätze der Eidechsen untersucht. Die Datenaufnahme wurde in Brandenburg durchgeführt. Im Ergebnis zeigte sich, dass die Aktionsräume von Zauneidechsen im Frühjahr nach der Winterruhe am kleinsten und im Sommer am größten sind. Unterschiede in der Größe der Aktionsräume zwischen Männchen und Weibchen waren nicht signifikant. Die Größe des Aktionsraums ließ sich am besten durch die Kalenderwoche vorhersagen, da in warmen Sommermonaten im Schnitt größere Aktionsräume verzeichnet wurden als im Frühjahr und Spätsommer. Die Kernlebensräume der einzelnen Tiere befanden sich direkt entlang der Bahnlinie. Die meisten Schlafplätze wurden in der Böschung und im Gleisschotter festgestellt. Insbesondere im Sommer stellte der Schotter den meistgenutzten Schlafplatz dar, während sich die Schlafplätze im Frühjahr und Spätsommer hauptsächlich in der Böschung und am Waldrand befanden. Unsere Studie zeigt, dass Bahngleise und die angrenzenden Böschungen eine hohe Strukturvielfalt aufweisen und damit ganzjährig von Zauneidechsen besiedelt werden können, während die genaue Lebensraumnutzung je nach Jahreszeit variiert. Darüber hinaus geben wir detaillierte Einblicke in die Nutzung verschiedener Mikrohabitate als Versteck- und Schlafplätze.

Schlüsselwörter. Autokorrelierte Kerndichteschätzung, Mikrohabitat, Schlafplatz, Radiotelemetrie.

Introduction

Linear infrastructure, such as roads and railways, causes landscape fragmentation, leading to habitat degradation and loss (Forman & Deblinger 2000), isolation of populations and collision-related mortality of wildlife (Borda-de-Água et al. 2017). However, there is ongoing debate over the extent of these effects. In contrast to the negative effects of roads and railways, these linear structures may also increase habitat connectivity (Henle & Rimpp 1994, Graitson 2006, Penone et al. 2012, Moroń et al. 2014, Popp & Hamr 2018, Ament et al. 2023), and thus species diversity in their surrounding areas (Debinski & Holt 2000). In addition, some linear structures themselves have the potential to provide novel habitats and ecosystems (Moroń et al. 2014, Wrzesień et al. 2016, Ouédraogo et al. 2020). Therefore, research is required to identify what causes positive effects of linear infrastructure and how these effects can be maintained or even improved.

While most studies on the ecological effects of linear infrastructure have concentrated on roads, there has been a recent increase in research on the ecology of the biocoenosis along railway tracks (Dorsey et al. 2015, Barrientos et al. 2019). For example, moose and bears were the focus of research on railway-animal relationships, as these species frequently collide with trains and cause severe damage to railway traffic. However, railway tracks can offer suitable habitat conditions for other taxa, such as grasshoppers (Miedreich 2000, Vandevelde & Penone 2017), butterflies (Kalarus & Bąkowski 2015), and reptiles (Graitson 2006, Graitson et al. 2020). Habitat suitability for these species relies on a regular but extensive mowing scheme along railway tracks that prevents trees and shrubs from growing, thus conserving open land vegetation with many flowering plants (Tikka et al. 2000) that attract pollinators (Moroń et al. 2014) and other insects.

For the Sand Lizard (*Lacerta agilis* Linnaeus, 1758), a Eurasian squamate species, it has been suggested that railways are currently among the most important novel habitats (Mutz & Donth 1996, Blanke 1999, English Nature 2004, Graitson 2006, Kühnel 2008, Borda-De-Água et al. 2017). Sand lizards are original inhabitants of forest steppe (Bischoff 1981). Nowadays they inhabit a variety of semi-open, warmer habitats that provide a small-scale mosaic of multiple vegetation structures. Due to widespread population decreases the species is strictly protected being listed in the Annex IV under the FFH directive ('European Habitats Directive') throughout the countries of the European Union (Council of Europe 2006). In Germany, both short-term and long-term population trends show a strong decline for Sand Lizards (Blanke et al. 2020), which is why action is required to bring this species to a favorable conservation status – in its natural habitats as well as in novel habitats such as railway tracks.

Railways are subject to regular interventions, such as maintenance of the track superstructure or modernization of the signalling system. As railways are frequently inhabited by Sand Lizards, these interventions must be conducted without killing or disturbing Sand Lizards or destroying their reproduction sites or resting places, as defined in the 'European Habitats Directive'. This results in a set of mitigation measures that are carried out frequently to protect affected Sand Lizard populations (English Nature 2004, Natural England 2011, Peschel et al. 2013, Schneeweiss et al. 2014). However, detailed knowledge of how Sand Lizards use their habitat along railways is essential to assess possible threats of construction activities and to evaluate the effectiveness of mitigation measures like e.g., translocation of animals. In this context, detailed knowledge of the species' home range specifications would enable a better understanding of habitat use (Bradley et al. 2023). Home range data of animals provide important information for habitat conservation or restoration (Horne et al. 2020, Rubke et al. 2022), and additionally are used to assess the size and quality of ecological compensation sites (Rubke et al. 2022, Bradley et al. 2023).

Therefore, our study's objective was to apply home range concepts to enhance our understanding of how Sand Lizards use the novel habitat railway tracks. More specifically, our research questions were: (a) Home range size: How large are home ranges of Sand Lizards that live along railway tracks, and how does size of home ranges differ across seasons and between sexes? What are possible environmental drivers of home range size? (b) Microhabitat use: What microhabitats are included in home ranges along railway tracks? What microhabitats are used as sleeping sites for Sand Lizards during different seasons?

The majority of previous studies reporting on home range size and movements of Sand Lizards were based on repeated visual encounters of the same, known animals (House & Spellerberg 1983, Olsson 1986, Nicholson & Spellerberg 1989, Elbing 1995, Märtens 1999). Here, the number of recaptures is rather small, with usually long intervals (weeks to months) between captures. Using this approach, resting sites (including sleeping sites, hibernation sites or diurnal resting sites) are only detected by chance (Blanke & Frese 2021). This could result in an underrepresentation of resting sites, which are crucial for the lizard survival. Therefore, we decided to study home ranges of Sand Lizards using radiotelemetry (Boitani & Fuller 2000, Dodd 2016). This enabled us to study Sand Lizards in their natural environment over different time periods during the year along a railway track in eastern Brandenburg.

Materials and methods

Study site

Our study was carried out in Neißemünde, Germany, at the German-Polish border (52°04'31–41" N, 14°41'26–50" E, Fig. 1A). The mean annual temperature is 9.7 °C, with an annual precipitation of 553 mm (Deutscher Wetterdienst 2023). The investigated two-track railway was built in 1846 and runs parallel to the river Oder. We collected data along an east to west orientated, 400 m long railway section in 2020 and 2021 (Table 1, Fig. 1C). Local trains pass the track every hour, additional freight trains drive daily on the track.

Within the study site we distinguished five different 'location types' that classify the main habitat elements that usually occur along railway tracks: track ballast, sideway, embankment, forest / forest edge and open land (compare Fig. 1B). The track ballast consists of crushed stones (ranging from 2 to 6.5 cm in size). The sideway, which is about 50 cm wide and runs on both sides along the railway tracks, consists of bare soil (gravel, 0.5 to 2 cm size) with scattered herbs. The embankment is alongside the sideway paths and approximately 4 to 8 m wide. The northern embankment is facing south, while the southern embankment is north-facing. Due to the annual mowing of the embankment, a diversity of herbs, grasses and shrubs has developed, with patches of bare soil in-between. Adjacent to both embankments broad leaf forest with native Scots pine (*Pinus sylvestris*), common oak (*Quercus robur*), and silver birch (*Betula pendula*), and non-native robinia (*Robinia pseudacacia*) can be found. Extensively managed grassland is present in the north-eastern area of the study site (Fig. 1C).

In addition to the different location types, we examined the microhabitat structures that Sand Lizards use. We mapped the different vegetation types in our study site and categorized them into nine different microhabitat types (Supplementary Table S1). All these microhabitat types have been identified as important for Sand Lizards in previous studies (e.g., House & Spellerberg 1983, Märtens 1999, Amat et al. 2003, Heltai et al. 2015). Additionally, we divided our study site into eight habitat sections, which comprise different abiotic and biotic factors (microhabitat type, aspect, and slope). These sections extend from the middle of the railway track 15 m into the surrounding area, illustrated in Fig. 1C. For every section we calculated the proportion of microhabitat structures, as well as mean slope and mean aspect (aspect, in this context meaning the compass direction a terrain surface is facing).

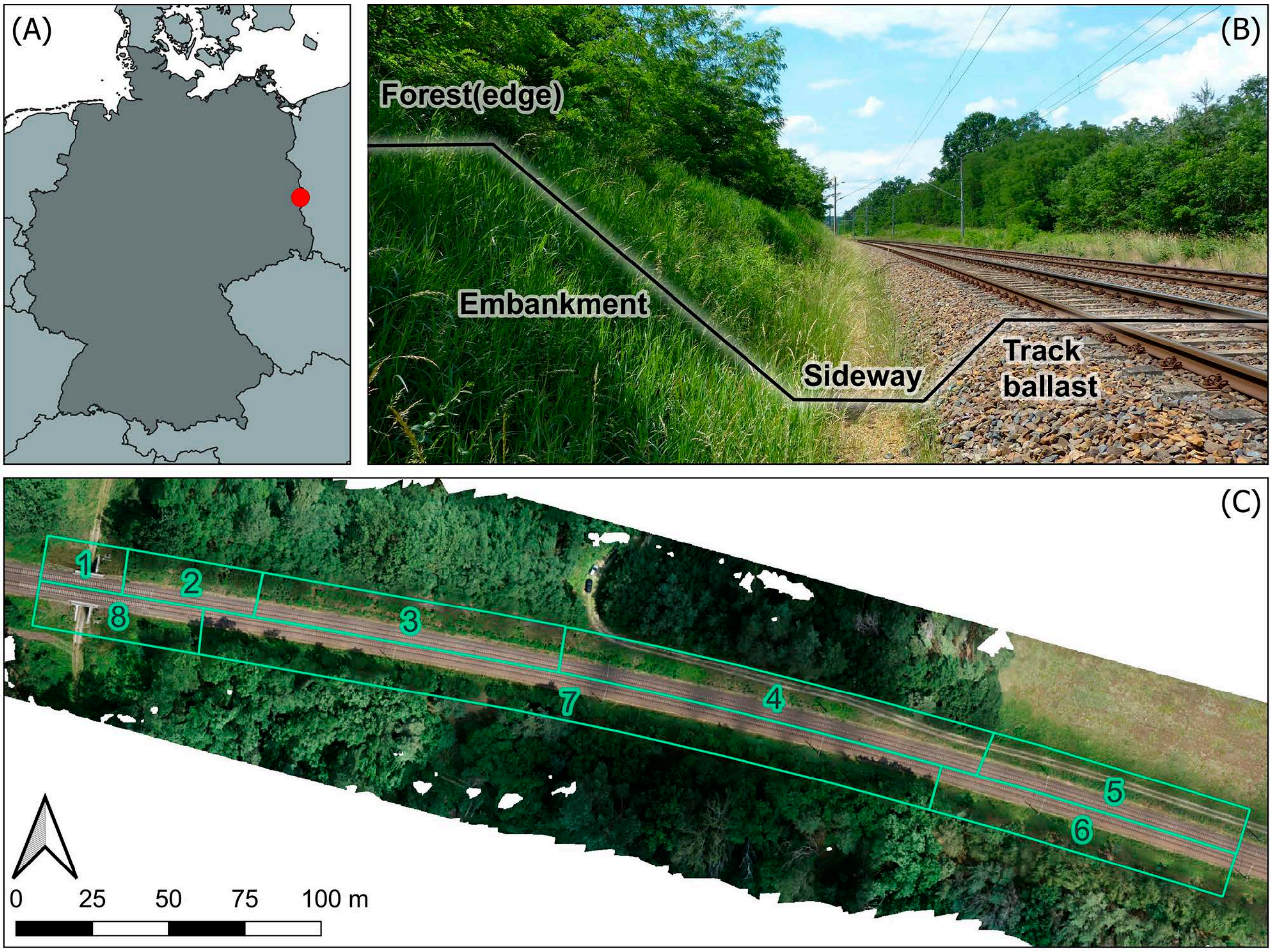

Figure 1. (A) Location of the study site in Neißemünde, Brandenburg, Germany. (B) Cross section of study site showing different locations: track ballast, sideway, embankment and forest(edge). (C) Aerial view of study site, a 400 m railway section. Numbers from 1 to 8 mark our divisions into habitat sections representing different biotic and abiotic conditions (composition of microhabitats, mean slope and mean aspect) that were analysed in the regression model (see Table 2). Aerial orthophoto: DB Engineering & Consulting GmbH.

Table 1. Summary of four different sampling periods (summer 1, summer 2, late summer and spring) during 2020 and 2021 with information on time, mean daily temperature and mean daily precipitation. For every sampling period the number of sampled Sand Lizards is provided, as well as the phenology of Sand Lizards and the daily lizard activity that was recorded during that period.

Sampling period	Timeframe	Mean daily temperature	Mean daily precipitation	No. of sampled lizards	Sand Lizard phenology	Daily lizard activity
Spring	19.04.–29.04.2021	7.6 °C (min. -4.8 °C, max. 18.1 °C)	1 mm	1 ♀ 17 ♂	Shortly after hibernation	09:30 am – 6:00 pm
Summer 1	09.06.–24.06.2020	19.0 °C (min. 6.3 °C, max. 34 °C)	4 mm	6 ♀ 10 ♂	Females gravid, oviposition	8:00 am – 7:30 pm
Summer 2	21.07.–04.08.2020	18.9 °C (min. 8.1 °C, max. 29.4 °C)	0 mm	10 ♀ 10 ♂	After mating season	08:30 am – 6:00 pm
Late summer	24.08.–12.09.2020	16.7 °C (min. 4.5 °C, max. 27.1 °C)	2 mm	12 ♀ 4 ♂	During beginning of hibernation	09:30 am – 05:30 pm

An aerial orthophoto of the entire area was recorded with an unmanned aircraft system (DJI Phantom 4 RTK) in June 2020 and provided by DB Engineering & Consulting GmbH. Additionally, a digital surface model with a resolution of 1 m was downloaded from LGB Brandenburg (© GeoBasis-DE/LGB, dl-de/by-2-0) to extract slope and aspect of the study site.

For our study periods, we obtained meteorological data from a weather station in Coschen (Station-ID: 6170, approx. 3 km from the study site). Weather data included in the home range analyses were mean daily air temperature (in °C) at a height of 2 m above ground and daily amount of precipitation (in mm) (Deutscher Wetterdienst 2023).

Sand Lizard data

Specimens were recorded in 2020 and 2021 during four different periods (subsequently labelled: “spring”, “summer 1”, “summer 2”, “late summer”), that represented different phases in the activity period of Sand Lizards (Table 1). At the beginning of every sampling period, we caught between 16 and 20 adult Sand Lizards (in total: 70; 29 females, 41 males) along the track, by hand or with a noose. We measured snout–vent length (SVL) and total length using a calliper (in mm, to the closest 0.5 mm), and body mass using a spring scale (1–30 g, 0.5 g increments). All animals were photographed with a Panasonic DMC-FZ150 camera for individual pattern recognition. Animals weighing a minimum of 6.0 g were tagged with a very high frequency (VHF) transmitter (LB-2X by Holohil). These transmitters measure 11 × 5 × 2.8 mm (L × W × H) and weigh 0.31 g. The battery of the transmitter lasts up to 21 days. Tagging of Sand Lizards with radiotelemetry transmitters has been successfully conducted by Clement et al. (2022) and Wieczorek et al. (2020), where the transmitter was attached dorsally to the animals. We applied a divergent tagging method, based on the method of Brazeau & Hecnar (2018), where the transmitter was attached with medical tape (synthetic band-Aid 3MTM TransporeTM) lateral to the lizard’s tail base (Supplementary Figure S2). The antenna of the transmitter was shortened to 5 cm to avoid entangling in vegetation. The tagging method was tested prior to fieldwork and showed no negative effects on locomotion and health of adult Sand Lizards (Janssen et al. 2024). After attaching the transmitter, all animals were released at the catching spot. By visual pattern recognition we assured that no animal was tagged twice. Sampling (i.e., locating every animal by radiotelemetry) started four to 12 hours after releasing the lizards. Throughout the seasons, daily sampling began one hour before anticipated lizard activity (depending on season, sun exposition, and air temperature (Blanke & Fearnley 2015) and ended one hour after the last active lizard was recorded (Table 1). Radiotracking was conducted with an Alinco DJ-X11 receiver, a HB9CV antenna and a Yagi antenna. All animals were located between one and seven times per day (average 3.4), by carefully approaching the animal following the received signal to the closest point – either until the animal was sighted or until the hiding spot was located with 0.4 m^2 to 1 m^2 accuracy (depending on quality of signal and respective depth of transmitter in the ground). The individual lizard ID, GPS coordinates and time stamp were recorded as ‘fixes’, together with the information if the respective animal was sighted or not. If the same location for one individual was recorded in one evening and the consecutive morning without seeing an active animal, this location was classified as an ‘overnight fix’. Overnight fixes were assessed infrequently. We tried to re-catch all animals that remained tagged until the end of a sampling period and removed the transmitter and tape. These animals showed no signs of negative impact by the transmitters. All sampled animals are listed in Supplementary Table S3, including size and weight of the animal, duration of sampling, number of fixes recorded and transmitter history.

Data analysis

To calculate home range estimates, we used area-corrected, autocorrelated kernel density estimation ($AKDE_C$; Fleming et al. 2015), a method that is robust to infrequent sampling with radiotelemetry and reliable for relatively small sample sizes (Fleming et al. 2019). Additionally, we calculated home range sizes by simple minimum convex polygons (MCP) to compare our results to previous studies on Sand Lizard home ranges (Blanke 1995, Märtens 1999, Clement et al. 2022, Wieczorek et al. 2020). However, the MCP method is sensitive to outliers polygon size tends to increase with sampling time (Börger et al. 2006) and polygons might include unused areas within home range boundaries (Fieberg & Börger 2012).

The main assumption for home range estimation is that animals show range residency. We tested every lizard with at least 16 fixes for range residency by calculating the semi-variance function (SVF). The resulting function was plotted in a variogram, using the 'continuous-time movement model' (ctmm) package in R 3.5.0 (Calabrese et al. 2016). We visually inspected the variograms for autocorrelation structure of the fixes. A range-resident animal should have a variogram that approaches an asymptote, which is proportional to home range size (Calabrese et al. 2016). If the variogram does not converge to an asymptote, this indicates either an insufficient sampling duration or shifting movements without range residency of the respective animal. Fixes of animals without range residency were excluded from home range estimation.

Calculation of home ranges with $AKDE_C$ was done stepwise. For every individual, we chose the best-fit movement model via maximum likelihood (ML) as well as perturbative Hybrid REML (pHREML) estimations, based on Akaike's Information Criterion adjusted for small sample sizes (AICc). Those models were fitted to the data to estimate usage density functions via $AKDE_C$. Fixes were weighted to determine home ranges based on irregular sampling schedules or missing data. During our study period, only one animal crossed the two-tier railway track, probably migrating to a hibernation site. All other animals used only the outer part of the rocky railway body and were never found in-between rails. Therefore, we took the middle of the railway track as a hard boundary for calculating home ranges. Subsequently, home range size was determined by the 95% $AKDE_C$ isopleth for every individual, as well as a core area with 50% $AKDE_C$ isopleth.

For the comparison with other Sand Lizard studies and home range sizes, we estimated conventional 95% MCP home ranges using the 'adehabitatHR' package in R (Calenge 2006). To assess the quality of home range sizes calculated with the MCP, we tested the dependency of the MCP home range size on an increasing number of fixes. For every Sand Lizard with more than 16 fixes we created 20 sets of data with its fixes in a random order and calculated the 100% MCP home range size for five to all fixes. Then we calculated the percentage of home range size that was reached for every combination of the random fixes in comparison to the 100% MCP of all fixes we collected. Finally, we summarized the values of every random set from all animals and fitted the accumulation curve with confidence interval (Supplementary Figure S4). At 16 fixes, the asymptote reaches 65% of mean percentage of home range size, converging at a fictive maximum of 110%. Therefore, home ranges of lizards with at least 16 fixes calculated with a 100% MCP polygon account for approximately two third of the total home range size (calculated with MCP) of the specific animal.

To test for differences in home range sizes between seasons and sexes, we computed a Wilcoxon rank-sum test, each for the MCP home range sizes and the $AKDE_C$ home range sizes. P-values were adjusted (in the following labelled "p_{adj}") with the Bonferroni-Holm method to account for multiple comparisons in each group. We used a linear model (LM) to test for the influence of different explanatory variables on home range size. All variables that were considered as explanatory are listed in Table 2. We chose SVL and sex, according to findings of Märtens (1999) and Wieczorek et al. (2020) who recorded differences in activity for Sand Lizards of different size and sex. Additionally, season was included in the model as a continuous variable, represented by mean weighted calendar week during which the sampling was conducted. As ectotherms, activity of Sand Lizards can strongly depend on weather. Therefore, we calculated mean daily temperature and mean daily precipitation during sampling for every lizard and included it in the analysis. Additionally, we wanted to test if the number of fixes had an influence on the calculated home range size and included number of fixes in the model. The latter can indicate if the time of sampling was sufficient for calculating robust home range estimates. To account for differences in microhabitat availability in our study section, we assigned every lizard to one habitat section (see Fig. 1C, 'study site'), based on where it was caught and had its main habitat (based on $AKDE_C$) during sampling. This allowed us to include the mean proportion of ruderal herbs and grasses (ruderal meaning early colonizer species), ruderal herbs and grasses with blackberry, forest and forest edge as explanatory variables in the model. At last, we included mean slope and mean aspect of the habitat section in which an animal lived. Aspect (usually measured in degrees) was transformed into the two variables northness and eastness to remove circularity in the data (see Olaya 2009).

If necessary, explanatory variables were square-root transformed (mean daily precipitation, cover of tall ruderal herbs, cover of ruderal herbs with blackberry, cover of forest and forest edge, cover of shrubs) to achieve normal distribution. As the 95% $AKDE_C$ and 95% MCP were highly correlated (Spearman's $\rho = 0.96$), we chose the 95% $AKDE_C$ (square-root transformed) as a response variable for home range size in the LM. Mean calendar week during sampling was used as a quadratic term in the LM, as it had an obvious non-linear relationship with home range size. Potential collinearity among explanatory variables was checked with variance inflation factors (R-package 'car', Fox & Weisberg 2019). Mean temperature and mean calendar week

Table 2. Explanatory variables that were considered for analysis of Sand Lizard home range size in the regression model. Variables that could not be used due to collinearity are marked.

Explanatory variable	Unit	Range	Median	Mean ± SD	Inclusion in linear model
Mean (weighted) calendar week	calendar week	16.5–35.9	30.28	26.50 ± 7.44	Yes
Sex of animal	category	female / male			Yes
Snout-vent-length	cm	6.0–8.5	7	7.18 ± 0.68	Yes
No. of fixes	count data	16–52	36	35.96 ± 9.20	Yes
Mean daily temp	°C	6.98–20.23	17.09	15.15 ± 5.10	No, collinearity with calendar week
Mean daily precipitation	mm	0.08–6.62	1.22	1.53 ± 1.57	Yes
Cover of ruderal herbs and grasses	%	0.18–48.88	15.2	19.99 ± 18.26	No, collinearity with cover of blackberry
Cover of ruderal herbs and grasses with blackberry	%	0.05–28.3	6.37	9.36 ± 10.17	Yes
Cover of shrubs	%	2.89–43.8	16.48	18.02 ± 12.69	Yes
Cover of forest	%	0.1–14.05	1.96	4.41 ± 5.12	No, collinearity with northness
Mean slope	°	4.13–13.03	8.79	8.44 ± 3.12	Yes
Mean northness	numerical	-1.00–0.9	0.55	-0.29 ± 0.67	Yes
Mean eastness	numerical	-1.00–0.83	0.03	0.13 ± 0.68	Yes

induced high variance inflation factors among each other, as did the cover of tall ruderal herbs with cover of shrubs and northness with cover of forest. Therefore, we removed mean temperature, cover of tall ruderal herbs and cover of forest from the model. In the adjusted model, variance inflation factors were consistently < 4 indicating that collinearity was unlikely (see Dormann et al. 2013).

In a last step, for testing the influence of different explanatory variables on home range size, we examined the relative importance of explanatory variables for explaining the response variable 95% AKDE_C by using model averaging (Grueber et al. 2011) in the R-package 'MuMIn' (Barton 2015). For each combination of the explanatory variables included in the full model, a single model was created. All models were then ranked by AICc. The best models (all within two AICc units from the model with lowest AICc) were averaged by using the full average weighted by each candidate models' relative explanatory weight. Residuals of all LMs were visually screened for assumptions of normality, which we met.

Finally, we used a path model to test if the effect of season on home range size was direct or if it was mediated indirectly via changes in environmental variables (mean temperature, mean precipitation), sex of the sampled animal, or number of fixes (i.e., control for sampling). Thus, an a priori path model with the direct paths of season (represented as calendar week), mean temperature, sex (different probability of catching male or female Sand Lizards), and number of fixes was constructed. An alternative model was also calculated, in which the effect of season (mean calendar week) on home range size was indirect via influence on mean temperature, mean precipitation, number of fixes, and sex. As mean calendar week and mean temperature had a non-linear relationship, they were both included with a quadratic term. Path models were calculated with the R-package 'lavaan' (Rosseel 2012) and model fit was tested using chi-square test (χ^2), comparative fit index (CFI), Tucker-Lewis index (TLI), root mean square error of approximation (RMSEA), and standardized root mean square residual (SRMR) (Hu & Bentler 1999). The path model used the same data as the linear model. Covariances were fitted between linear and quadratic calendar week, linear and quadratic mean temperature and between precipitation and mean temperature.

Results

Individual animals were radio-tracked between one and 18 days (mean: 8.5 days ± 4.4 SD). Out of all 70 tagged individuals, 49 had a minimum of 16 fixes each and showed range residency and were therefore considered for further analyses (73% of deployed tags). These 49 animals (22 females, 27 males) were tracked between three and 18 days (mean: 10.7 days ± 3.2 SD) and were located between 16 to 52 times (mean: 36 fixes ± 9.3 SD). Nineteen animals had less than 16 fixes and were excluded from further analysis, as well as two animals with more than 16 fixes but without range residency. In total, we included 1711 valid fixes for further analyses. Out of all datapoints, 218 overnight fixes could be evaluated. Only one animal crossed the railway track, while all other animals stayed on their original side of the track. Two untagged female Sand Lizards were observed during oviposition at the sideway during summer 1.

Home range size

We calculated home range sizes for 49 Sand Lizards during four different seasons (spring, summer 1, summer 2,

Table 3. Sand Lizard home range sizes calculated with the 95% AKDE$_C$, 50% AKDE$_C$ and 95% MCP for female and male Sand Lizards during spring (SP), summer 1 (S1), summer 2 (S2) and late summer (LS; compare Table 1). Home range sizes are given as mean home range size (in m^2) including standard deviation (SD) for each season and sex (females = ♀, males = ♂).

	SP ♀	SP ♂	S1 ♀	S1 ♂	S2 ♀	S2 ♂	LS ♀	LS ♂
Sample size	1	14	3	5	8	6	10	2
Ø 95% AKDE$_C$ (m^2)	12	50	108	339	347	268	69	192
SD	NA	39	24	153	236	97	42	146
Ø 50% AKDE$_C$ (m^2)	3	10	22	75	84	56	14	45
SD	NA	7	8	41	70	24	8	31
Ø 95% MCP (m^2)	5	20	57	160	125	110	24	101
SD	NA	17	20	86	112	46	16	79

Table 4. Results of the averaged linear model testing for relationship between explanatory variables and Sand Lizard home range size (95% AKDE$_C$). Given are model estimates (± SE), Z values, the probability P of the Z statistics, and the relative importance of a variable in the averaged model. Variables are sorted by decreasing relative importance. Note: Significant relationships (at $p < 0.050$) are given in bold. [a)] Square-root-transformed before analyses.

Variable	Estimate ± SE	Z value	P value	Relative importance
Week	5.796 ± 0.827	6.823	< 0.001	1.0
Week^2	-0.106 ± 0.016	6.415	< 0.001	1.0
Sex	1.757 ± 1.762	0.985	0.325	0.64
Northness	-0.643 ± 0.997	0.638	0.523	0.41
Eastness	0.500 ± 1.142	0.435	0.664	0.25
Mean slope in main habitat	0.073 ± 0.233	0.312	0.755	0.11
Cover of blackberry[a]	-0.148 ± 0.478	0.308	0.758	0.11
Mean precipitation[a]	-0.071 ± 0.377	0.185	0.853	0.09

late summer; Table 1). Over all seasons, home range sizes calculated by 95% AKDE$_C$ ranged from 0.7 m^2 to 885 m^2 (mean: 167 ± 170 m^2), while home range sizes calculated with 95% MCP ranged from 0.2 m^2 to 387 m^2 (mean: 68 ± 76 m^2). Home range sizes calculated with the 95% MCP was consistently smaller than home range sizes calculated with 95% AKDE$_C$ (see Supplementary Table 3 for individual home range sizes calculated with MCP and AKDE$_C$). Irrespective of the estimation method, the largest home ranges (by average) were recorded in summer 2, while in spring animals had the smallest home ranges (Table 3). Maps showing all estimated home ranges along the railway track calculated with the 50% and 95% AKDE$_C$ are provided in Supplementary Figure S5.

Home range sizes were compared between males and females during different time periods. Home range sizes calculated with either 95% AKDE$_C$ or 95% MCP did not differ between males and females (Wilcoxon rank test, p-values adjusted with Bonferroni-Holm method) (Fig. 2A). For females, both 95% AKDE$_C$ and 95% MCP were significantly larger in summer 2 compared to late summer (AKDE$_C$: $p_{adj} = 0.001$, MCP: $p_{adj} = 0.007$). For males, both estimates indicated significantly larger home ranges in summer 1 (both estimates $p_{adj} = 0.002$) and 2 (AKDE$_C$: $p_{adj} < 0.001$, MCP: $p_{adj} = 0.001$) compared to spring.

Core areas calculated with the 50% AKDE$_C$ averaged 37 m^2 ± 43 m^2 SD. Core areas were largest in summer 2 (average of 72 ± 55 m^2), while in spring animals had the smallest core areas (average of 9 ± 7 m^2). Home range size of 95% AKDE$_C$ and core area size of 50% AKDE$_C$ were strongly correlated (Spearman, $\rho = 0.973$). Accordingly, significant differences in core area size were similar to 95% AKDE$_C$ data.

Predictors of home range size

Home range size was best predicted by season, which was represented by the numeric variable calendar week as a quadratic term. Model selection revealed seven best fit models (all within two AICc units of the model with lowest AICc), which included calendar week (as a quadratic term), sex, mean slope, northness, eastness, cover of blackberry, and mean precipitation as relevant explanatory variables (Table 4). Once averaged across these seven models, only calendar week had a significant effect on home range size (Fig. 2B).

The path analysis indicated that the effect of season (represented here by mean calendar week) on home range size (95% AKDE$_C$) is not a direct one but mediated indirectly via differences in mean temperatures (Fig. 3). Furthermore, sex of an animal had a weak significant effect ($p = 0.042$) on home range size, while precipitation had none. The path model had a good fit, supported by Chi-square test ($p > 0.5$), comparative fit index (CFI > 0.90), Tucker-Lewis index (TLI > 0.95), root mean square error of approximation (RMSEA < 0.08), and standardized root mean square residual (SRMR < 0.08), indicating support for the hypothesized relationships.

Location and microhabitat composition of core areas

We analysed the location and the proportion of microhabitat types in the core areas of all animals during different seasons. The location of core areas partially shifted from locations close to the railway track in spring to locations slightly farther away of the railway track in summer 2 and late summer: In spring core areas were located mainly on

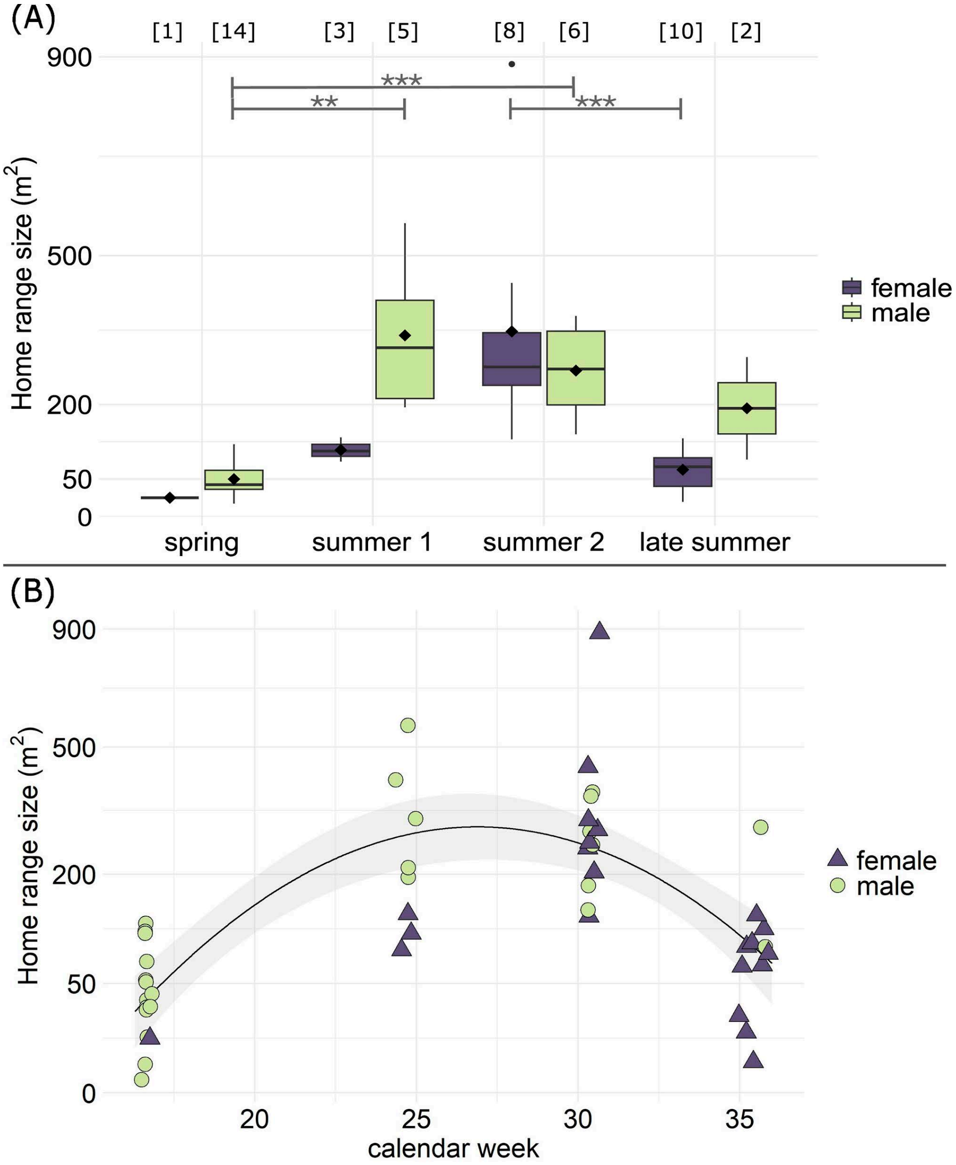

Figure 2. (A) Differences in home range size for male (green) and female (dark purple) Sand Lizards during the four sampling periods: spring, summer 1, summer 2 and late summer (compare Table 1), calculated with 95% $AKDE_C$. Given are median of home range sizes and mean home range size (black diamond; compare Table 3) for each group. Sample sizes are given in square brackets above each boxplot, Wilcoxon rank test results of comparisons between sexes and seasons are given with level of significance (**: $p < 0.01$; ***: $p \leq 0.001$). (B) Home range size of individual Sand Lizards (females: dark purple triangles, males: green circles) during spring (calendar week 16–17, April), summer 1 (calendar week 24–25, June), summer 2 (calendar week 30–31, July/August) and late summer (calendar week 35–36, August/September). The black regression line indicates the prediction of the linear model for home range size; the 95% confidence interval is displayed as grey-shaded ribbon. Note that the y-axis in (B) is square-root transformed.

the embankment, which in average comprised more than 75% of all core areas, and additionally consisted of small proportions railway track and sideway. In summer 1 and summer 2 the proportion of embankment that was included in the core areas decreased to approximately 30 to 40%. In summer 2 and late summer, forest was a component of core areas (average 15% in summer 2 to 25% in late summer), which was not the case in spring and summer 1. Changes in the location of the core area were not significant (Wilcoxon rank test with Bonferroni-Holm correction), but the use of the sideway was almost significantly higher (p_{adj} = 0.061) in summer 2 compared to spring.

We observed different microhabitat composition in the core areas during the year (Fig. 4). Overall, the core areas contained mainly five microhabitat types: track ballast, sideway, ruderal herbs and grasses, ruderal herbs and grasses with blackberry and shrubs. Forest edge, forest, and field path were included only in few core areas and accounted for small percentages in general. The microhabitat type construction was not part of core areas. In summer 1 and summer 2 the coverage of microhabitat types in the core area was rather equal (the mean proportion for every microhabitat type in core areas was below 26%), while in spring and late summer the main component of core areas were shrubs, comprising on average 42 to 44% of individual core areas. Differences in the percentage of shrubs in the core area throughout the year were not significant, though. A Wilcoxon rank test did not reveal any significant differences in the coverage of different microhabitat types in the core areas during different seasons.

The railway track is running from east to west, and almost all sites parallel to it are either facing north or south. Irrespective of railway site (north or south), core areas showed a mean aspect to south (aspect between 135° and 225°) for most (65%, 33 of 51 animals) animals. The Wilcoxon rank test showed a significant difference in mean core area aspect in spring (Ø 183 ± 49°), compared to summer 1 (Ø 117 ± 62°, p = 0.021), summer 2 (Ø 114 ± 60°, p = 0.000) and late summer (Ø 158 ± 45°, p = 0.036). The mean slope of core areas was higher in late summer and spring (both 13°) than summer 1 and 2 (both 10°), although these differences were not significant.

Sleeping sites

Sleeping sites were mostly located inside the core areas of the animal's home ranges. In spring, sleeping sites were found mainly (89%, 49 of 55 recorded locations) within the embankment (Fig. 5A). Interestingly, in summer 1 and summer 2 the track ballast was the most used sleeping site, with 81% of all sleeping sites in summer 1 (26 of 32 recorded locations) and 65% in summer 2 (45 of 69 recorded locations). In late summer, the embankment gained more importance as a sleeping site again. Here, 40% of all sleeping sites (25 of 62 recorded locations) were found in the embankment, with forest representing another 40%. Other microhabitats that were used as sleeping sites, were shrubs in spring and late summer, as well as herbs and grasses (with or without blackberry) in spring, and forest and forest edge in late summer (Fig. 5B).

The sleeping sites were similarly orientated than core areas, with most (62%) over the whole study period directing south (135–225°). Twenty-eight percent of sleeping sites

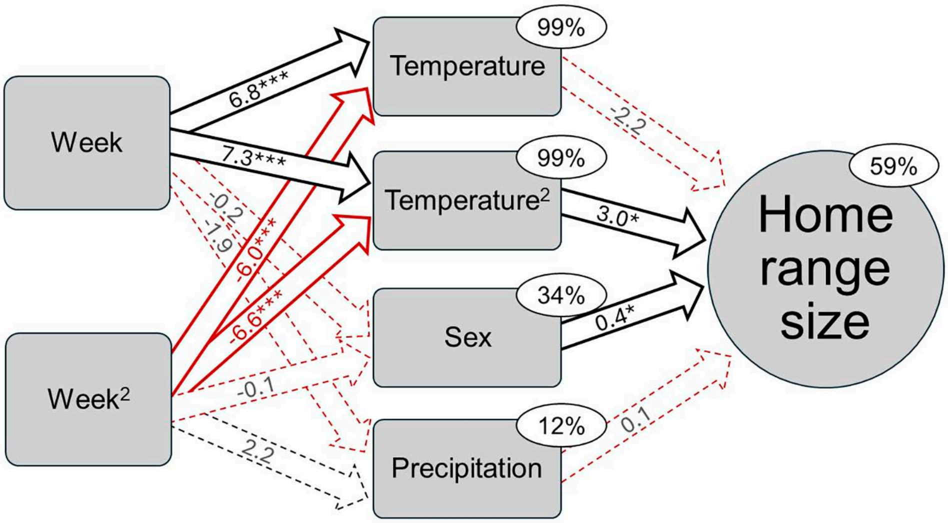

Figure 3. Illustration of the path model, showing that Sand Lizard home range size (estimated with 95% $AKDE_C$) is influenced indirectly by calendar week via changes in mean temperature. As mean calendar week and mean temperature show a non-linear relationship, they were included with a quadratic term. Numbers in arrows give the path coefficients. Contour of arrows corresponds to the strength of the respective path: Significant paths (*: $p < 0.05$, ***: $p < 0.001$) are indicated by bold arrows, non-significant paths ($p > 0.05$) are illustrated by dashed lines. Black arrows indicate positive relationships, red arrows indicate negative relationships. The circled numbers above endogenous variables are the sum of the variances (R^2) explained by all causal paths on a variable.

were north-facing slopes (315–360°, 0–45°). These were mostly located in the northern edge of the railway track that was used in summer 1 and in summer 2. During these periods, the railway track was the most used sleeping site.

Sleeping sites were found in places with slopes of up to 21°. On average, slopes of sleeping sites were steepest in spring (13.7 ± 6.5° SD) and summer 1 (13.1 ± 5.0° SD), followed by summer 2 (12.2 ± 7.3° SD) and late summer (11.1 ± 8.1° SD). These differences were not significant.

Discussion

The aim of our study was to understand how Sand Lizards along railways use their habitat throughout the year by applying radiotelemetry and the home range concept. We found that home ranges in general were largest in summer and smallest in spring. Female Sand Lizards used larger home ranges only after egg deposition (summer 2), whereas males had similar large home ranges throughout summer (summer 1 and summer 2). Calendar week was the only significant driver for home range size. The path analysis revealed that this relation is not direct, but indirect via changes in air temperature. The core areas of tagged Sand Lizards were located directly along the railway track. Only towards summer 2 and late summer core areas shifted partly to the close forest edge. Based on that, microhabitat use in core areas of home ranges varied partly throughout the year. In spring and late summer shrubs on the embankment comprised the biggest parts of the core areas, while in summer different microhabitat types were rather equally used. Sleeping sites were found in the embankment or in the track ballast, which was used especially in summer 1 and summer 2. Most sleeping sites were facing south, with only a few sites found facing north in summer 1 and 2.

Home range size

We compared home ranges sizes of Sand Lizards between seasons and sexes. In spring (April), males used relatively small home ranges and were found mostly sun basking. We

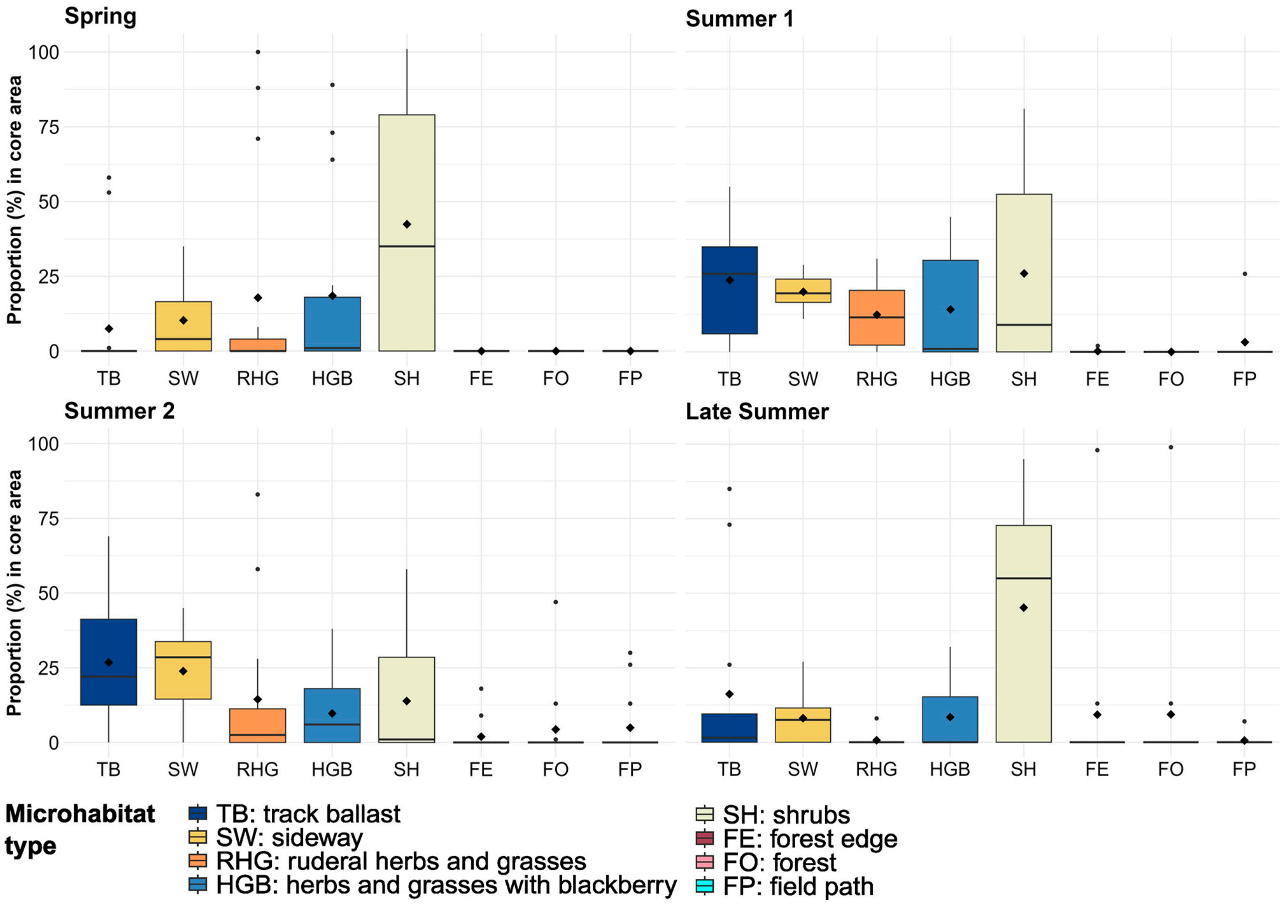

Figure 4. Composition of microhabitat types during spring, summer 1, summer 2 and late summer (compare Table 1) in core areas of Sand Lizard home ranges. For every season, the boxplots display the proportion of microhabitat types (TB = track ballast, SW = sideway, RHG = ruderal herbs and grasses, HGB = ruderal herbs and grasses with blackberry, SH = shrubs, FE = forest edge, FO = forest, FP = field path) recorded in the core areas of all Sand Lizards. Mean proportion of every microhabitat type is displayed in a black diamond. Microhabitat type construction was not part of any core area and is not shown.

caught only one female during that season (Table 1), making it impossible to compare male and female home ranges. Apparently, we caught animals in the first days after hibernation, because they were all at the beginning of shedding, males were not green coloured yet and movements in the habitat were only recorded infrequently. Two male Sand Lizards appeared regularly in front of their hiding place, but didn't move away from it during spring sampling. This resulted in two home ranges with a size below 1 m² (calculated with 95% MCP). Male Sand Lizards are known to end their hibernation in spring about one or two weeks before females and spend most of the time sun basking, without greater movements (Bischoff 1981, van Nuland & Strijbosch 1981, Nicholson & Spellerberg 1989, Olsson & Silverin 1997, Märtens 1999, Gvozdík 2000, Amat et al. 2003). During this time, costs for basking (high predation risk, energy) are weighted up for enhanced spermatogenesis (Nicholson & Spellerberg 1989). This is accompanied by an intensification of male coloration (Olsson & Silverin 1997).

During summer 1 (June) all home ranges of females were smaller than those of males, although this difference was not significant. It is well documented that females show reduced and lower activity when gravid, and adequate sites for oviposition are available nearby (Nicholson & Spellerberg 1989, Elbing 1995, Amat et al. 2000, Olsson et al. 2000, Wieczorek et al. 2020), which conforms with our data. Reduced activity is most likely due to the high costs of egg production and an increased risk of predation when moving, particularly when in a gravid state (Amat et al.

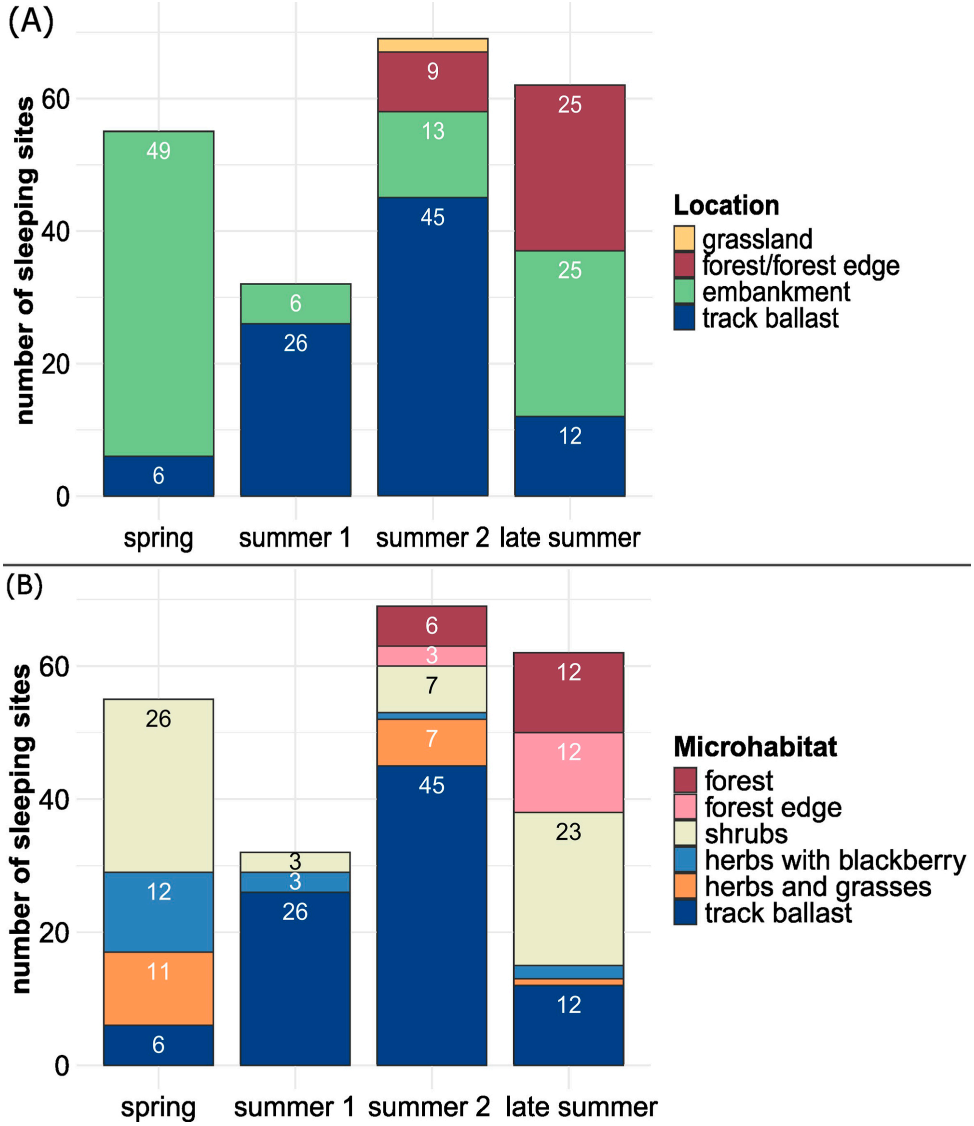

Figure 5. Number of Sand Lizard sleeping sites (A) per location, (B) per microhabitat. Numbers inside the bars give the exact number for every type of sleeping site location or microhabitat. Three microhabitat types were not recorded as sleeping sites (sideway, field path, construction), as they do not offer hiding places.

2000, 2003). At the same time, males are known to increase activity and thus home range size during reproduction in order to increase the number of possible mating partners (van Nuland & Strijbosch 1981, Wieczorek et al. 2020).

In summer 2 (July/August), following oviposition, the size of female home ranges increased, being equal to those of males. These results agree with Nicholson & Spellerberg (1989), who reported the highest activity of Sand Lizards (based on animals caught in pitfall traps) between June and August. Likewise, Elbing (1995) documented the largest home ranges for males in August (based on visual encounter and pattern-identification) and for females in the second half of July to mid-August. In late summer (August/September), we did not detect a difference in home range sizes between males and females. This is similar to results of Clement et al. (2022), who sampled Sand Lizards during the same time of the year with radiotelemetry.

Model averaging indicated that home range size was determined by season, respectively calendar week, but not by other explanatory variables. The effect of calendar week was, as revealed by path analysis, indirect and mainly explained by changes in air temperature. In the path analysis the overall variation in home range size was not related to the sex of an animal, similar to results of the regression analysis. A strong influence of temperature on home range size is not surprising, because ectotherm animals like the Sand Lizard strongly depend on their environmental temperature, which affects metabolic rates and thereby animal activity (Huey 1982). While environmental temperature "sets fundamental limits on reptile activity", movement patterns are further influenced by a "complex interaction involving the behavioral repertoire of an individual, its physiological capacities […], and certain ecological constraints (e.g., risk of predation)" (Huey 1982). Therefore, reptiles have evolutionarily developed different adaptation techniques to buffer effects of non-favourable environmental temperatures on behaviour and performance (Castilla et al. 1999, Amat et al. 2003). In our case the explanatory variables in the path model (mainly temperature) explained 59% of home range size of Sand Lizards, indicating that additional variables that were not represented in the model account for differences in home range sizes as well. Schmitz et al. (2022) found that movement patterns of Sand Lizards in a central German heath land were not influenced by climate or weather conditions, habitat composition or sex and size of an animal. The authors conclude that patterns in habitat use partly depend on the ontogeny of individuals and that seasonal habitat shifts are more extreme at edges of the distributional range but not in the core. Our findings generally seem to be consistent with that conclusion, as habitat use of Sand Lizards in north-eastern Germany in a continental region is more temperature dependent than those of Schmitz et al. (2022) in an Atlantic climate.

In general, a larger home range is representing either less resources in the environment (food, availability of spots for thermoregulation, oviposition or overwintering) or a bigger overlap with possible mating partners and therefore enhanced reproduction success (Olsson & Madsen 2001, Olsson et al. 2011). When comparing our results of home ranges (calculated with 95% MCP) to other studies, mean home range sizes over the whole study period were comparably small (males: 0.2–249 m², Ø 72 ± 73 m² SD; females: 1–387 m², Ø 64 ± 82 m² SD). Similar results of home range sizes, calculated with 100% MCP are found in Blanke (1995) for Sand Lizards in a sand pit (males: 4–329 m², Ø 107 ± 73 m² SD; females: 5–790 m², Ø 269 ± 74 m² SD) and in Märtens (1999) for Sand Lizards in semi-dry grassland and wasteland (males: 0.5–370 m², Ø 98 m²; females: 0.5–506 m², Ø 57 m²). In these two studies animals were located by visual encounters, what probably led to an underrepresentation of the home range size, when animals could not be detected actively at all times. In two other studies, where animals have been located via radiotelemetry, home ranges were larger. Clement et al. (2022) recorded mean home range sizes (estimated with 95% MCP) for males and females of 808 m² (no SD given, 295–1757 m²) for Sand Lizards in a heathland, and Wieczorek et al. (2020) recorded the largest known home ranges for Sand Lizards in extensive agricultural land. The mean size (calculated with 100% MCP) for males was 35,000 m² ± 22,000 SD (9000–80000 m²), and 10000 m² ± 15000 SD (3000–48000 m²) for females. Although direct comparison with other studies is difficult, due to variations in sampling methods and habitats, the sizes of the Sand Lizard home ranges in our study appear comparably small, indicating high resource availability along the railway track. The track environment consists of different substrates, slope directions, and vegetation patterns (see next chapter), offers a presumably high insect diversity, and numerous rodent burrows (as hiding places), and therefore likely represents optimal habitat quality for Sand Lizards, allowing Sand Lizards to live in small home ranges throughout the year.

Microhabitat use

The core areas of tagged Sand Lizards were located along the railway track throughout the year, comprising the track ballast, the sideway, and the adjacent embankment. This demonstrates that the railway track, along with the sideway and embankment nearby, provides essential habitat components for Sand Lizards all year round. Various substrates heat up separately during the day, allowing the Sand Lizard to quickly move between patches of different microclimatic conditions (House & Spellerberg 1983, Castilla et al. 1999, Märtens 1999). Embankments as well as the sideway attract different kinds of insects that Sand Lizards prey on. And, as the observation of two female Sand Lizards without transmitters showed, the sideway can even serve as a habitat for egg deposition, which has already been supposed by Blanke (1999).

Inside the core areas, the composition of microhabitats varied slightly throughout the year. The proportion of track ballast and sideway in core areas was highest during summer 1 and summer 2, compared to spring and late summer. In summer, the railway track's surface can reach temperatures of above 50 °C (Menius & Matthews 2020), making it unsuitable for Sand Lizards (Bauwens et al. 1995, Eckert et al. 2002). However, the stones of the track ballast store heat and therefore are warmer than the rest of the environment in the evening. This makes them an attractive sleeping site for Sand Lizards living along the track.

Sand lizards inhabit a variety of different habitats, including heathland, forest edges, grassland, or extensively used meadows, as well as urban habitats like parks and gardens (e.g., see Dent & Spellerberg 1988, House & Spellerberg 1988, Märtens 1999, Amat 2003, Becker & Buchholz 2016, Mizsei et al. 2020). It is known that the structural complexity of a habitat is more important than plant species diversity for the abundance of Sand Lizards (House & Spellerberg 1983, Blanke & Fearnley 2015). The ruderal vegetation on the embankment in our study site varies in size; herbs are often interspersed with budding trees or blackberry bushes, or vegetation is sparse and holds places for sun-bathing next to hiding spots. Ruderal vegetation also offers habitat to a diverse arthropod fauna that Sand Lizards prey upon (Penone et al. 2013, Wrzesień et al. 2016, Toffolo et al. 2021). Embankments contain high structural diversity in combination with the adjacent sideway and the railway stones, which explains why Sand Lizards often occur in high abundances along railway tracks (Mutz & Donth 1996, Blanke 1999, English Nature 2004).

Since we only caught Sand Lizards along the railway track and not in the surrounding region, we have to consider the possibility that our results, which show that core areas are in the direct environment of the railway track are biased. As the surrounding area offers suitable habitats as well, the results may not be representative for all animals in the local population. Nevertheless, our results show that home ranges including the core area of some individuals may entirely be restricted to railway tracks.

An important habitat element of Sand Lizards, which is usually neither mentioned nor investigated, is sleeping sites. With the use of telemetry, we detected more than 200 sleeping sites along the railway track. In summer 1 (June) and summer 2 (July/August) a high number of Sand Lizards chose the track ballast as sleeping site, and on certain nights, we found almost all our study animals there. During summer 1 and summer 2 the sleeping sites in the railway track were chosen irrespectively of slope orientation. In contrast to that, sleeping sites in spring and late summer were mainly south-facing. This indicates that differences in substrate are important for sleeping site choice in summer when the stones of the track ballast serve as a heat storage and are warmer in the evening than the adjacent embankment. But due to fewer hours of sunshine and lower insolation in spring and late summer, there is no temperature difference between embankment and track ballast like in summer and therefore the choice of a sleeping spot is determined rather by a southern slope than the type of substrate. Therefore, the track ballast holds a special function as a sleeping site, especially in summer. In order to complement our findings about sleeping site locations of Sand Lizards, additional research on the location and quality of hibernation sites is required.

Conclusions

The availability of various microhabitats (characterised by different vegetation as well as different substrates) that railway tracks offer on a small scale, in combination with a presumed high food supply, indicate railway tracks as habitats of good quality for Sand Lizards. Therefore, high densities of Sand Lizards can be observed here. Based on our findings we recommend for future conservation actions that accompany constructions at railway tracks: If railway tracks hold a high structural diversity and are inhabited frequently by Sand Lizards, it has to be considered that (1) stones of the track ballast represent an important sleeping habitat in summer, even though these areas are not used during the day. This means that maintenance of track superstructure should be avoided on summer nights without considering additional mitigation measures; that (2) construction work – throughout the whole year – that affects the railway track as well as sideway and embankment directly impact the core habitats of Sand Lizards living along the track, making disturbances and killing likely. Furthermore, mitigation translocations of Sand Lizards, often done to avoid killing of Sand Lizards during constructions, need to consider that home range size varies during different seasons and animals use different microhabitat types throughout the year. As home range sizes in our study were comparably small, likely because of a high structural diversity along the railway track, home range sizes in newly created ecological compensation sites would probably increase, if ecological compensation sites offer less habitat quality. The use of stones as structural habitat element on ecological compensation sites has been controversial at least in reptile conservation practice in Germany (Zahn 2017), as stones do not offer much cover from predators. We could demonstrate that this is not applicable for stones of the track ballast, which provide places to sleep and sunbathe along with hiding places in close proximity. As a result, larger aggregations of stones may also improve the functional and structural diversity of ecological compensation sites. Overall, we observed the use of comparatively small home ranges of Sand Lizards throughout the year, which originates from small scale availability of different microhabitat structures along railway tracks. Thus, this is a good example of how linear infrastructure may provide valuable habitat features and thereby counteract habitat loss and fragmentation for certain species like the Sand Lizard.

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Supplementary data

The following data are available online:

Supplementary Table S1. Different microhabitat types in the study area.

Supplementary Figure S2. Picture of a tagged Sand Lizard.

Supplementary Table S3. Information on all Sand Lizards that were tracked in the study.

Supplementary Figure S4. Accumulation curve for randomized home range sizes calculated with MCP.

Supplementary Figure S5. Boundaries of Sand Lizard home ranges, calculated with 50% and 95% AKDE_C, during spring, summer 1, summer 2 and late summer.