Home range and ecology of a palaearctic lacertid

Combining novel and old approaches to assess *Lacerta agilis* LINNAEUS, 1758 in the centre of its distribution with considerations for conservation

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Biodiversitätswandels

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Summary

Effective species conservation requires a thorough understanding of a species’ ecology as it reveals the requirements a species has of its environment. In this thesis I combine established methods like visual encounter surveys and the processing of local weather data with novel methods like radio-telemetry on sand lizards and habitat mapping by UAV to make an ecological profile for a population of *Lacerta agilis* from the centre of its range. In several papers, me and my colleagues analyse different aspects of sand lizard ecology: The spatio-temporal patterns in microhabitat and weather preferences, the weather dependent detection probability, and the home range and habitat selection. Before that, I summarize previous studies of home range and habitat selection in vertebrates to identify the allocation of focus towards vertebrate orders and topics and to understand, where the study of *Lacerta agilis* fits into previous work. In summary, allocation of focus on vertebrate orders in home range and habitat studies is independent of species diversity within the order as well as relatedness between orders or portion of vulnerable species within orders. Furthermore, many marine turtles and mesocarnivores were among the most studied species and topics most studied in concordance with home range and habitat selection are conservation/human influence, intraspecific differences, and home range shifts and exploratory behaviour. In the following, the thesis focuses on establishing an ecological profile of *L. agilis.* First, the data shows, that the studied central population varies greatly in spatio-temporal patterns of microhabitat and weather preferences from much studied populations at the ranges edge. Overall, the spatio-temporal patterns in habitat selection of *L. agilis* in this population cannot be explained by season, weather or microclimate and only very minor differences between ontogenetic stages, sexes or daytime can be observed. Overall, *L. agilis* of this population occupy a broad niche but are most active in dry and sunny conditions with low windspeeds after air temperatures reached values around 20°C for a few hours. In terms of habitat, lizards favour incorporating blackberry bushes into their home range while avoiding large areas of sand and tall vegetation. My results show the need for local data in conservation and help improving conservation of local populations by detailing weather dependent encounter rates and fine-scale habitat selection. I furthermore supply a combination of methods many of which are designed to remain useful for a multitude of organisms and applicable in conservation and management work. From 2018 to 2020, me and my collaborators accumulated 220 days of field work, 10 of which were dedicated to radio-telemetry and 5 to drone flights not counting

the days dedicated to testing and preparation. In this time, we recorded 947 sand lizard encounters not counting the relocations during the radio-telemetry study.

Introduction

This illustration was made by MANUEL SCHUMACHER and commissioned by the author of this thesis. The artist consented to the inclusion and publication of the illustration.

Rationale

Conservation has long been past the point of the assumption, that nature will sort itself out if we leave large parts of it alone (FIEDLER 2012). Our influence on this planet can be felt in even the remotest locations and today, it is widely accepted, that in order to mitigate the potentially disastrous consequences of our modern existence, humankind must manage nature to prevent the further loss of diversity (FIEDLER 2012). However, conservation requires knowledge first. Understanding the “why” and “how” of nature is fundamental to conservation as it lays the groundwork for every subsequent decision. With climate change and habitat destruction often being recognised as among the most pressing problems in conservation, information on habitat selection and weather preferences is needed for effective conservation and the prediction of population trends (TRAVIS 2003). It is beneficial to have this information from local populations as ecological requirements can change drastically over the geographic range of a species (KÜHNELT 1965, BROWN et al. 1996, GASTON 2009, PRIETO-RAMIREZ et al. 2018).

This thesis aims at establishing an ecological profile for a population of *Lacerta agilis* at the Dellbrücker Heide in Cologne by providing information on spatiotemporal patterns of activity, weather dependent detection probability, home range, and habitat selection. In addition, the thesis provides a review of previous studies on vertebrate orders concerned with home range and habitat selection which highlights the allocation of focus in the field.

I used established methods like visual encounter surveys and new approaches like habitat assessment via UAV and radio-telemetry on small lizards in order to formulate a profile relevant to conservation and easy to replicate with other populations and animals.

As an introduction, I first establish the background of some topics, relevant to the overall thesis: I talk about the niche concept and its application in this thesis, the study subject *Lacerta agilis*, examples on how monitoring surveys work in conservation, and the use of unmanned aerial vehicles in ecology. After the base of knowledge is established, I go more into detail on the abovementioned aims and scope of the thesis.

An introduction to the niche concept and its application in this thesis

One goal of this thesis is to establish an ecological profile of *Lacerta agilis* with relevance to conservation. The way, ecology defines an organism’s interaction with its environment is most often via the ecological niche. As niche concepts are varied and diverse, it is advantageous to clarify the idea of a niche and to clarify the concept applied in each chapter.

According to the OXFORD ENGLISH DICTIONARY (2023), the ecological niche is described as "The actual or potential position of an organism within a particular ecosystem, as determined by its biological role together with the set of environmental conditions under which it lives." This definition already shows that multiple approaches to the niche concept exist. The niche can be seen as an actual representation of an organism's position or the position it could potentially occupy. It can focus on the impact an organism has on its environment, on the requirements it has of its environment, or on both. Several niche concepts exist, each focusing on different aspects and definitions. One of the oldest niche concepts is often called the Grinnellian niche and is defined as the sum of the suitable environmental conditions that allow a species to survive and reproduce (GRINNELL 1917, POCHEVILLE 2015). Per contrast, the Eltonian niche defines the niche of an animal as "its place in the biotic environment, it's relation to food and enemies" (ELTON 1927). In other words, the Eltonian niche focuses on an organism's effect on its environment including other organisms and its role in the ecosystem it inhabits (ELTON 1927, SOBERÓN 2007, POCHEVILLE 2015). The Grinnellian niche concept often concerns itself with more broad scale ecologic and geographic attributes of a species while the Eltonian niche concept focuses primarily on interactions between organisms and between consumers and resources at a local scale (SOBERÓN 2007). A further concept combining both approaches is the Hutchinsonian niche, which defines the niche as an "n-dimensional hypervolume" with each dimension being an environmental variable, like a condition or a resource that define an organism's ecological requirements to survive and reproduce successfully in perpetuity (HUTCHINSON 1957). HUTCHINSON's niche concept also attributes the niche to an animal (be it species or population) rather than attributing animals to a pre-defined niche as GRINNELL and ELTON did (COLWELL & RANGEL 2009). HUTCHINSON's niche concept further distinguishes between the fundamental niche and the realized niche. The fundamental niche is closer to the Grinenllian niche concept as it describes all conditions that allow an organism to survive and reproduce while the realized niche excludes those conditions in which the species is not found in reality. The realized niche is hence narrower and seen as a result of competition from other organisms outcompeting it in certain areas and forcing it to limit itself to the conditions it is most adapted to (HUTCHINSON 1957, POCHEVILLE 2015). In these remaining conditions, its adaptations allow it to be most likely to outcompete others in turn linking it to the Eltonian niche (HUTCHINSON 1957, POCHEVILLE 2015). HUTCHINSON's niche concept has been used as the basis of MACARTHUR & LEVINS' approach to express the niche as a resource utilization distribution and be visualised as a histogram along the axes established by Hutchinson (MACARTHUR & LEVINS 1967, POCHEVILLE 2015). Today, we do not see the niche as exclusively reliant on competition or solely defined as the number of variables needed for an organism or its role in the food chain. In 1995, LEIBOLD proposed to split the niche into two distinct components: the "impact" niche, corresponding to ELTON's niche concept, and the "requirement" niche, corresponding to HUTCHINSON's definition. As concluded by CHASE & LEIBOLD in 2009, we recognize the niche of an organism as the combination of the requirements an organism has of its environment as well as its influence on said environment bringing us back to the initial definition (CHASE & LEIBOLD 2009). The multitude of concepts, of which many more slight variations exist show the controversial nature of the exact details of describing what a niche really entails and how to measure it. In conclusion, in almost all cases, the analysis of a species niche must forsake any pretence of completeness and instead focus on what is deemed important and possible for the question at hand. In part B of the thesis, my collaborators and I investigate the ecology of *Lacerta agilis*. In chapter 2, we investigate on a broad scale, the ecology of *L. agilis* in the context of Grinnellian niche concepts by comparing environmental factors of a central population of L*acerta agilis* with those reported in literature for populations at the species' edge. We also investigate biotic interactions as is common for the Eltonian niche, albeit it being intraspecific differences between males, females and subadults. Chapters 3 and 4 then focus mainly on the niche concept as a selection of relevant habitat and weather variables, ignoring interactions between groups safe for a short comparison between males and females in chapter 4. In the entirety of the work, I take a mostly Hutchinsonian approach to the niche concept as being a collection of variables and attribute the niche to the animal rather than the animal to the niche. Due to my ambition to provide a framework of practical use in conservation in this collection of studies, the variables are chosen based on their ability to be recorded in the wild in a practical manner for conservation projects which mostly excludes Eltonian species interactions as these require very extensive field studies on communities rather than focus on one species (SOBERÓN 2007). The focus species, *Lacerta agilis*, is well studied in many parts of its range and a lot of general information about morphology, systematics, distribution, and ecological niche is available (e.g., YAKOVLEVA 1964, GLANDT 1979, NICHOLSON 1980, HOUSE & SPELLERBERG 1983b, MOULTON & CORBETT 1988, SPELLERBERG 1988, EDGAR & BIRD 2006, GROZDANOV et al. 2014, BLANKE & FEARNLEY 2015). While individual populations can differ throughout the range of the species, it is nevertheless important to get a general idea on the study subject and what is universally known throughout its range.

The study subject: *Lacerta agilis* LINNAEUS, 1758

As part B focuses on the ecology of *Lacerta agilis*, having an extensive description of the species throughout its range is helpful as it puts the methods and discussions into context. The following section is a profile of *Lacerta agilis* and serves as the base on which I try to expand with these findings.

Figure 0.1: *L. agilis* of different age from the Dellbrücker Heide in Germany: Hatchling (top left), subadult (top right), adult female (bottom left), and adult male (bottom right). Fotos by Vic F. Clement.

Morphology

Lacerta agilis is of a stocky build with short legs for a lacertid and on average 18cm – 25cm in total length with the tail being approximatively 1.5 times the snout-vent-length (EDGAR & BIRD 2006) (Figure 0.1). *L. agilis* is the smallest member of the *Lacerta* genus (BLANKE & FEARNLEY 2015). Males often have more pronounced heads then females and immature individuals (BRAÑA 1996). Like most lacertids, sand lizards are capable of caudal autotomy in case of danger. Juveniles, subadults and females are a brown or brownish-grey all year while males develop bright green flanks during the breeding season which usually fade before hibernation (EDGAR & BIRD 2006) (Figure 0.1). Males also have black spots along the side while females have a more monochrome background colour (EDGAR & BIRD 2006) (Figure 0.1). All sexes have a predominantly dark vertebral band composed of numerous irregular brown and/or black and/or white/tan markings which are specific to the individual (EDGAR & BIRD 2006) (Figure 0.1). The band is usually framed by bright white or tan stripes to either side (EDGAR & BIRD 2006) (Figure 0.1). Usually, dark spots with bright centres occur in rows at the sides of the animals (EDGAR & BIRD 2006) (Figure 0.1). Colour and pattern can vary across the range of the species and natural morphs like red-backed "erythronotus" morphs or completely green forms are known within wild populations (EDGAR & BIRD 2006).

Systematics and distribution

Lacerta agilis is a member of the family Lacertidae and the type species for the genus *Lacerta* (UETZ & HOSEK 2019). It is closely related to other Eurasian lizards like *Lacerta bilineata, Lacerta viridis, Lacerta trilineata,* etc. The genus is often collectively referred to as green lizards (BLANKE & FEARNLEY 2015).

Lacerta agilis has a palaearctic distribution and is native to large parts of Europe and Central Asia (EDGAR & BIRD 2006). The species occurs from central France, the Pyrenees and Great Britain in the West to Mongolia and Northwest China in the east (EDGAR & BIRD 2006). Their most northern distributions are Great Britain, Denmark, South Sweden and Russia while their southern distribution reaches towards countries like Kazakhstan, Ukraine, Turkey, Bulgaria and Greece (IUCN 2020). They are absent from most of the Mediterranean and Iberic peninsula except the eastern coasts of the Adriatic Sea (i.e., Bosnia and Herzegovina and Montenegro) and the eastern Pyrenees (EDGAR & BIRD 2006, IUCN 2020). With that distribution, *Lacerta agilis* is among the most widely distributed palaearctic reptiles together with *Zootoca vivipara* (IUCN 2020). *Lacerta agilis* is thought to have originated from the Caucasus between the late Miocene and the early Pliocene (PETERS 1958) and likely spent cold periods in Transcaucasia, the southern Balkans, Crimea and Southern France from where it subsequently recolonised afterwards (BISCHOFF 1988).

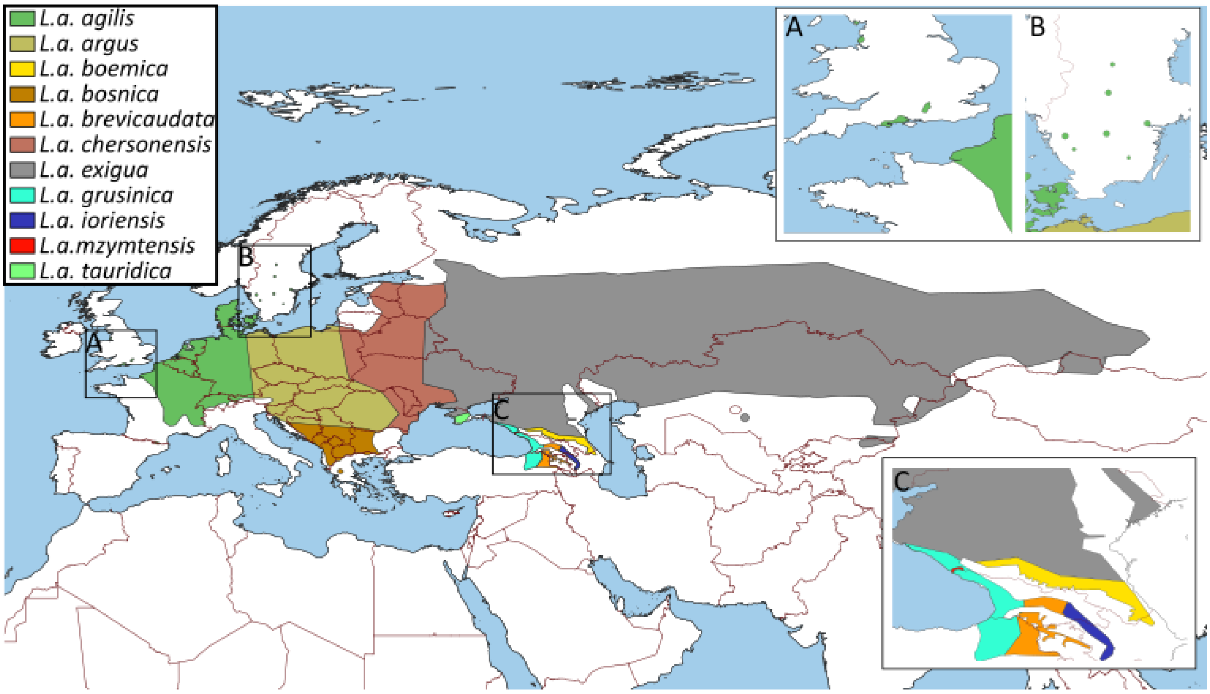

Figure 0.2: Approximate distribution of *Lacerta agilis* subspecies redrawn after ANDRES et al. 2014 and BISCHOFF 1988. Data drawn from (IUCN 2020) and drawn with Natural Earth Free vector and raster map data (NATURAL EARTH 2022). Zones of overlap exist according to ANDRES et al. and BISCHOFF but have been neglected in this depiction for clarity.

The reptile database (UETZ & HOSEK 2019) accepts eleven subspecies of *Lacerta agilis: L. a. agilis* LINNAEUS, 1758, *L. a. argus* LAURENTI, 1768, *L. a. boemica* SUCHOW, 1929, *L. a. bosnica* SCHREIBER, 1912, *L. a. brevicaudata* PETERS, 1958, *L. a. chersonensis* ANDRZEJOWSKI, 1832, *L. a. exigua* EICHWALD, 1831, *L. a. grusinica* PETERS, 1960, *L. a. ioriensis* PETERS & MUSKHELISCHWILI, 1968, *L. a. mzymtensis* TUNIYEV & TUNIYEV, 2008, and *L. a. tauridica* SUCHOW, 1926. Subspecies can have wide distributions or localized ones (Figure 0.2). *L. a. agilis* is the westernmost occurring subspecies and can be found primarily in Central and Northern Europe up until Central Germany in the east (ANDRES et al. 2014, BISCHOFF 1988) (Figure 0.2). Here it is replaced by *L. a. argus* which occurs in the eastern half of Germany in the west, to most of Poland in the east and Romania, Serbia and Croatia in the south (BISCHOFF 1988, ANDRES et al. 2014) (Figure 0.2). South of the distribution of *L. a. argus* up until central Greece occurs *L. a. bosnica* while the distribution of *L. a. chersonensis* starts to the east of *L. a. argus'* distribution and ranges across the Baltic states and the easternmost parts of Russia bordering them, most of Belarus, the western Ukraine, Moldavia and western Romania (BISCHOFF 1988, ANDRES et al. 2014) (Figure 0.2). The largest part of the eastern complex is composed of *L. a. exigua* whose distribution borders *L. a. chersonensis* in the west and ranges all across Asia to the eastern edges of the species' distribution (BISCHOFF 1988, ANDRES et al. 2014) (Figure 0.2). *L. a. tauridica* occurs on the southern half of the Crimean Peninsula in Ukraine. Additionally, five subspecies with small distributions can be found in the Caucasus between the black sea and the Caspian Sea (Figure 0.2, especially 0.2C): The distribution of *L. a. boemica* borders that of *L. a. exigua* to the north and reaches towards the Elbrus mountains in the south and the Caspian Sea in the east (BISCHOFF 1988, ANDRES et al. 2014) (Figure 0.2). *L. a. grusinica* and *L. a. mtymtensis* can be found along the easternmost coasts of the black sea with *L. a. mzymtensis* occurring at the upper basing of Mzymta River and *L. a. grusinica* occurring around that in Russia, Georgia, and Northern Turkey (BISCHOFF 1988, TUNIYEV & TUNIYEV 2008, ANDRES et al. 2014) (Figure 0.2). *L. a. iorinensis* is found in eastern Georgia along the upper Iori river and *L. a. brevicaudata* occurs in montanous areas in Georgia, Armenia, and northeastern Turkey (BISCHOFF 1988, ANDRES et al. 2014) (Figure 0.2).

Ecology: Habitat, activity, and behaviour

Habitat choice and weather preference of *L. agilis* are especially important to part B of this thesis. Although throughout its range, *L. agilis* can be found in a multitude of conditions, it does show a generalized ecological niche throughout its range. Across its range, *L. agilis* occupies a variety of habitats (BLANKE & FEARNLEY 2015). The common characteristics of sand lizard habitats are that they are sun exposed and structure rich and have batches of bare ground for egg incubation (HOUSE & SPELLERBERG 1983a, BLANKE & FEARNLEY 2015). These habitats can be for example heathlands, shrublands, forest edges, clearings, sand dunes, alpine meadows, pastures, urban habitats like gardens or cemeteries, or linear habitats like along rivers or railways. (YAKOVLEVA 1964, GROZDANOV et al. 2014, BLANKE & FEARNLEY 2015). Important prerequisites for habitats are that opportunities for basking and cooling off can be found in relatively close proximity as well as that prey, shelter, winter quarters, and suitable egg laying sites be present (BLANKE & FEARNLEY 2015). For that reason, ideal sand lizard habitat is structurally diverse on a small scale, so it provides those requirements within microhabitats or transition zones in close proximity to each other (HOUSE & SPELLERBERG 1983b, CORBETT 1988, SPELLERBERG 1988, BLANKE & FEARNLEY 2015). As such, *L. agilis* is synanthropic and has favoured the open, bushy border structures humans create at the edges of their agricultural and developmental areas since the Middle Ages (BISCHOFF 1988).

In general, vegetation structure is more important than specific plant species to *L. agilis* and many plant species can fulfil similar structural compositions in different habitats (Glandt 1979, House & Spellerberg, 1983b, Dent & Spellerberg 1987, Blanke & Fearnley 2015). While sand lizards can be found in most of the habitats listed above in the centre of their distribution, at the northern edges of their distribution (I.e., Great Britain, Sweden, and parts of Russia) sand lizards are restricted to sandy habitats such as dunes and heathlands (House & Spellerberg 1983b, Dent & Spellerberg 1987, Edgar & Bird 2006). South-exposed slopes and old-growth dry heath with structurally diverse vegetation to provide hides and basking spots present the most ideal conditions for northern populations due to thermoregulatory constraints (House & Spellerberg 1983b, Dent & Spellerberg 1987, Edgar & Bird 2006). In the Pyrenees, *L. agilis* is restricted to subalpine meadows (Amat et al. 2003). Sand lizards are mostly terrestrial although they can climb and often do climb low vegetation in order to bask (Edgar & Bird 2006). Basking sites should be close to cover and ideally on a surface that has high heat capacity like wood, sand, or rock (House et al. 1979, Blanke 1999, Meister 2008, Blanke & Fearnley 2015). Shelters serve as refuges for bad weather, during the night and sometimes as winter quarters (Blanke & Fearnley 2015). Although *L. agilis* can excavate burrows itself to serve as shelters (Simms 1970), they prefer to spare the effort and look for pre-existing shelters (Blanke & Fearnley 2015). As such, burrows of mammals, gaps between stones and in walls or hollow wood are popular options (Blanke & Fearnley 2015) (Figure 0.3). Additionally, tree bark, leaf litter or other structures are used as short-term retreats to escape predators (Blanke & Fearnley 2015) (Figure 0.3).

Figure 0.3: Sand lizards use a variety of structures as retreats or shelters. Left: Female in a turned-over piece of metal debris. Right: Male looking out from a burrow.

Sand lizards occupy home ranges ranging from a few square meters to over 1000m^2 depending on resource distribution (BLANKE & FEARNLEY 2015). Sand lizards do not defend their home range but may defend certain sites within it if they are especially suitable (SIMMS 1970). Otherwise, most evidence points towards animals being tolerant of each other's presence and things like overnight shelters have been observed to host multiple lizards (e.g., NICHOLSON 1980, MOULTON & CORBETT 1988). Sand lizards are mostly sedentary and disperse at a slow rate (HARTUNG & KOCH 1988) but disperse faster in poor environmental conditions as individuals travel in search of better habitats (KLEWEN 1988). Passive transportation as for example by river floods and floating debris might also contribute to the dispersal of sand lizards along riverbanks (BLANKE & FEARNLEY 2015).

Lacerta agilis are strictly diurnal and usually emerge in the morning when temperatures are high enough to bask in sun exposed spots close to cover and sheltered from the wind (EDGAR & BIRD 2006). Sand lizards are then active throughout the day until late afternoon where they retreat into their burrows. *L. agilis* is known as a "shuttling heliotherm" (SPELLERBERG 1976) and thermoregulates by shuttling between sun exposed and shadowy microhabitats throughout the day. On hot days, sand lizards adapt a bimodial activity pattern and hide during the midday hours and be more active in the morning and afternoon. They can however switch to a unimodal pattern when conditions are colder (HOUSE et al. 1979). For *L. agilis,* reported ideal temperatures can vary between 17°C air temperature (AMAT et al. 2003) and 32°C near ground temperature (HELTAI et al. 2015) although most results point to a preferred air temperature around 20°C for most populations (e.g., HOUSE et al. 1979, BLANKE 1999, AMAT et al. 2003, FEARNLEY 2009) and a preferred body temperature between 23°C-38°C (SPELLERBERG 1976, BLANKE & FEARNLEY 2015). *L. agilis* prefer dry weather over rain and low humidity and sunny weather over overcast conditions (HOUSE et al. 1979, KURANOVA et al. 2003, FEARNLEY 2009). The heliothermic species usually basks in full sunlight by radiation and convection (AVERY 1979, FEARNLEY 2009) and are generally more thermophilic than *Zootaca vivipara, Podarcis muralis,* or *Anguis fragilis,* which often occur in the same area.

Sand lizards hibernate in burrows from autumn to spring. While exact times can vary between locality, animals usually emerge from hibernation from March to April (OLSSON 1988) with males emerging around 10-14 days before females in order to start sperm production (EDGAR & BIRD 2006). Hibernation then starts from September to October with juveniles being active longer (EDGAR & BIRD 2006). Activity times throughout the year shift slightly due to sunrise and sunset times and temperature (BLANKE & FEARNLEY 2015). Animals are also more active during the mating season (AMAT et al. 2003). During the mating season between March and May, males are aggressive towards each other and will attempt to mate with as many females as possible (EDGAR & BIRD 2006). Males sometimes guard females for a period of time after mating to prevent other males from mating with the same females (OLSSON 1992). Females lay 4-14 eggs in a burrow. In northern clines the burrows are dug in sand while elsewhere, burrows may be dug in soil instead (EDGAR & BIRD 2006). Seven to twelve weeks later, hatchlings emerge which can then live up to 12 years in the wild (EDGAR & BIRD 2006). While sand lizards have a general life expectancy around six years in the wild (NATURE CONSERVANCY COUNCIL (GREAT BRITAIN) WILDLIFE ADVISORY BRANCH 1983), alpine populations have been observed to have slightly higher life expectancies (ARAKELYAN & JENDEREDJAN 2003, ROITBERG & SMIRINA 2006a, ROITBERG & SMIRINA 2006b).

Sand lizards are insectivorous and are active hunters as well as sit-and-wait ambush predators (HUEY & PIANKA 1981, NEMES 2002, BLANKE & FEARNLEY 2015). Ambush tactics are more often used during spring, when lizards are basking and when prey is abundant (BLANKE & FEARNLEY 2015). When foraging, prey is quickly seized with open mouth (SIMMS 1970). They rely mostly on vision and olfaction to hunt (NICHOLSON 1980). *L. agilis* is a generalist that mainly feeds on arthropods with beetles and their larva being an important part of their diet while the contribution of other groups of arthropods is varying depending on environment (BLANKE & FEARNLEY 2015). Additionally, sand lizards are known to practice filial cannibalism on occasion (CORBETT & TAMARIND 1979, EDGAR & BIRD 2006). For hydration, sand lizards usually drink dew from surfaces but can also recognise standing water as a water source (BLANKE & FEARNLEY 2015).

Sand lizards are commonly predated on by a wide range of animals. Foxes, mustelids, house cats, birds of prey, corvids and snakes prey frequently on sand lizards while domesticated fowl like phaesants and chickens occasionally do so as well (SIMMS 1970, BISCHOFF 1984, EDGAR & BIRD 2006). Eggs are also eaten by badgers or even other sand lizards when found (BISCHOFF 1984). Habitats overlap with *Zootoca vivipara* and *Anguis fragilis* but competition is rarely observed (EDGAR & BIRD 2006). Competition with other green lizards of the genus *Lacerta* as well as with wall lizards *Podarcis sp.* has been observed (HEYM et al. 2013, HELTAI et al. 2015).

Conservation status and threats (non-natural)

Lacerta agilis is listed as “least concern” in the IUCN Redlist of species with the last assessment being in May 2018 (IUCN 2020, AGHASYAN et al. 2021). It is listed as least concern due to its large range and adaptability to habitat modification of some populations. The assessors recognise however, that populations in certain parts of the range are declining (IUCN 2020, AGHASYAN et al. 2021). *L. agilis* is listed in Appendix IV of the FFH Habitats Directive of the European Union and is therefore to be put under strict protection across their entire range within the EU.

Common threats to *Lacerta agilis* include human influence on the habitat, that lead to its degration, fragmentation or destruction as structure rich habitats are being replaced by structurally unsuitable developed areas like agriculture, arboriculture, or urbanization (e.g CORBETT & TAMARIND 1979, EDGAR & BIRD 2006, BLANKE & FEARNLEY 2015). Afforestation, intensification of agriculture, urbanisation, roads, and the lack of utilization of heathland in agriculture are important factors for the decline of *L. agilis* throughout its range (BLANKE & FEARNLEY 2015). Similarly, although *Lacerta agilis* is a commonly known synanthropic species since the Middle Ages (BISCHOFF 1984, BISCHOFF 1988), modern pollution through overfertilization, erosion as well as disturbance by people and predation by pets degrades habitat further (EDGAR & BIRD 2006). As habitats grow smaller and more isolated, populations become more and more inbred leading to a loss of genetic variability as immigration and emigration become less and less likely (BLANKE & FEARNLEY 2015). As *L. agilis* lives so close to humans and in areas predominantly managed by humans, they also depend on proper habitat management and can be one of the first species to suffer if management is neglected (CORBETT & TAMARIND 1979). Their proximity to humans and their protection status makes them common subjects of environmental impact assessments and compensatory measures (CLEMENT et al. 2022) and as such, the species is often monitored. Monitoring is often conducted according to guidelines made by experts based on available data. It is of great benefit to a scientist wishing to contribute new information to improve monitoring to understand what published data is required and how it is being used.

How monitoring surveys for conservation are conducted (an example from German guides)

In part B of this thesis, my collaborators and I have monitored *Lacerta agilis* via visual encounter surveys which are one of the most common monitoring techniques used in conservation (ALBRECHT et al. 2013). Targeted species monitoring like in this thesis often done in the context of development projects as an impact assessment or in subsequent compensatory measures. We define monitoring as the act of surveying an environment, population, or community in the field by means of a field study that assesses presence or abundance. Initial monitoring is meant to inform, whether further, long-term monitoring or specific measures are necessary to secure the survival of the subject of the survey before continuing the project. One example of the this is the environmental impact assessment. According to Article 3 of the directive 2011/92/EU of the European parliament and the council of 13 December 2011 on the assessment of the effects of certain public and private projects on the environment, environmental impact assessments are meant to "identify, describe and assess […] the direct and indirect effects of a project on the following factors: (a) human beings, fauna and flora; (b) soil, water, air, climate and the landscape; (c) material assets and the cultural heritage; (d) the interaction between the factors referred to in points (a), (b) and (c)." Monitoring of regional abundance is the most common monitoring in conservation with things like determination of range, identification of key habitat features and interspecies interactions often taking a complementary role (ALBRECHT et al. 2013). In general, monitoring is conducted by experts based on guidelines commissioned by the state and/or developed between said experts with input from professional experience, science, politics, and other fields and adhering to the legislatives of the concerned area, country, and/or international community (MARKUS DIETZ from the Institut für Tierökologie und Naturbildung in Gonterskirchen pers. comm.).

Techniques for abundance and presence monitoring are most often species or group specific and rely on numerous techniques (ALBRECHT et al. 2013). Glue traps with sweet lures can be used to get hair from *Muscardinus avellanarius* or *Glis glis* while the search of relevant habitat structures, nests or burrows of birds and mammals can sufficiently prove the presence of certain fauna in the affected area (ALBRECHT et al. 2013). Bats and frogs can be located via audio tracking along transects or around breeding ponds (ALBRECHT et al. 2013). Many commonly used methods exist and are used based on the area and questions and are chosen based on experience and existing scientific knowledge.

As my focus is mainly based on visual encounter surveys of *Lacerta agilis*, I want to take some time to look at the methods for first assessment surveys proposed by SCHNITTER et al. 2006, ALBRECHT et al. 2013, LÜTTMANN et al. 2017, and HESSEN MOBIL 2020 in more detail. *Lacerta agilis* is lumped in with all other reptiles by ALBRECHT et al. 2013 and HESSEN

MOBIL 2020 with some elaborations distinguishing it from others. All four guides focus on the collection of data via visual encounter study and ALBRECHT et al. 2013 and LÜTTMANN et al. 2017 highlight the importance of identifying adults by their unique back pattern to estimate population size and both propose mark and recapture studies as a good way to further estimate population size. All guides explain that the use of artificial hides is rather unsuccessful for *Lacerta agilis* but ALBRECHT et al. 2013 confirms that they are worth checking if they have been established because of other species. ALBRECHT et al. 2013, LÜTTMANN et al. 2017, and HESSEN MOBIL 2020 highlight the importance of the right weather to maximise encounters with ALBRECHT et al. 2013 and HESSEN MOBIL 2020 stating very broadly for all reptiles that there should be no precipitation and temperatures should be between 22°C and 30°C during surveys and LÜTTMANN et al. 2017 stating that days should be hot and humid but without rain and further stresses that surveys at midday should be avoided especially on hot days. In any case, not much more in-depth information is given on thermal ecology which leads to the assumption, that this knowledge is to be taken from literature and experience. Guides list the minimum number of necessary surveys as four (ALBRECHT et al. 2013, HESSEN MOBIL 2020) or six (SCHNITTER et al. 2006, LÜTTMANN et al. 2017) but ALBRECHT et al. 2013 agree that six would be better. SCHNITTER et al. 2006, ALBRECHT et al.2013, and HESSEN MOBIL 2020 highlight the necessity of also surveying the range of suitable habitat in and around the concerned area with suitable area only being defined briefly by SCHNITTER et al. 2006 which leads to the assumption again, that this information is to be taken from literature and experience.

Looking at the guidelines of *Lacerta agilis* and many others shows that considerable knowledge on the ecology and behaviour of a species is a prerequisite for successful monitoring. For example, weather dependent activity is highlighted as an important factor for all reptiles including *Lacerta agilis* and knowledge of the terrestrial habitat and aquatic spawning ground preferences of amphibians are important to determine likely migration routes. In many such cases, knowledge on the ecology is assumed to be already known from literature. Similarly, selecting areas for relocation efforts are mostly based on available literature on the requirements of the species (see e.g., HACHTEL et al. 2017). However, new techniques in ecology allow for very fast assessment of weather preferences or habitat use even parallel to monitoring. Such techniques allow also to incorporate more species specific and even population specific information into monitoring guides. Unmanned aerial vehicles (UAVs) for example are one of those techniques, that allow for quick habitat assessment via the provision of high-resolution habitat maps (see Chapter 4). UAVs can therefore provide population specific data on habitat choice instead of relying solely on generalized data from literature. UAVs further provide a method to scientifically quantify and register habitat preferences which many conservation practitioners usually learn informally from experience.

A review on the use of unmanned aerial vehicles in ecology

In Chapter 4, I use an unmanned aerial vehicle (also called UAV or drone for short) to monitor the vegetation at a very high resolution in order to determine habitat use of *L. agilis* at a scale relevant to the animal. The use of UAVs in ecology is a comparably novel approach, but in the past decade, great steps have been made in developing new applications aimed to facilitate the collection of data in ecological studies (Stephenson 2020). A search in the web of science core collection (Clarivate Analytics 2022) for the topics “UAV” or “unmanned aerial vehicle” over the entire timespan from 1945-2021 in the Categories Ecology or Zoology reveals 326 publications most of which were released after 2014 (Figure 0.4). Additionally, up to the 11th of February 2022, six publications were found for 2022. Publications using UAVs and the citations thereof have rapidly increased in the seven years following 2014 (Figure 0.4) which is not only due to new applications being developed but also due to increasing accessibility and affordability of UAVs.

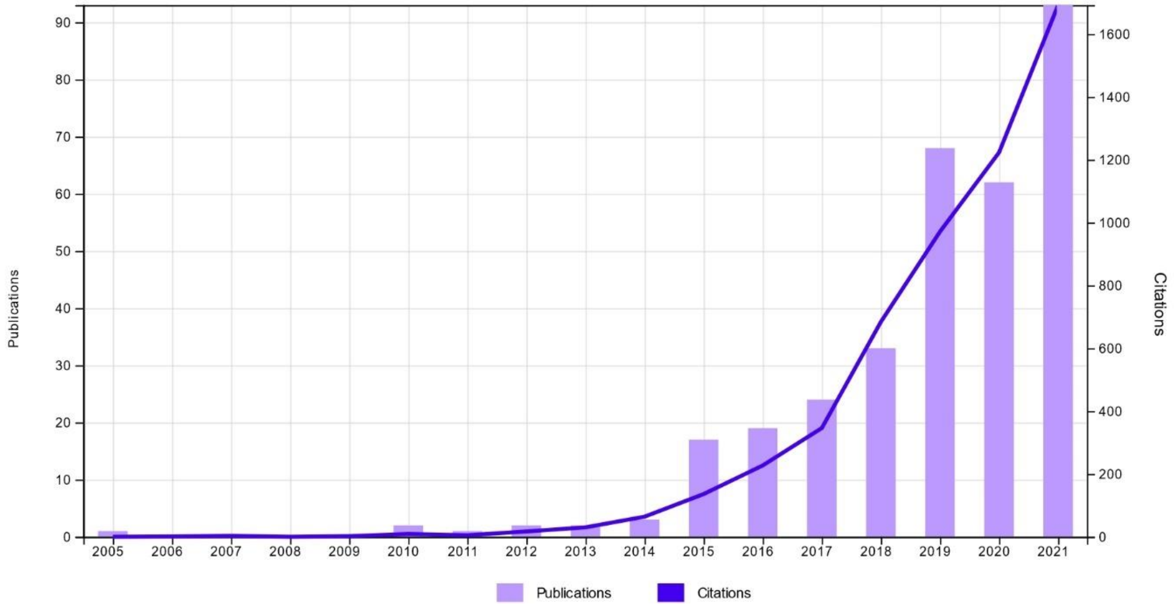

Figure 0.4: Number of publications and citations in web of science for the topics “UAV” or “unmanned aerial vehicle” over the entire timespan from 1945-2021 in the categories Ecology or Zoology (Source: Web of Science Clarivate Analytics 2022, date of access 11.02.2022)

The publication which was by far the most cited in the Web of Science search was by ANDERSON & GASTON from 2013 in which they not only reviewed current technologies and types of UAVs but also highlighted both current and potential future uses of UAVs. At that point a big drawback of unmanned aerial vehicles was the fact that collected data would still have to be interpreted manually for the most part as pattern recognition software for interpreting collected footage was not yet widely available (ABD-ELRAHMAN et al. 2005, ANDERSON & GASTON 2013). JONES et al. were one of the first to use UAVs to locate animals in 2006 but had trouble as the UAVs and cameras used where not yet capable of capturing georeferenced footage and were difficult to deploy in the wilderness. Nevertheless, JONES et al. highlighted the potential for UAVs. They said in their publication from 2006 that “For small UAVs to be useful as management or research tools, they should be durable, modular, electric powered, launchable and recoverable in rugged terrain, autonomously controllable, operable with minimal training, and collect georeferenced imagery.” This list of demands would come to be largely met over the following years and since those early days, more sophisticated algorithms and more powerful and affordable UAVs have allowed for a multitude of applications. Most common applications for UAVs are animal monitoring and vegetation mapping. The latter also finds use in animal ecology as habitat mapping, which is what I used UAVs for in chapter 4 of this thesis. However, there is a large variety of applications within these fields worth considering.

The vast majority of studies within the web of science search used UAVs for the detection, observation or counting of animals from the air. The ability to detect animals swiftly and precisely from the air is an enticing prospect for several reasons. UAV surveys can be cheaper and safer compared to manned aerial surveys (ADAME et al. 2017, HODGSON et al. 2017, GENTLE et al. 2018, LETHBRIDGE et al. 2019). Furthermore, UAVs can reach hard-to-access places and facilitate monitoring in habitats like rivers (BISERKOV & LUKANOV 2017, COLLAS et al. 2020), treetops (VAN ANDEL et al. 2015, ANDREW & SHEPHARD 2017, BONNIN et al. 2017), mountains (HE et al. 2020), marshlands (MCKELLAR et al. 2021, NIWA 2021), Antarctic islands (KORCZAK-ABSHIRE et al. 2018), or the ocean (see CASTELBLANCO-MARTÍNEZ et al. 2019 for a review). UAVs can also be a time efficient alternative to detect animals or their burrows compared to ground-based surveys. The primary concerns for the feasibility of these studies are most often evaluating detection probability and disturbance to the animals. In general, detection probability and disturbance are mostly compared to current best practices and should at least be comparable to them. Over the years, studies have reported varying degrees of success for different animal groups with some studies reporting very different results for the same type of surveys in quick successions (e.g., GENTLE et al. 2018, LETHBRIDGE et al. 2019, OLD et al. 2019, COX et al. 2021). In general, one of the most common reason for failure to reach results comparable to usual survey methods like ground based visual encounter surveys is vegetation cover (e.g., VAN ANDEL et al. 2015, BONNIN et al. 2017, OLD et al. 2019).

Whether or not animals are disturbed by UAVs is an important concern. UAVs can stress animals by virtue of being a loud, unknown, and erratically moving object in their vicinity (VAS et al. 2015, MUSTAFA et al. 2018, DUPORGE et al. 2021, LABORIE et al. 2021). In 2018, MUSTAFA et al. asked the important question, whether disturbance is to be defined as “impact on survival or reproduction” or as any “measurable change in behaviour or physiological status”. The former definition might be a more realistic criterion for assessing the permissibility of drones especially when keeping in mind the fact that alternatives like ground-based surveys might also stress animals (DYCK & BAYDACK 2004, HAHN et al. 2017, PENNY et al. 2019, SCHOLTEN et al. 2019, GALLEGO & SARASOLA 2021). The latter definition however can also be a valuable reminder, that even though UAVs might not impact survival or reproduction directly, applications still do have an impact, which can be important for policies on recreational use as it is applied for eco-tourism in the Arctic and Antarctic regions to watch animals (DYCK & BAYDACK 2004, LEARY 2017, MUSTAFA et al. 2018). Although comparing disturbance by UAV and disturbance by humans and assessing which one would be preferable can be challenging, it is important to assess in order to make informed policies as blanket prohibition or unregulated permission of UAVs are both unviable options. Despite their potential influence on animal behaviour, UAVs have been used to study animal behaviour as well (NYAMURYEKUNG’E et al. 2016, SCHOFIELD et al. 2017, KHOKTHONG et al. 2019, FRIXIONE et al. 2020, EJRNÆS & Sprogis 2021). The stress, UAVs elicit from animals can also be used to trigger avoidance behaviour and thus prevent animal-human conflicts from elephants entering farmland (HAHN et al. 2017) or make rhinoceros flee from places targeted by poachers (PENNY et al. 2019). Despite detection and monitoring of animals being the most common use of UAVs, it is mostly applicable to large animals or areas with very sparse cover options for the animals. For a small animal living in an area with lots of cover options that has to be wary of aerial predators, like *Lacerta agilis*, detection via UAV has a lot of challenges. This thesis does not aim to tackle those challenges but instead focuses on the second common use of UAVs in ecology, which is vegetation/habitat mapping.

In vegetation mapping, UAV generated high resolution images allow to quantify vegetation cover (LIANG et al. 2017) but also investigate structure of plant communities (BELMONTE et al. 2020). Vegetation diversity can be measured indirectly via the use of spectral sensors and calculating spectral diversity (HEUMANN et al. 2015, ROSSI et al. 2022) or by distinguishing individual plant species (e.g., KNOTH et al. 2013, JAMES & BRADSHAW 2020). Using high resolution imagery from UAVs, vegetation can also be classified in categories relevant to the study and categorical maps can be generated (ZWEIG et al. 2015, GONÇALVES et al. 2016, KATTENBORN et al. 2020, CLEMENT et al. 2022). Identification of species also allows the location of invasive plants via aerial surveys (DASH et al. 2019, ELKIND et al. 2019, DATTA et al. 2021) or documenting the phenology of a specific plant species (NEUMANN et al. 2020). UAVs also allow monitoring of vegetation in difficult to reach habitats just like for animals (e.g., KNOTH et al. 2013, HUSSON et al. 2014, ZWEIG et al. 2015, BRIGNOLI et al. 2018, BERTACCHI et al. 2019, NAHIRNICK et al. 2019, DURGAN et al. 2020, MORGAN et al. 2020, RÄSÄNEN et al. 2020, STRUMIA et al. 2020, ALDOUS et al. 2021, MORA-SOTO et al. 2021, ZHANG et al. 2021). Areas especially vulnerable to disturbances by on-foot surveys can also be reached with minimum impact by UAVs (MALENOVSKÝ et al. 2017). The methods and applications used in studies with botanical focus can also be used to map animal habitat and microhabitat at high resolutions (e.g., HABEL et al. 2016, CLEMENT et al. 2022). This is the exact approach I took in this thesis as I established categorical habitat maps to analyse the preference of *L. agilis* for certain habitat structures (see chapter 4 of the thesis). The high-resolution imagery allows for the detection and mapping of plant species certain insects require for oviposition (HABEL et al. 2016) or map fine scale habitat structures of animals as I did (FRITZ et al. 2018, OOSTHUIZEN et al. 2020, CLEMENT et al. 2022). The main benefits of this approach are control over temporal and spatial resolution as well as the independence of satellite imagery. In one instance (STARK et al. 2018) UAV supported mapping of proboscis monkey habitat revealed recent clearing of forest habitat that was of large importance to the group of monkeys, which would have been overlooked when using only satellite images. This led to a swift protection of remaining habitat (STARK et al. 2018). STARK et al. demonstrated the benefit of UAVs to have control over the timeframe of collected data. UAVs can also provide images when satellites are often obscured by clouds like in Antarctica (GOEBEL et al. 2015). Another application lies in the tracking of habitat modification or degradation over time as has been done for sea turtle nesting beaches where beach topography could be tracked thanks to the ability of UAVs to collect time sensitive data quickly. UAVs were also used to study foraging utilization via point clouds from collected UAV-imagery by livestock, which can give pasture wide insights instead of having to focus on sample locations within the pasture (GILLAN et al. 2019). Furthermore, UAVs provide insight into habitat selection of flighted birds from the bird's perspective and help determine which factors influence decisions of birds (KAMM & REED 2019).

In conclusion, UAVs can be a valuable tool in ecology. The control over spatial and temporal resolution as well as the potential for collecting a lot of data in relatively short surveys times, putting the resources into post-survey analysis instead are attractive for monitoring of animals and habitat. The potential for less disruptive and safer methods of survey also show promise. However, UAVs also face challenges for example in the requirement of technical knowledge for determining correct parameters. Other challenges include UAVs not being equally good in detecting animals than humans might be in dense vegetation and the fact that disturbances to animals might be neglected. As a new tool for ecological surveys whose popularity has increased rapidly over the past years, focus in UAV research lies in developing new applications, ironing out kinks, compensating for shortcomings, assessing impact on animals and developing best practice policies. This study is one of only a few studies using UAVs to assess the ecology of a very small animal with high site fidelity. As such, the use of an UAV was to reap the benefit of high temporal and spatial resolution in vegetation mapping. Small animals with high site fidelity like *L. agilis* benefit greatly from the increased resolutions as they allow for a very detailed analysis of the microhabitat within their home range. In my opinion, small scale habitat use by UAVs will improve our understanding of animal space use when it comes to conservation and allow for the identification of structures which are especially important. Instead of limiting ourselves to broadly described habitat requirements, like "open habitat with occasional bushes", UAVs allow us to really quantify use of specific structures by the animals. So far, *Lacerta agilis* may be too small and its habitat too diverse to be reliably detected from UAVs that fly high enough not to also disturb the animals, but to my knowledge, attempts at detecting lizards with UAVs are being made (e.g., SAHU 2019, HUERTA et al. 2020).

Aims, scope and overview

As established previously, information on habitat selection and weather preferences is important for effective conservation and the prediction of population trends (TRAVIS 2003) with local populations being the most reliable source for applicable information. To repeat the aim of the thesis established in the beginning:

“This thesis aims at establishing an ecological profile for a population of *Lacerta agilis* in the Dellbrücker Heide in Cologne by providing information on spatiotemporal patterns of activity, weather dependent detection probability, home range, and habitat selection. In addition, the thesis provides a review of previous studies concerned with home range and habitat selection which highlights the allocation of focus in the field. “

In the following part A, consisting of chapter 1, I first address the allocation of focus to vertebrate orders in home range studies, to assess previous work and how the rest of my study fits into established literature. After that in part B, I take a look at the ecology of *Lacerta agilis*. In chapter 2, I examine spatiotemporal patterns in habitat and weather preferences of *Lacerta agilis* to confirm, that they are indeed different from much studied populations from the edges of the species’ range. Finally, I will establish the weather and habitat preferences of the subject population in the chapters 3 and 4 respectively. A syntax in form of a flowchart depicting the workflow, central questions and results of each part and chapter can be found in Figure 0.5 for ease of reference.

The home range concept is often used for studying habitat selection as it provides a definable area, in which an individual can fulfil all its daily needs (BURT 1943). Modern home range calculations usually also consider intensity of space use within home ranges (e.g., WORTON 1989, SILLERO et al. 2021). Thus, home range studies are an invaluable first step for studying habitat selection of an animal. Home range studies are also versatile and can focus on a variety of additional topics like animal movement, population dynamics and inter- or intraspecific interactions. Many studies also discuss the implications for conservation as they identify important habitat structures (e.g., SCHOFIELD et al. 2010) or study the changes of home range in human-altered landscapes (e.g., GUERRERO-SANCHEZ et al. 2022). Home range studies are common in vertebrates, but it is fair to assume, that not all vertebrate clades are studied equally. Identifying gaps in knowledge and strongly studied clades or topics can help shed light on potential opportunities for further research. Therefore, part A of this thesis titled:

Part A: Allocation of focus in regard to vertebrate orders and topics in home range and habitat studies.

consists of one chapter, which is a review titled:

Playing favourites - A review and discussion on the allocation of vertebrate orders and foci in home range and habitat selection studies.

In this first chapter, I am analysing the allocation of interests in vertebrate orders and topics of home range and habitat publications. For this part, I reviewed 903 publications from 1980 to 2018 that concerned themselves with home range and habitat selection of vertebrates and describe the allocation of focus towards vertebrate orders and topics. This part highlights the relation between publication numbers and species richness and shows, that allocation of focus in vertebrate orders is independent of species richness, relatedness or portion of threatened species within the order. Furthermore, I have identified conservation and human influence, intraspecific differences, and home range shifts/exploratory behaviour as the topics most often studied in concordance with home range and habitat preferences. I thereby highlight the allocation of focus in the field of home range studies and discuss some potential reasons for the distribution while proposing further research opportunities.

The further chapters of the thesis, that constitute part B called:

Part B: An ecological profile of *Lacerta agilis* LINNAEUS, 1758 - Spatio-tempoal patterns, weather preferences, habitat selection, and home range.

focus on establishing an ecological profile for a population of *Lacerta agilis* LINNAEUS, 1758 in the centre of its distribution in the Dellbrücker Heide in Cologne. I chose *Lacerta agilis* as study subject, as it is easily accessible but also a frequent target of compensatory measures and management questions due to its synanthropic nature and proximity to humans (RÖDDER et al. 2016). Numbers of *L. agilis* are overall declining (IUCN 2020, AGHASYAN et al. 2021). In the profile, we include home range, habitat selection, weather dependent detection probability and sex and age dependent differences in spatio-temporal patterns. In chapter 2 titled:

Spatiotemporal patterns of habitat use by the sand lizard (*Lacerta agilis* LINNAEUS, 1758): Effects of climatic seasonality?

I explore together with collaborators data on distance to habitat structures, microhabitat, microclimate and weather collected during a visual encounter survey of *Lacerta agilis*. We focus on identifying potential seasonal, sex and age dependent patterns in habitat use for this central population of *Lacerta agilis*, which have been reported from the edges of the species' distribution (e.g., JACKSON 1978, HOUSE & SPELLERBERG 1983b, AMAT et al. 2003, NEMES et al. 2006, ČEIRÂNS 2007, GROZDANOV et al. 2014, WOODFINE et al. 2017, PRIETO-RAMIREZ et al. 2018). We used generalized linear models to detect, whether finding distance from certain habitat features or microhabitat at the finding point could respectively be explained by a combination of the other values and seasonal variables. We used density estimation to test if there was a significant difference between microhabitat and distance data between morning, midday and afternoon findings. We calculated hypervolume overlap between males, females and subadult lizards to locate ontogenetic or sex specific differences in weather and habitat preferences within the population. We show that movement patterns of the individuals can neither be described by time differences (seasonal or daily), climatic conditions or habitat composition. Furthermore, movement patterns do not show habitat or weather-related differences between sexes or age safe for a small difference in habitat use between ontogenetic stages. These findings contrast with those reported from populations at the edges of the distribution and show, that much less studied central populations of sand lizards differ from their conspecifics at the edges of the species' range. This highlights the need to know local populations for management and conservation.

Weather conditions are essential determinators of activity, and consequently detection probability of animals, especially ectotherms. Knowing when detection probability is highest is a core requirement for successful monitoring and management of ectothermic species like *Lacerta agilis* but in many cases, listed optimal weather conditions are vaguely defined or lumped in with all other reptiles (SCHNITTER et al. 2006, ALBRECHT et al. 2013, LÜTTMANN et al. 2017). While studies for *Lacerta agilis* are numerous, most focus on the edges of the species' distribution. As shown in the previous chapter, results from across the wide range of the species cannot be accepted as blanket solutions to all populations. It is therefore important to have information on detection probability of local populations and to have means to visualise the complex interactions of different weather variables comprehensively. Chapter 3 of the thesis titled:

Weather-related detection probability of *Lacerta agilis* LINNAEUS, 1758 within the core range in western Germany

focuses on determining weather-based detection probability using a multitude of weather variables, both from the time of finding and hours before. Bayesian models are used to identify the weather variables that best explain the detection probability during conducted visual encounter studies. Furthermore, variable interactions are depicted in an easy-to-understand regression tree model for ease of use. Sand lizards have shown to be more active during dry conditions with low windspeeds, after sunny weather, and at temperatures around 20°C. Rainfall in the previous 24 hours also increased detection probability. The unpruned regression tree explores variable interactions, gives concrete variable values and highlights at which conditions to expect good detection probability. Aside from providing concrete information, the method used is useful for both post-survey analysis and for determination of best survey conditions and only requires data on findings and weather data which can be supplied by an external source. It can thus be added to many monitoring projects.

As discussed previously, home range and habitat selection are key factors for effective conservation and management. Given the disastrous effect of habitat destruction on global diversity, understanding habitat requirements of animals is of utmost importance in conservation. However, smaller animals with small home ranges like *Lacerta agilis* require fine scale assessments. In chapter 4 of the thesis titled:

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

I focus on using unmanned aerial vehicles to record high resolution maps. One of the biggest advantages of unmanned aerial vehicles is their ability to control spatial and temporal resolution of the maps and fit them to the requirements of a study. A Maxent algorithm was used to define habitat categories on the map. My collaborators and I also calculated home ranges of individual lizards with the help of radio-telemetry and define a procedure to attach radio transmitters to *Lacerta agilis*. We used multiple home range calculations to ensure comparability with other studies. We then combine resulting home ranges with the categorical map to compare habitat composition within the home range with available habitat in the area to assess, which habitat structures are favoured compared to-, avoided compared to- or used according to available habitat. Overall, *Lacerta agilis* in the area favour blackberry bushes while underutilizing high vegetation and sand within their home ranges. Low vegetation and grass are used according to individual preferences that average out around neither being preferred nor avoided. This study provides a method to assess small vertebrate habitat preferences with high spatial resolution which can be used in planning population specific habitat management or compensatory measures.

All in all, it took 220 days of fieldwork over three years for all chapters of the thesis combined (Table 0.1). The different chapters are comprised of publications which are published in international journals (Table 0.2).

Figure 0.5: Overview of the thesis from aims and goals to the main conclusions. Different chapters are separated by colour and start with the central question to the chapter followed by the methods and finally be the main results. Weather data supplied by the DWD (Deutscher Wetterdienst).

Table 0.1: Workload of fieldwork per year in days.

Year	**Days of Fieldwork** **visual encounter surveys**	**radio-telemetry**	**drone flights (incl. training flights)**
2018	67	0	0
2019	45	10	5
2020	93	0	0
Sum	205	10	5

Table 0.2: Publications corresponding to the chapters of the thesis.

Chapter	**Publication/Submission**	**Status**
1	**CLEMENT, V.F.,** & D. RÖDDER (2021): Playing favourites – a review and discussion on the allocation of vertebrate orders and foci in home range and habitat selection studies. – North-Western Journal of Zoology, **17(1)**: 134–148.	Published
2	SCHMITZ M.L., **V.F. CLEMENT**, P. GINAL, & D. RÖDDER (2022): Spatiotemporal patterns of habitat use by the sand lizard *(Lacerta agilis* LINNAEUS, 1758): Effects of climatic seasonality? – Salamandra **58(4)**: 302-316	Published
3	**CLEMENT, V.F.**, J. EDANACKAPARAMPIL, L.M. SCHMITZ, R. SCHLUCKEBIER, & D. RÖDDER (2022): Weather-related detection probability of *Lacerta agilis* LINNAEUS, 1758 within the core range in western Germany. – Basic and Applied Herpetology **38**: 1-21. doi: https://doi.org/10.11160/bah.242.	Published
4	**CLEMENT, V.F.**, R. SCHLUCKEBIER, & D. RÖDDER (2022): About lizards and unmanned aerial vehicles: assessing home range and habitat selection in *Lacerta agilis*. Salamandra **58(1)**: 24–42.	Published

Part A

Allocation of focus in regard to vertebrate orders and topics in home range and habitat studies.

This illustration was made by MANUEL SCHUMACHER and commissioned by the author of this thesis. The artist consented to the inclusion and publication of the illustration.

Chapter 1

Playing favourites - A review and discussion on the allocation of vertebrate orders and foci in home range and habitat selection studies.

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Published as: CLEMENT, V.F. & D. RÖDDER (2021): Playing favourites – a review and discussion on the allocation of vertebrate orders and foci in home range and habitat selection studies. – North-Western Journal of Zoology, **17**: 134–148.

This illustration was made by MANUEL SCHUMACHER and commissioned by the author of this thesis. The artist consented to the inclusion and publication of the illustration.

Preface summary and author contributions

This chapter has been published in the North-Western Journal of Zoology as:

CLEMENT, V.F. & D. RÖDDER (2021): Playing favourites – a review and discussion on the allocation of vertebrate orders and foci in home range and habitat selection studies. – North-Western Journal of Zoology, **17(1)**: 134–148.

All authors agreed to the inclusion of this publication into this doctoral thesis. As copyright holder, the journal was asked to allow the inclusion as well to which they consented.

As preface, I first give a summary of the publication's background, contents, results, and conclusions and highlight my contributions to this publication. The original publication can be found in the appendix under the name Publication_S1. Please note that numbers of figures and tables were changed from the original publication to fit the structure of the thesis. Additionally, spelling mistakes that slipped through proof-reading in the publication may have been corrected.

Home range and habitat selection are known as important topics in the study of animal ecology as they define space use and resource management while also laying the groundwork for further behavioural and ecological research. The study of animal movement, population dynamics, and inter-/intraspecies interactions are some examples of fields benefiting from a solid understanding of the subject's use of space. Furthermore, a clear understanding of an animal's space use is also a prerequisite for the development of effective conservation measures. Thus, home range and habitat selection have continuously been a focus of ecological studies on many different taxa over the years. In this review, we ask two questions. We first want to know which vertebrate groups and species were most studied in terms of home range and which were so far neglected. Second, we want to know which ecological topics were studied alongside home range and habitat selection. For that we have reviewed 903 publications across all extant vertebrate clades incorporating some form of home range and habitat selection in their methods from 1980 to the first quarter of 2018. We reviewed the publications by reading through the abstract and scanning the main text for key words like "home range" or "habitat selection" and if found, we note the subject species of the work as well as the ecological topics discussed in the publication. The species were then grouped into corresponding orders while the topics were divided into: Habitat use/quality, conservation/human influence, population density, reproductive behaviour, territoriality/aggression, home range shifts and exceptions, intraspecific differences, interspecific interactions, and reviews. A quantitative analysis then revealed the foci of the studies. For the single species, we highlighted the most studied species and for the orders, we compared proportion of studies to proportion of species within the order to see whether species rich orders would get more attention than species poor orders. Similarly, we analysed whether closely related orders get more attention than distantly related ones or whether orders with a high relative amount of threatened species would get more attention than orders with relatively fewer threatened species. For the ecological topics, we highlighted the proportion of studies including a certain topic. Overall, we have observed, that the allocation of attention towards vertebrate orders is independent of species richness, relatedness, and portion of threatened species for most orders. In our discussion we speculate on possible reasons for the observed results and highlight further opportunities for research. Furthermore, we have shown that topics often studied in concordance with home range and habitat selection are conservation and human influence, intraspecific differences, and home range shifts/exploratory behaviour, while topics like population density, reproductive behaviour, territoriality/aggressive behaviour, and interspecific interactions are studied less often. We also discuss these topics and thus highlight opportunities for further research. In conclusion, this review highlights and discusses the current distribution of focal points in studies concerning home range and habitat use while identifying less studied fields and taxa - thereby emphasizing potential opportunities for further research.

As primary author, my contributions to this study were numerous and I was involved in all steps of the study. I conceptualized the idea for the study together with DENNIS RÖDDER as a part of my doctoral thesis as an introduction to which studies have been done before and where our planned studies on *Lacerta agilis* fit into previous work on home range and habitat selection. I analysed the papers and sorted them into the categories and phylogenies used in this work. Statistical and quantitative analysis was done by me with help and explanations of DENNIS RÖDDER. The first interpretation of the results was done by me with DENNIS RÖDDER giving input along the way. I wrote the original draft of the manuscript and reviewed it together with DENNIS RÖDDER to finalise the manuscript for submission.

Abstract

Home range and habitat selection are key subjects when studying animal ecology. Defining the space use and resource management of an animal establishes a solid basis for further behavioural and ecological research, as well as conservation management. Studies focusing on determining home range and habitat selection often include further questions regarding for example conservation, animal movement, population dynamics, and inter- or intraspecific interactions. It is therefore unsurprising that home range and habitat selection have been the focus of numerous studies on different vertebrate taxa over the years. We have reviewed 903 publications on all extant vertebrate clades focusing on these topics from 1980 to the first quarter of 2018. We have observed that allocation of vertebrate orders is independent of species richness, relatedness, and portion of threatened species within the order. We have highlighted the relation between publication numbers and species richness and offer ideas for future research in proposing possible causes for the observed allocation and in highlighting understudied clades. Furthermore, we have observed that topics often studied in concordance with home range and habitat selection are conservation and human influence, intraspecific differences, and home range shifts/exploratory behaviour. Meanwhile, topics like population density, reproductive behaviour, territoriality/aggressive behaviour, and interspecific interactions seem to be less studied. This review highlights and discusses the current distribution of focal points in studies concerning home range and habitat use while identifying less studied fields and taxa - thereby emphasizing potential opportunities for further research.

Keywords. Home range, habitat selection, vertebrate, behavioural ecology, study subject preference, topic preference

Introduction

The concept of home range was first introduced by BURT in 1943. BURT defined the home range as “that area traversed by the individual in its normal activities of food gathering, mating, and caring for young”. He further emphasized that “Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range.” Since then, the definition might have been deemed too imprecise by some, but the core ideas of the definition have never been seriously challenged or altered (BOITANI & FULLER 2000). The reasons for animals to have home ranges can be numerous. For example, familiarity increases safety, as escape paths and hideouts become known to the point of automatism (STAMPS

1995). In addition, as the location of necessary resources becomes known, staying in the vicinity guarantees the availability of resources, while migrating into new, previously unknown territory lacks this reliability (BOITANI & FULLER 2000). There are a multitude of other reasons for animals to establish home ranges, but in the end they all come down to one general reason: The benefits of establishing a home range exceed the associated costs, i.e., remembering the layout and potentially defending the resources. The study of home range is therefore closely associated with the study of habitat selection, as animals' home ranges reflect their ecological requirements.

The study of home range and habitat selection can reveal important information needed to understand animal space requirements. Since the home range of an animal includes everything it requires to survive on a day-to-day basis, investigating the size of the home range and what habitats and microhabitats it contains gives researchers a solid base for assessing animal ecology. From here, numerous more detailed approaches can be executed. Home range overlap and density can for instance be used to infer population sizes (e.g., GREEN et al. 2000, BENSON et al. 2006) while habitat structure can be used to study resource requirement (e.g., MURPHY & DOWDING 1995), identify critical areas (e.g., INGRAM & ROGAN 2002, WALDRON et al. 2006), or quantify effects of anthropogenic influences (e.g., DE MAYNADIER & HUNTER JR. 2000, FAHRIG & RYTWINSKI 2009). Even though it is by far not the only way to study a species ecology, it provides a first look on species behaviour and ecology and is an essential requirement for creating a complete image of a species' ecology.

This review provides a general overview on studied vertebrate clades and the topics included in publications that combined home range analysis and habitat selection. We further give an overview of the amount of attention each order of vertebrates has received since 1980, as well as the foci highlighted in said publications. We expect the amount of attention attributed to the various groups and topics to be very variable, and independent of species richness, relatedness of the orders, and number of threatened species within orders. This review aims to give first insights on the focal points of home range and habitat selection studies and to give a starting point to identify opportunities for new research.

Methods

For every large vertebrate class, a search on Web of Science (CLARIVATE ANALYTICS 2018) was conducted using the parameters shown in Table 1.1. The classes were: Non-tetrapod vertebrates (in the following called fish), amphibians, non-avian diapsids (in the following called reptiles), birds and mammals. All searches were conducted in the Web of Science Core Collection within the entire time range from 1980 to the first quarter of 2018.

The abstract of each search result was considered and searched for specific foci (Table 1.2) in order to later distinguish different home range related topics of research. For studies to be considered in this review, they had to (1) calculate some form of home range and (2) study habitat use or quality meaning to quantify the use or avoidance of biotic and/or abiotic environmental conditions, describing the influence of environmental conditions on home range, or evaluating the quality of the environment. (as described in Table 1.2). In the case where the abstract was hinting at a topic but was inconclusive about its inclusion, the main text was analysed. Similarly, whenever it was not apparent from the abstract whether home range had been calculated, the study was scanned for the terms “home range”, “home-range”, “range”, “polygon”, and “kernel” in order to find passages that might describe the home range estimation. “Polygon” and “kernel” were included because minimum convex polygon and kernel density estimation are the most common methods to calculate home range. Search results that did not meet these requirements or did not include the required taxonomic groups were excluded. We recorded overall publications per class and per year as well as counting the number of publications treating a certain focus.

Table 1.1: Search terms, refining Web of Science categories and access date of every Web of Science search conducted.

Taxonomic group	Seach terms	Web of Science categories	Date accessed
Fish	TOPIC: ("home range*" OR "home-range*") AND TOPIC: ("habitat use" OR "habitat selection") AND TOPIC: (fish)	Marine Freshwater Biology OR Limnology OR Fisheries OR Biodiversity Conservation OR Biology OR Ecology OR Multidisciplinary Sciences OR Oceanography OR Zoology OR Environmental Sciences OR Behavioral Sciences	27.02.2018
Amphibians	TOPIC: (home range* OR home-range*) AND TOPIC: (habitat use OR habitat selection) AND TOPIC: (amphibia* OR anura* OR caudata OR gymnophiona OR frog* OR salamander* OR newt* OR caecilian* OR toad*)		13.03.2018
Reptiles	TOPIC: (home range* OR home-range*) AND TOPIC: (habitat use OR habitat selection) AND TOPIC: (reptile* OR testudines OR sphenodontida OR squamata OR crocodylia OR tortoise* OR turtle* OR tuatara* OR lizard* OR snake* OR crocodile* OR alligator*)	Zoology OR Ecology OR Evolutionary Biology OR Environmental Studies OR Biodiversity Conservation OR Marine Freshwater Biology OR Limnology OR Environmental Sciences OR Biology OR Oceanography OR Forestry OR Multidisciplinary Sciences OR Behavioral Sciences OR Fisheries	19.03.2018
Birds	TOPIC: (home range* OR home-range*) AND TOPIC: (habitat use OR habitat selection) AND TOPIC: (bird* OR aves)	Ecology Or Marine Freshwater Biology Or Veterinary Sciences Or Ornithology Or Oceanography Or Zoology Or Biodiversity Conservation Or Agriculture Multidisciplinary Or Environmental Sciences Or Environmental Studies Or Behavioral Sciences Or Evolutionary Biology Or Multidisciplinary Sciences Or Urban Studies Or Biology Or Agriculture Dairy Animal Science Or Forestry	27.03.2018
Mammals	TOPIC: (home range* OR home-range*) AND TOPIC: (habitat use OR habitat selection) AND TOPIC: (mammalia OR mammal*)	Ecology OR Marine Freshwater Biology OR Zoology OR Oceanography OR Biodiversity Conservation OR Agriculture Multidisciplinary OR Environmental Sciences OR Environmental Studies OR Multidisciplinary Sciences OR Urban Studies OR Biology OR Behavioral Sciences OR Forestry OR Evolutionary Biology	05.04.2018

Table 1.2: Evaluation topics looked for in the search results, with explanation.

Topic	Explanation
Habitat use/Quality	The study quantifies the use or avoidance of biotic and/or abiotic environmental conditions, describes the influence of environmental conditions, or evaluates the quality of the environment.
Conservation/Human influence	The study explicitly examines anthropomorphic effects on populations or tests the effectiveness of conservation measures.
Population Density	The study measures population density or studies the effects of population density on home ranges.
Reproductive Behaviour	The study examines behaviour associated with the reproduction such as courting behaviour, mating behaviour, breeding behaviour or raising young.
Territoriality/Aggression	The study examines the effects of territoriality and aggression between individuals.
HR Shifts and Exceptions	The study describes shifts in home range, excursions outside the home range, or migratory/sedentary behavior
Intraspecific differences	The study aims to identify differences between sexes, onthogenetic stages or populations.
Interspecific interactions	The study describes interactions between different species
Review	The study is a review

Within each class (fish, amphibians, reptiles, birds, mammals), study subjects were classified into orders. The classification system was chosen according to the ITIS global Catalogue of Life database in order to have one single reference for species numbers (RUGGIERO et al. 2015, ROSKOV et al. 2019). We are aware, that the taxonomic classification used in the data base is controversial but having one single reference for systematics and species numbers brings considerable advantages. For one, combining multiple systematics from different sources is likely to result in counting species multiple times and towards different orders. Furthermore, phylogeny of many clades is unclear and combining them sensibly into a complete vertebrate tree of life would be worthy of an entirely separate review. Lastly, the Catalogue of Life is a publicly accessible data base allowing everyone to quickly assess the order each species is allocated to in this review. Squamates were divided into snakes and lizards and studied separately due to the traditional separation and different ecology. For the same reasons, the Cetartiodactyla were also divided into Cetacea and Artiodactyla. Using the online species databases (ROSKOV et al. 2019, UETZ & HOSEK 2019, FROESE & PAULY 2000), the number of different species in each order was acquired. Then, for each order, two proportions were calculated: The proportion of studies concerning the respective order within the search results of the corresponding class (proportion of publications) and the proportion of species within the class that belong to that order (proportion of species). In the following, these expressions will describe the proportions within the class. Fisher’s exact test with a Monte Carlo simulation with 2000 repetitions was used to test whether the distribution of species and publications within orders are the same. The test was limited to orders that had publications allocated to them to avoid having a lot of entries with zero publications and non-zero species numbers. For Amphibia, where only 2 orders were studied, the Monte Carlo simulation was cut since it did not apply to a 2x2 table. Since fisher’s exact test requires mutually exclusive data in every entry to be applicable, we technically cannot apply it to a data set which included publications considering multiple orders. However, the number of publications considering multiple orders was relatively small (22 publications). Therefore, the test was calculated two times: once treating publications considering x orders as x separate publications and once excluding said publications. If both distributions prove to be significantly different from the distribution of species, we assume that the difference, the publications considering multiple orders make is negligible.

A phylogenetic tree was manually build using TreeGraph 2 (STÖVER & MÜLLER 2010) after (FROESE & PAULY 2000, LAPOINTE & KIRSCH 2001, BETANCUR et al. 2013, PRUM et al. 2015, NELSON et al. 2016, TARVER et al. 2016). Using R (R CORE TEAM 2020) and the R packages: picante (KEMBEL et al. 2010), ape (PARADIS & SCHLIEP 2019), adephylo (JOMBART & DRAY 2010), ade4 (CHESSEL et al. 2004, DRAY et al. 2007, DRAY & DUFOUR 2007, BOUGEARD & DRAY 2018), phylobase (HACKATHON et al. 2020), geiger (PENNELL et al. 2014), and phytools (REVELL 2012), proportion of publications was mapped onto the tree as a continuous variable with the function contMap from the phytools package. BLOMBERG’s K (BLOMBERG et al. 2003) was calculated to estimate phylogenetic signals with proportion of publications treated as potential signal in order to assess whether closely related orders have received similar attention.

In order to assess whether the portion of threatened species within an order dictates the attention an order was given, data from the IUCN red list of species website was requested (IUCN 2020). After adapting the phylogeny to the phylogeny used with the rest of the data, the portion of species listed as vulnerable or above within an order were determined. We compared the portion of vulnerable or above species with the portion of publications across all publications (not just within a class) using fisher’s exact test once more in order to determine whether the allocation of attention was similar to the distribution of at-risk species.

Finally, orders without any publications were listed as well.

In order to assess which species received the most attention, species with five or more publications were highlighted and discussed separately. We chose 5 as a cut-off as it constitutes 20 species (approx. 2.5% of all species studied) and the amount is still reasonable to discuss within the frame of this review.

Results

Distribution of publications within classes and over time

In total, the Web of Science searches yielded 1599 results. There were 289 studies found for fish, 85 for amphibians, 337 for reptiles, 474 for birds, and 414 for mammals. Out of all of these, the number of suitable studies was 139 for fish, 39 for amphibians, 207 for reptiles, 300 for birds and 218 for mammals, effectively resulting in 903 relevant publications that studied home range and habitat selection. The full list of considered publications as well as suitable publications is available in the supplementary material under Supplementary Material Table S1.1. The proportions of relevant studies are represented in Figure 1.1A.

As Figure 1.1B shows, searches yielded almost no results in the time period from 1980 to the early 90s. The earliest publications in the results were from 1992 for fish, 1994 for amphibians, 1990 for birds and 1993 for mammals. For reptiles, a single paper from 1984 was found, but after that, the next oldest paper was from 1991. Publications per year tended to fluctuate but overall, the number of studies for all taxonomic groups increases over the course of the years as can be seen in Figure 1.1B.

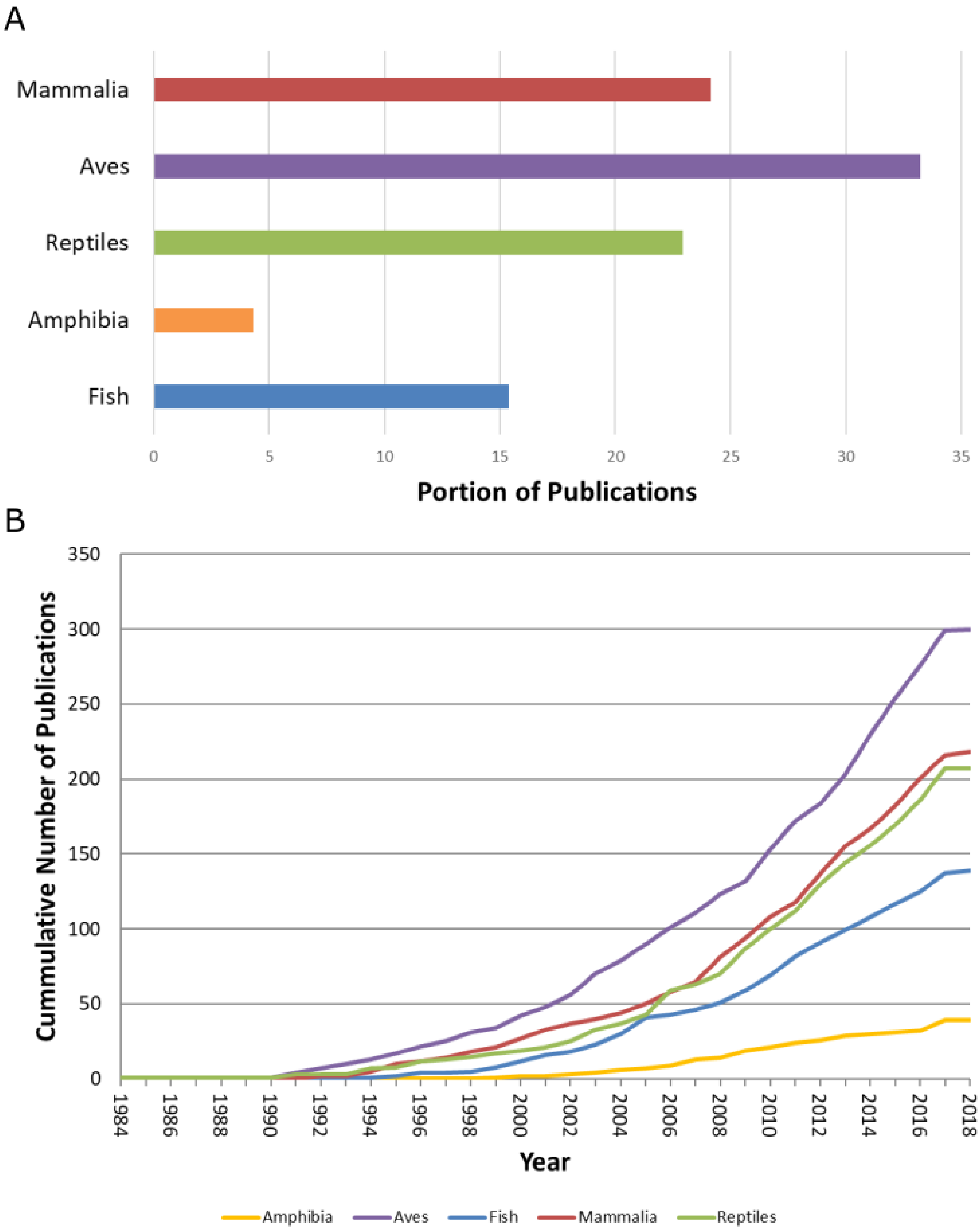


Figure 1.1: Allocation of suitable papers (A) towards the five major taxonomic groups and (B) over time towards the five taxonomic groups.

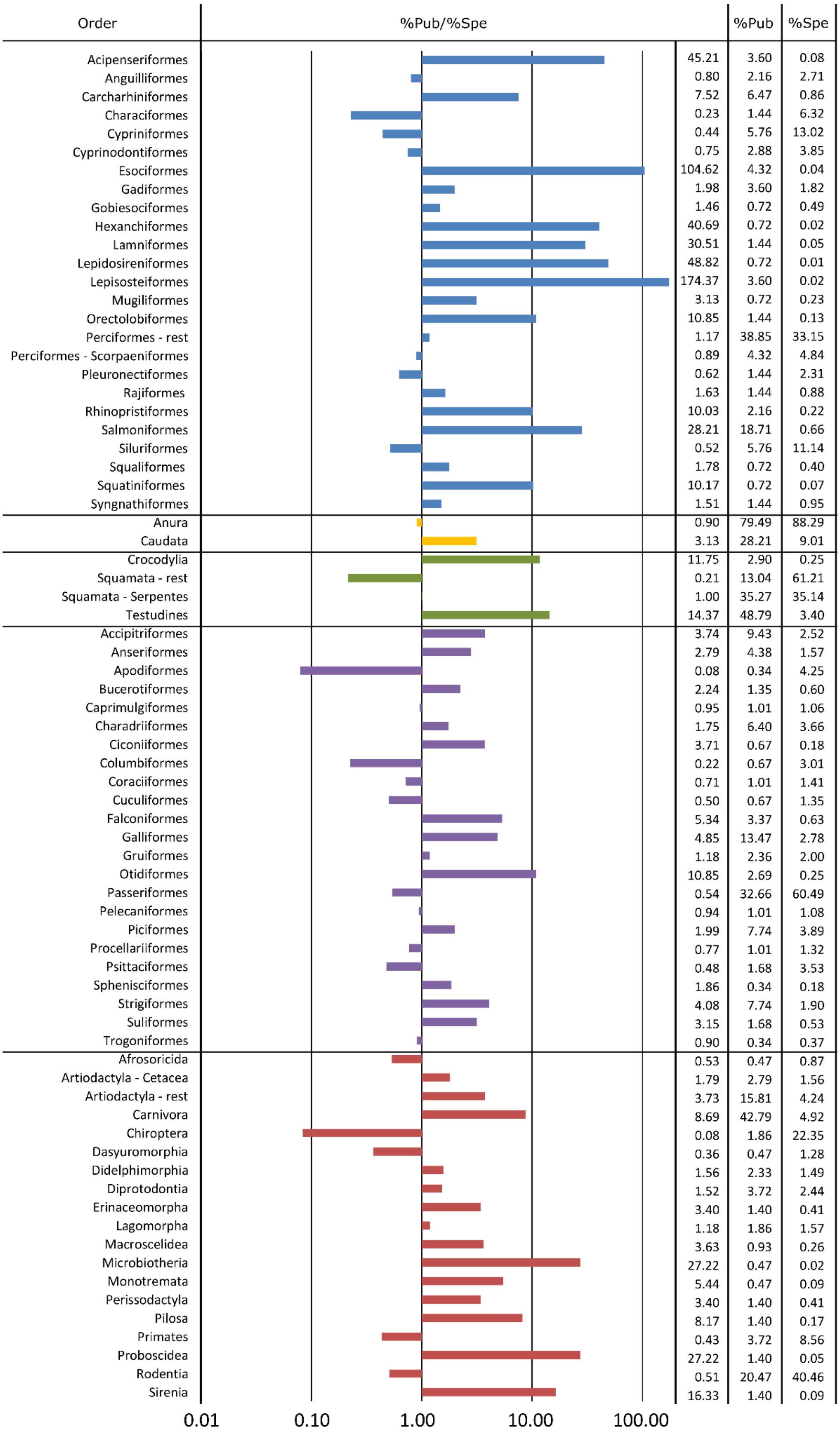
Allocation of orders within classes

Studied orders

All comparisons using fisher’s exact test were significantly different with p-values of $p<0.001$ for every pair of distributions except for the Amphibia pairs. For Amphibia, in both cases the distributions were also significantly different from each other ($p<0.001$ for the test including publications considering multiple orders and $p=0.01581$ for the test excluding publications considering multiple orders). This means that the observed differences between the distribution of studies and species within classes are significant and cannot be explained solely by chance.

Figure 1.2 shows the proportion of publications divided by the portion of species for each order in graph and number as well as the actual proportions. Absolute numbers of species and publications can be found in the Supplementary Material Table S1.1. In most orders, proportion of publications is higher than proportion of species. In Lepisosteiformes and Esociformes, proportion of publications is over a hundred times higher than proportion of species. In Lepidosireniformes, Acipenseriformes, Hexanchiformes, Lamniformes, Salmoniformes, Microbiotheria, Proboscidea, Sirenia, Testudines, Crocodylia, Orectolobiformes, Otidiformes, Squatiniformes, and Rhinopristiformes, proportion of publications is over 10 times higher than proportion of species. Meanwhile, proportion of publications is ten times smaller than proportion of species only in Apodiformes and Chiroptera. The proportion of species is only roughly equal to the proportion of publications in snakes. In Caprimulgiformes and Pelecaniformes, proportions are also very similar with factors of 0.95 and 0.94 respectively.

Figure 1.3 shows the proportional allocation of publications per class over the vertebrate tree of life for orders with at least one publication. The tree is not to be seen as a representative vertebrate tree of life as it is built around the orders used by the ITIS tree of life data base (RUGGIERO et al. 2015, ROSKOV et al. 2019) and some of those orders are controversial. Orders that are used in this review but are not up to date to the used phylogenies are therefore placed where the majority of the species allocated to them would be now. The tree only contains orders represented by at least one publication in the sample. Calculating a BLOMBERG’s K (999 randomizations) with proportion of species as signal reveals that the distribution does not represent a phylogenetic signal ($K=0.055727$, $p=0.226226$). Therefore, there is no evidence that suggests that closely related orders receive similar attention.



Order	%Pub/%Spe	%Pub	%Spe
Acipenseriformes	45.21	3.60	0.08
Anguilliformes	0.80	2.16	2.71
Carcharhiniformes	7.52	6.47	0.86
Characiformes	0.23	1.44	6.32
Cypriniformes	0.44	5.76	13.02
Cyprinodontiformes	0.75	2.88	3.85
Esociformes	104.62	4.32	0.04
Gadiformes	1.98	3.60	1.82
Gobiesociformes	1.46	0.72	0.49
Hexanchiformes	40.69	0.72	0.02
Lamniformes	30.51	1.44	0.05
Lepidosireniformes	48.82	0.72	0.01
Lepisosteiformes	174.37	3.60	0.02
Mugiliformes	3.13	0.72	0.23
Orectolobiformes	10.85	1.44	0.13
Perciformes - rest	1.17	38.85	33.15
Perciformes - Scorpaeniformes	0.89	4.32	4.84
Pleuronectiformes	0.62	1.44	2.31
Rajiformes	1.63	1.44	0.88
Rhinopristiformes	10.03	2.16	0.22
Salmoniformes	28.21	18.71	0.66
Siluriformes	0.52	5.76	11.14
Squaliformes	1.78	0.72	0.40
Squatiniformes	10.17	0.72	0.07
Syngnathiformes	1.51	1.44	0.95
Anura	0.90	79.49	88.29
Caudata	3.13	28.21	9.01
Crocodylia	11.75	2.90	0.25
Squamata - rest	0.21	13.04	61.21
Squamata - Serpentes	1.00	35.27	35.14
Testudines	14.37	48.79	3.40
Accipitriformes	3.74	9.43	2.52
Anseriformes	2.79	4.38	1.57
Apodiformes	0.08	0.34	4.25
Bucerotiformes	2.24	1.35	0.60
Caprimulgiformes	0.95	1.01	1.06
Charadriiformes	1.75	6.40	3.66
Ciconiiformes	3.71	0.67	0.18
Columbiformes	0.22	0.67	3.01
Coraciiformes	0.71	1.01	1.41
Cuculiformes	0.50	0.67	1.35
Falconiformes	5.34	3.37	0.63
Galliformes	4.85	13.47	2.78
Gruiformes	1.18	2.36	2.00
Otidiformes	10.85	2.69	0.25
Passeriformes	0.54	32.66	60.49
Pelecaniformes	0.94	1.01	1.08
Piciformes	1.99	7.74	3.89
Procellariiformes	0.77	1.01	1.32
Psittaciformes	0.48	1.68	3.53
Sphenisciformes	1.86	0.34	0.18
Strigiformes	4.08	7.74	1.90
Suliformes	3.15	1.68	0.53
Trogoniformes	0.90	0.34	0.37
Afrosoricida	0.53	0.47	0.87
Artiodactyla - Cetacea	1.79	2.79	1.56
Artiodactyla - rest	3.73	15.81	4.24
Carnivora	8.69	42.79	4.92
Chiroptera	0.08	1.86	22.35
Dasyuromorphia	0.36	0.47	1.28
Didelphimorphia	1.56	2.33	1.49
Diprotodontia	1.52	3.72	2.44
Erinaceomorpha	3.40	1.40	0.41
Lagomorpha	1.18	1.86	1.57
Macroscelidea	3.63	0.93	0.26
Microbiotheria	27.22	0.47	0.02
Monotremata	5.44	0.47	0.09
Perissodactyla	3.40	1.40	0.41
Pilosa	8.17	1.40	0.17
Primates	0.43	3.72	8.56
Proboscidea	27.22	1.40	0.05
Rodentia	0.51	20.47	40.46
Sirenia	16.33	1.40	0.09

Figure 1.2: Proportion of publications (%Pub) and proportion of species (%Spe) for all orders containing publications and ratio between them. Orders within classes arranged alphabetically.

Table 1.3a and Table 1.3b show the portion of publications and the number of species classified as vulnerable or above by the IUCN red list within each order. The fisher's exact test comparing those distributions states, that the distributions are significantly different from one another ($p<0.001$) meaning the observed allocation of attention is unrelated to the number of threatened species within an order.

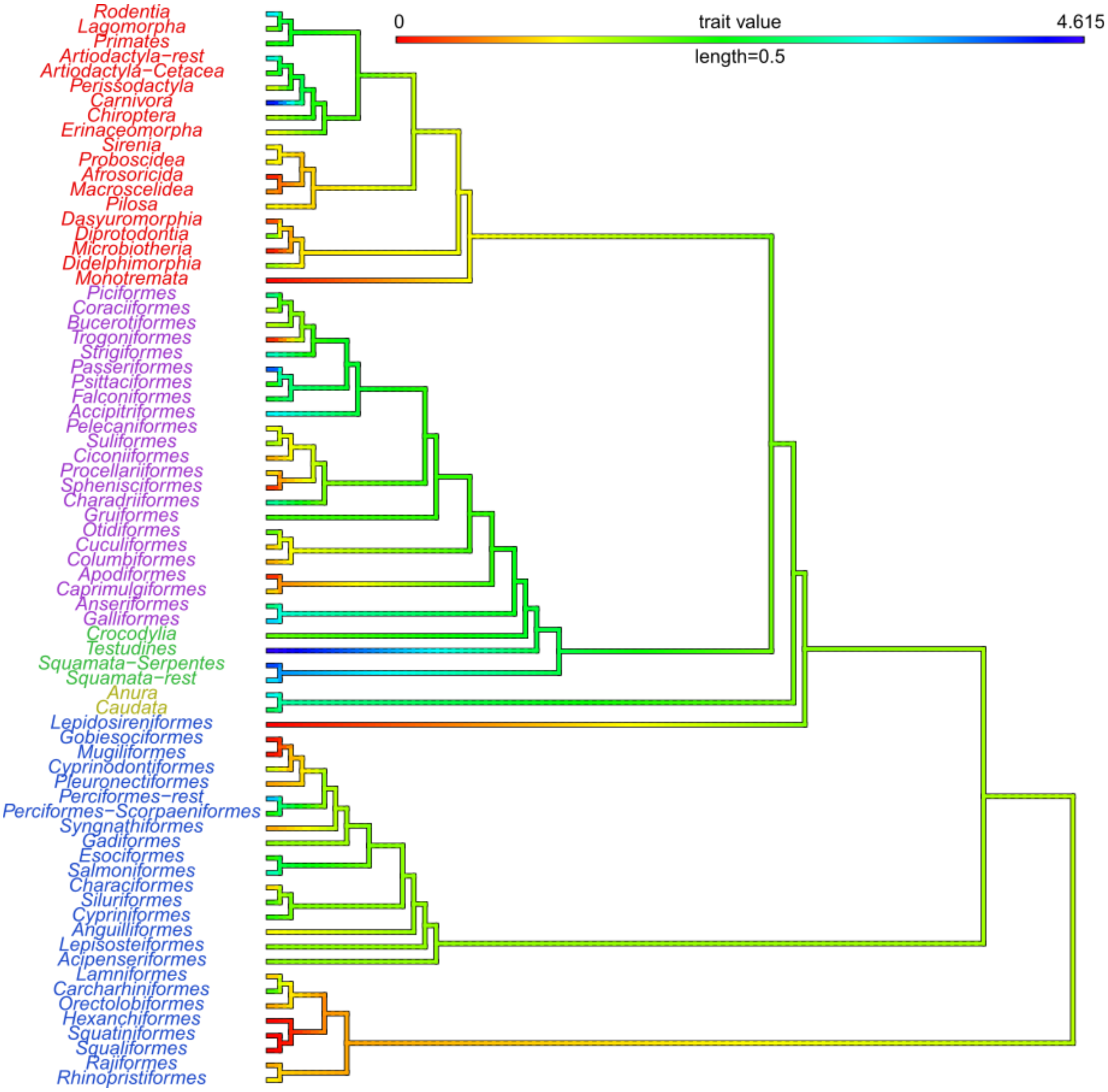


Figure 1.3: Taxonomic tree of vertebrates showing the Log10(number of publications) mapped as continuous character via the function contMap of the phytools package. Outdated orders are placed where most representatives of that order are placed today.

Table 1.3a: Portion of publications out of all publications (PoP) and portion of species classified as vulnerable or above (Voa) by the IUCN red list within each order. Ordered alphabetically (A-L).

Order	**PoP**	**Voa**	**Order**	**PoP**	**Voa**
Accipitriformes	9.43	21.71	Columbiformes	0.67	19.51
Acipenseriformes	3.60	85.19	Coraciiformes	1.01	11.17
Afrosoricida	0.47	30.91	Crocodylia	2.90	47.83
Albuliformes	0.00	10.00	Cuculiformes	0.67	7.28
Amiiformes	0.00	0.00	Cypriniformes	5.76	26.23
Anguilliformes	2.16	1.41	Cyprinodontiformes	2.88	40.15
Anseriformes	4.38	17.61	Dasyuromorphia	0.47	13.70
Anura	79.49	31.15	Dermoptera	0.00	0.00
Apodiformes	0.34	9.83	Didelphimorphia	2.33	8.70
Apterygiformes	0.00	80.00	Diprotodontia	3.72	35.37
Artiodactyla	15.81	41.63	Elopiformes	0.00	11.11
Ateleopodiformes	0.00	0.00	Erinaceomorpha	1.40	12.50
Atheriniformes	0.00	38.81	Esociformes	4.32	11.11
Aulopiformes	0.00	0.00	Eurypygiformes	0.00	50.00
Batrachoidiformes	0.00	19.15	Falconiformes	3.37	11.86
Beloniformes	0.00	12.10	Gadiformes	3.60	2.60
Beryciformes	0.00	1.42	Galliformes	13.47	25.40
Bucerotiformes	1.35	32.88	Gasterosteiformes	0.00	14.81
Caprimulgiformes	1.01	7.50	Gaviiformes	0.00	0.00
Carcharhiniformes	6.47	16.18	Gobiiformes	0.72	12.12
Cariamiformes	0.00	0.00	Gonorynchiformes	0.00	14.71
Carnivora	42.79	26.35	Gruiformes	2.36	25.91
Casuariiformes	0.00	0.00	Gymnophiona	0.00	8.20
Caudata	28.21	51.90	Gymnotiformes	0.00	10.34
Ceratodontiformes	0.00	100.00	Heterodontiformes	0.00	0.00
Cetacea	2.79	22.22	Hexanchiformes	0.72	0.00
Cetomimiformes	0.00	0.00	Hyracoidea	0.00	0.00
Characiformes	1.44	10.16	Lagomorpha	1.86	25.00
Charadriiformes	6.40	13.28	Lamniformes	1.44	66.67
Chimaeriformes	0.00	2.13	Lampriformes	0.00	0.00
Chiroptera	1.86	15.00	Lepidosireniformes	0.72	0.00
Ciconiiformes	0.67	30.00	Lepisosteiformes	3.60	0.00
Cingulata	0.00	10.00	Leptosomiformes	0.00	0.00
Clupeiformes	0.00	6.85	Lophiiformes	0.00	2.06
Coelacanthiformes	0.00	100.00			
Coliiformes	0.00	0.00			

Table 1.3b: Portion of publications out of all publications (PoP) and portion of species classified as vulnerable or above (Voa) by the IUCN red list within each order. Ordered alphabetically (M-Z).

Order	PoP	Voa
Macroscelidea	0.93	10.53
Mesitornithiformes	0.00	100.00
Microbiotheria	0.47	0.00
Monotremata	0.47	60.00
Mugiliformes	0.72	2.04
Musophagiformes	0.00	8.33
Myctophiformes	0.00	0.00
Myliobatiformes	0.00	34.21
Myxiniformes	0.00	11.84
Notacanthiformes	0.00	0.00
Notoryctemorphia	0.00	0.00
Ophidiiformes	0.00	2.04
Opisthocomiformes	0.00	0.00
Orectolobiformes	1.44	17.07
Osmeriformes	0.00	30.77
Osteoglossiformes	0.00	10.78
Otidiformes	2.69	30.77
Passeriformes	32.66	10.29
Paucituberculata	0.00	42.86
Pelecaniformes	1.01	15.52
Peramelemorphia	0.00	40.91
Perciformes	38.85	10.18
Percopsiformes	0.00	11.11
Perissodactyla	1.40	75.00
Petromyzontiformes	0.00	21.62
Phaethontiformes	0.00	0.00
Phoenicopteriformes	0.00	16.67
Pholidota	0.00	88.89
Piciformes	7.74	7.02
Pilosa	1.40	30.00
Pleuronectiformes	1.44	0.93
Podicipediformes	0.00	21.74
Polymixiiformes	0.00	0.00
Polypteriformes	0.00	0.00
Primates	3.72	60.77
Pristiophoriformes	0.00	0.00
Proboscidea	1.40	100.00
Procellariiformes	1.01	46.26
Psittaciformes	1.68	28.16
Pteroclidiformes	0.00	0.00
Rajiformes	1.44	11.54
Rheiformes	0.00	0.00
Rhinopristiformes	2.16	50.85
Rhynchocephalia	0.00	0.00
Rodentia	20.47	14.10
Saccopharyngiformes	0.00	0.00
Salmoniformes	18.71	48.03
Scandentia	0.00	8.70
Scorpaeniformes	4.32	2.78
Siluriformes	5.76	15.37
Sirenia	1.40	80.00
Soricomorpha	0.00	15.78
Sphenisciformes	0.34	55.56
Squaliformes	0.72	78.21
Squamata (Lizards)	13.04	18.93
Squamata (Serpentes)	35.27	11.78
Squatiniformes	0.72	50.00
Stephanoberyciformes	0.00	0.00
Stomiiformes	0.00	0.00
Strigiformes	7.74	56.79
Struthioniformes	0.00	50.00
Suliformes	1.68	27.78
Synbranchiformes	0.00	14.94
Syngnathiformes	1.44	5.96
Testudines	48.79	53.81
Tetraodontiformes	0.00	4.83
Tinamiformes	0.00	14.89
Torpediniformes	0.00	45.00
Trogoniformes	0.34	2.33
Tubulidentata	0.00	0.00
Zeiformes	0.00	0.00

Unstudied orders

Table 1.4 contains the unstudied orders as well as their species richness within their respective class. In fish, 39 out of 64 orders containing 15.72% of fish diversity had not been studied. In amphibians, the Gymnophiona containing 2.70% of amphibian diversity had not been studied. In reptiles, only the Rhynchocephalia containing only the tuatara and therefore only 0.01% of reptilian diversity had not been studied. In birds, 17 out of 40 orders containing 1.44% of avian diversity had not been studied and in mammals, 10 out of 29 orders containing 8.77% of mammalian diversity had not been studied. Most unstudied orders were fairly species-poor, containing less than 1% of species diversity (Table 1.4) within the class but some contained more than 1% of the species richness of their corresponding class. These orders were Atheriniformes, Clupeiformes, Lophiiformes, Ophidiiformes, Stomiiformes, Tetradontiformes, Gymnophiona, and Soricomorpha in mammals.

Table 1.4: Orders without any recorded publication including proportion of species richness (in %) within the class.

Order	Species Richness	Order	Species Richness	Order	Species Richness
Albuliformes	0.04	Polypteriformes	0.04	Gaviiformes	0.05
Amiiformes	0.00	Saccopharyngiformes	0.08	Leptosomiformes	0.01
Ateleopodiformes	0.04	Stephanoberyciformes	0.21	Mesitornithiformes	0.03
Atheriniformes	1.05	Stomiiformes	1.22	Musophagiformes	0.22
Aulopiformes	0.78	Synbranchiformes	0.35	Opisthocomiformes	0.01
Batrachoidiformes	0.24	Tetraodontiformes	1.29	Phaethontiformes	0.03
Beloniformes	0.80	Zeiformes	0.10	Phoenicopteriformes	0.06
Beryciformes	0.48	Petromyzontiformes	0.14	Podicipediformes	0.22
Cetomimiformes	0.10	Heterodontiformes	0.03	Pteroclidiformes	0.15
Clupeiformes	1.16	Myliobatiformes	0.72	Rheiformes	0.02
Elopiformes	0.03	Pristiophoriformes	0.02	Struthioniformes	0.02
Gasterosteiformes	0.09	Torpediniformes	0.21	Tinamiformes	0.45
Gonorynchiformes	0.11	Chimaeriformes	0.17	Cingulata	0.36
Gymnotiformes	0.69	Myxiniformes	0.24	Dermoptera	0.03
Lampriformes	0.07	Ceratodontiformes	0.00	Hyracoidea	0.07
Lophiiformes	1.06	Coelacanthiformes	0.01	Pholidota	0.14
Myctophiformes	0.75	Gymnophiona	2.70	Scandentia	0.34
Notacanthiformes	0.08	Rhynchocephalia	0.01	Soricomorpha	7.31
Ophidiiformes	1.57	Apterygiformes	0.05	Tubulidentata	0.02
Osmeriformes	0.96	Cariamiformes	0.02	Notoryctemorphia	0.03
Osteoglossiformes	0.75	Casuariiformes	0.04	Paucituberculata	0.10
Percopsiformes	0.03	Coliiformes	0.06	Peramelemorphia	0.36
Polymixiiformes	0.03	Eurypygiformes	0.02		

Most studied species

Table 1.5 shows the species with 5 or more publications. Most common among the list of species are Testudines and Carnivora. Turtles seem to have a special focus on sea turtles with the green sea turtle (*Chelonia mydas*), hawksbill sea turtle (*Eretmochelys imbricata*), and the loggerhead sea turtle (*Caretta caretta*) holding three of the top 4 most spots in the list. Additionally, two freshwater turtles (*Clemmys guttata* and *Emydoidea blandingii*) and one tortoise (*Testudo hermanni*) are represented. Carnivorans have as many representations as Testudines but the species have lower individual publications. The coyote (*Canis latrans*) has the third most publications out of all animals. Artiodactyla are represented by two species of cervids: the red deer (*Cervus elaphus*) and the white-tailed deer (*Odocoileus virginianus*).

Table 1.5: List of most all species with more than 4 publications allocated to them in the data set used for this study.

Class	**Order**	**Species**	**Publications**
Reptilia	Testudines	*Chelonia mydas*	14
Reptilia	Testudines	*Eretmochelys imbricata*	13
Mammalia	Carnivora	*Canis latrans*	11
Reptilia	Testudines	*Caretta caretta*	9
Mammalia	Carnivora	*Vulpes vulpes*	8
Reptilia	Testudines	*Clemmys guttata*	7
Mammalia	Artiodactyla	*Cervus elaphus*	6
Mammalia	Carnivora	*Felis catus*	6
Mammalia	Carnivora	*Lynx rufus*	6
Mammalia	Carnivora	*Ursus americanus*	6
Aves	Accipitriformes	*Aquila chrysaetos*	5
Aves	Calliformes	*Colinus virginianus*	5
Aves	Otidiformes	*Tetrax tetrax*	5
Mammalia	Rodentia	*Apodemus sylvaticus*	5
Mammalia	Carnivora	*Martes americana*	5
Mammalia	Artiodactyla - rest	*Odocoileus virginianus*	5
Reptilia	Crocodylia	*Alligator mississippiensis*	5
Reptilia	Testudines	*Emydoidea blandingii*	5
Reptilia	Squamata - Serpentes	*Heterodon platirhinos*	5
Reptilia	Testudines	*Testudo hermanni*	5

In birds, the golden eagle (*Aquila chrysaetos*), the Northern bobwhite (*Colinus virginianus*), and the little bustard (*Tetrax tetrax*) all have 5 publications allocated to them. Rodents are represented by the wood mouse (*Apodemus sylvaticus*) while non-turtle reptiles are the Mississippi alligator (*Alligator mississippiensis*) and the Eastern hognose snake (*Heterodon* *platirhinos*). No amphibians or fish species have more than 5 publications allocated to them. Fish species with the most publications were largemouth bass (*Micropterus salmoides*), Atlantic salmon (*Salmo salar*), and Lake trout (*Salvelinus namaycush*) with 4 publications each while the European green toad (*Bufo viridis*) and the wood frog (*Lithobates sylvaticus*) were the amphibians with the most publications with 3 each.

Allocation of foci

Figure 1.4 shows that, in general, conservation and human influence, home range shifts/home range exiting behaviour, and intraspecific differences were the most studied topics while there seemed to be far less studies on population density, reproductive behaviour, territoriality and aggression, or interspecific interactions. A full citation report including an overview which publications were allocated to which topics is found in the appendix in the appendix table S1.1 .

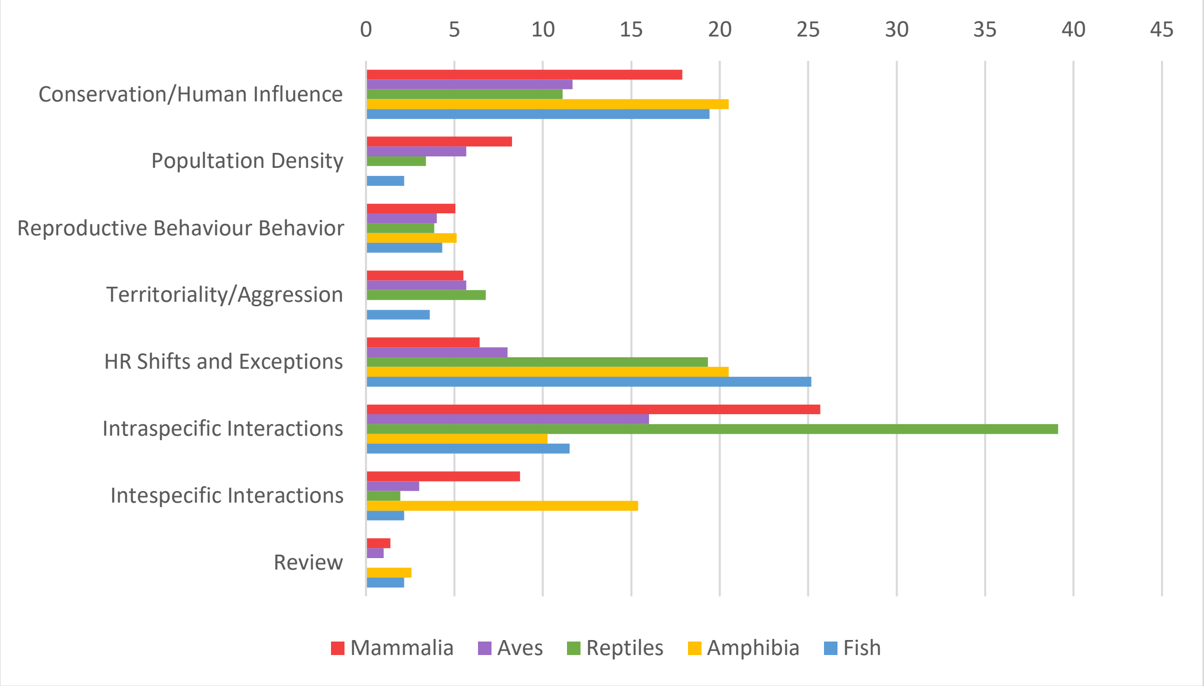


Figure 1.4: Percentage of publications covering different topics in different classes.

Within all classes, at least 10% of publications addressed the issue of conservation and human influence with studies concerning reptiles and birds staying close to 10% while studies concerning fish and mammals neared 20%, and studies concerning amphibians crossed the 20% mark. Population density was generally rarely studied in relation to home range and habitat selection, with birds and mammals being between 5% and 10% while in reptiles and fish, proportion of studies stayed under 5% and no studies were found for amphibians. Reproductive behaviour was studied in around 5% of publications for all classes. Territoriality and aggression were studied similarly as often as population density, while in reptiles, it was studied a little more frequently than population density and there were no cases of it being studied in amphibians. Home range shifts and exploratory behaviour were highly studied in fish, amphibians and reptiles and not so much in birds and mammals. Intraspecific differences were studied in roughly a third of cases in reptiles, with almost 40% of all studies discussing the topic in some way. In mammals, a little over a quarter of all studies included intraspecific differences. In the remaining clades, around 10%-16% of studies covered the topic. Interspecific interactions were generally not studied much but they were more present in studies about amphibians and mammals. Reviews on the topic remain rare with only three reviews for birds, fish, and mammals respectively, and one for amphibians.

Discussion

Distribution of publications over time

The apparent absence of publications before 1990 in the search results is very unlikely to be linked to an absence of interest in home range studies before that time period as evidenced by numerous publications in the field (ERIKSTAD 1985, ERNEST & MARES 1986, LITVAITIS et al. 1986, CEDERLUND & OKARMA 1988). However, the publication of Worton's kernel density estimation method to calculate home range based on utilization distribution in 1989 immediately precedes the first search results in the web of science search (WORTON 1989). As this method not only calculates the area the animal moves in, but also the intensity of utilization within the area (WORTON 1989), it is better suited to combine with the study of habitat selection. As searches were conducted for studies encompassing both home range and habitat selection, this could be a reason for the observed bias towards later years. Additionally, although no conscious effort had been made to search for newer studies, searching terms could have somehow favoured newer studies.

The rising numbers of publications in the field of home range assessment and habitat selection is not surprising and follows a much more general trend in the scientific community: Scientific publications generally increased over the course of the last decades (BJORK et al. 2009, BORNMANN & MUTZ 2015) due to the digitalization and globalization of science. It is easier than ever to access publications from all over the world and to make one's own publications accessible (BORNMANN & MUTZ 2015). Furthermore, the international competition prompts researchers to publish at higher frequencies (FIRE & GUESTRIN 2019). In future studies, it would be interesting to see whether home range and habitat studies have increased at a different pace than other fields and which factors affect the growth rate of a scientific field. One example of such a factor are advances in technology like telemetry and satellite data, which allow for the acquisition of large data sets with comparatively little effort (COCHRAN 1980).

Allocation of publications within classes and orders

The series of fisher’s exact tests suggest that the allocation of publications across orders within a class is significantly different from the distribution of species richness or portion of threatened species. This indicates, that neither the number of species, nor the portion of threatened species is a deciding factor in determining interest in an order. As the calculation of BLOMBERG’s K over the vertebrate tree reveals, closely related orders also do not receive similar levels of attention. We can therefore conclude that researchers neither concentrate nor avoid particular clusters of closely related orders. This however does not mean it could not be a deciding factor on other phylogenetic levels. There could be a relation between number of studies and relatedness within certain orders on family level. To test this, one would need a much larger sample size so it could be properly resolved on family level or be done in a more focused study.

Considering species richness, one thing must be kept in mind when doing the calculations this way: orders having exceptionally high or low species richness can show a more extreme relationship between proportion of species and proportion of publications. The large number of species within orders like Cypriniformes, lizards , and Chiroptera (FROESE & PAULY 2000, ROSKOV et al. 2019, UETZ & HOSEK 2019) renders achieving equilibrium between publications and species numbers very hard to achieve. To do so would mean, many less species rich clades would have to be ignored or studied very scarcely. This would lead to an overall worse representation of vertebrate biodiversity in the publication history. Extremely species poor orders, on the other hand, do easily seem overrepresented because number of species within these orders can be so small, that even very few studies within the 289 publications considered can lead to an overrepresentation. Rhinopristiformes, Orectolobiformes, Lamniformes, Lepidosireniformes, Lepisosteiformes, Acipenseriformes, Hexanchiformes, Squatiniformes, Microbiotheria, Proboscidea and Sirenia are only represented in five papers or less but still show a publication to species number ratio above

10 because of their low number of species compared to other orders within their classes. Low species richness can also cause orders to remain completely unrepresented within the considered publications as orders poor in species are less likely to be prioritized by publications. As Table 1.4 reveals, most of the unstudied orders constitute less than 1% of species diversity within their major classes. While the portion of threatened species within an order can be considered a good criterion for studies on habitat use and home range, it alone cannot explain the overall distribution we observed either as represented in the fishers' exact tests made with the data from Table 1.3.

It is likely, that there are other attributes allocated towards animals, that could explain the amount of attention a taxon receives. Attributes like animal size (COCHRAN 1980, KENWARD 2000), and mobility (MAYOR et al. 2009), that influence the difficulty of applying radio-telemetry could play a role in the attractiveness of species and even populations. Many small lizards for instance have small home ranges and hence habitat often needs to be quantified at extremely fine resolutions - up to the point where individual rocks and bushes can be distinguished (e.g., BALTOSSER & BEST 1990, DIEGO-RASILLA & PEREZ-MELLADO 2003). This could lead to favouring of larger and/or more mobile taxa like Carnivora, Crocodylia, Testudines or sharks and the avoidance or omittance of for example Apodiformes, Soricomorpha, or Atheriniformes. We suggest comparing size and/or mobility to number of publications would be a good way to test this hypothesis. We feel however, that this has to be done on a much finer resolution than order level as some orders contain species varying greatly in size.

Animal accessibility is also an explanation worth considering as it can be assumed that deep sea animals for instance (like Coelacanthiformes, Lophiiformes and Stomiiformes (LONG 1995, NELSON et al. 2016, BURTON & BURTON 2017) or primarily fossorial animals like Gymnophiona (WELLS 2010) are hard to track reliably.

Certain ecological features may make taxa more interesting to study in terms of home range behaviour and habitat selection. The high number of studies concerning Otidiformes could be due to their predominantly terrestrial lifestyle (STEAD 1965) which might make their home range and habitat selection behaviour different from other birds and make them easier to study with radio-telemetry. Furthermore, predators like elasmobranchs, crocodiles, mammalian carnivores, raptors, and maybe Esociformes and Lepisosteriformes could be more interesting as they may potentially serve as indicators of the state of local ecosystems (see e.g., VAN FRANEKER 1992, CARROLL et al. 2001).

The possibility of certain taxa being more or less popular or recognizable in the general eye and the scientific community also possibly plays an important role. General appeal of animals and public opinion might influence the intensity with which orders might be studied. As discussed by ROSENTHAL et al. in 2017, there is a bias towards large, perceived charismatic animals within the general public and the scientific community. The seeming popularity of orders such as sharks (Carcharhiniforms, Orectolobiformes, Lamniformes), turtles and tortoises (Testudines), crocodiles and alligators (Crocodylia), raptors (Accipitriformes, Strigiformes and Falconiformes), mammalian carnivores (Carnivora), elephants (Proboscidea) and sirens and dugongs (Sirenia) could be explained by their appeal. It has also been shown, that there is a positive correlation between popularity of an animal and its relatedness to humans (WARD et al. 1998, BATT 2009, BORGI & CIRULLI 2015, ROSENTHAL et al. 2017). Similarly, aversion to more distantly related taxa is present from early youth in humans (KUBIATKO 2012, BORGI & CIRULLI 2015). In their 2017 publication ROSENTHAL et al. showed that this bias was also present in ecological studies. This is reminiscent of the concept of flagship species which describes “a species used as the focus of a broader conservation marketing campaign based on its possession of one or more traits that appeal to the target audience.” (VERISSIMO et al. 2011). Aside from appealing species getting more attention, researchers could also strategically favour the study of charismatic species to raise interest in their publications and make them more relevant for conservation purposes. However, the lack of a statistical ranking of animal popularity makes this hypothesis difficult to verify.

Another valid consideration is the direct impact species have on human society as well as public interest in protecting certain species. Some fish species may be of commercial interest for fisheries, such as Salmoniformes (MATTHEWS et al. 1994, SCRUTON et al. 2005, YOUNG 1996, FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS 2005), Acipenseriformes (FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS 2005, GERRITY et al. 2008, BARTH et al. 2011, ACOLAS et al. 2017) or Esociformes (FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS 2005). Additionally, the study of mammals could also be favoured since large or potentially dangerous animals like wild boars (*Sus scrofa*), coyote (*Canis latrans*), foxes (e.g., *Vulpes vulpes*) or wolves (*Canis lupus*) can enter human settlements motivating studies quantifying contact or assessing damage and risks (e.g., TREVES et al. 2004, CAHILL et al. 2012, GEHRT et al. 2013, POESSEL et al. 2016, WALTON et al. 2017). Also, feral cats are considered to be amongst the most destructive invasive species (LOWE et al. 2000), which highlights the necessity to understand their spatial and habitat uses in many ecosystems for appropriate management as evidenced by several publications (e. g. HARPER 2007, GEHRT et al. 2013, DOHERTY et al. 2015).

Testing these factors would be an important next step in unearthing the reasons for the observed taxonomic bias. We suggest doing this on smaller scales at first as it would be easier to identify small scale causes and testing their applicability at larger scales than vice versa. It is important to find the correct scale to test hypotheses. Most of these factors work on species level and any statements on higher classifications are just generalizations of the taxa within just as the observed allocation in Figure 1.1A. is a further generalization of the observed allocation of orders. By choosing to investigate above species level, we trade precision for a larger sample size per taxonomic unit per workload. We expect no single factor to be solely responsible for the amount of interest in a taxon but rather expect there to be a complex web of factors individually raising or lowering the specific attractiveness of a tax on to researchers.

Most studied species

When looking at the list of most studied species, one striking observation is, that apart from sea turtles and house cats, every species occurs in North America and/or Europe (IUCN 2020). It could be, that many of these species are more intensely studied due to the overall high number of scientific publications in these regions. This could contribute to the popularity of some species as easily accessible model species or species of local conservation interest. *Heterodon platirhinos*, *Alligator mississippiensis*, *Aquila chrysaetos*, *Colinus virginianus*, *Tetrax tetrax*, *Clemmys guttata*, and *Emydoidea blandingii* do not have any special reasons listed within their publications that would not also apply to numerous other species. Their geographical range could therefore make them convenient study subjects.

As for sea turtles, all sea turtles are at least vulnerable (IUCN 2020). They have a complex life history with migratory stages and periods of site fidelity (GODLEY et al. 2003, BLUMENTHAL et al. 2009, HART et al. 2012). Most publications state that understanding their space use is especially important for the identification and protection of crucial areas (SEMINOFF et al. 2002, MAKOWSKI et al. 2006, BLUMENTHAL et al. 2009, HAWKES et al. 2011, GAOS et al. 2012). Modern technology like satellite telemetry allows the reliable tracking over marine megafauna like sea turtles (MAKOWSKI et al. 2006, HAWKES et al. 2011, HOENNER et al. 2012, CHRISTIANSEN et al. 2017).

Spotted turtles (*Clemmys guttata*), Blanding's turtles (*Emydoidea blandingii*) and Hermann's tortoises (*Testudo hermanni*) are declining in numbers (MILAM & MELVIN 2001, LITZGUS & MOUSSEAU 2004, INNES et al. 2008, EDGE et al. 2010, ROZYLOWICZ & POPESCU 2013). However, this applies to many turtle species. Reasons for these species to be preferred could be tied to their geographic distribution as both species occur in more northern clines where they have to deal with seasonal weather shifts that could influence space use in these ectothermic animals (see e.g., LUISELLI et al. 2009).

All but one of the carnivorans studied are mesocarnivores. A reoccurring topic among the mesocarnivore studies is interspecific interactions more specifically intraguild competition and how it affects habitat use (ARJO & PELTSCHER 2004, GEHRT & PRANGE 2007, GEHRT et al. 2013, MOLSHER et al. 2017). Additionally, the habitat use of those animals in proximity to human settlements or otherwise disturbed areas is often studied (PANDOLFI et al. 1997, FULLER & HARRISON 2005, GODBOUT & OUELLET 2008, GOAD et al. 2014, POESSEL et al. 2016). Animals like coyotes and foxes are stated as highly adaptable (PANDOLFI et al. 1997, GOSSELINK et al. 2003) which could make them more attractive to localized habitat utilization studies. Feral cats on the other hand are stated as a big conservation concern (HALL et al. 2000, FERREIRA et al. 2011). The only non-mesopredator on the list, the black bear might get attention due to a close proximity to humans and willingness to exploit their food resources (BECKMANN & BERGER 2003, MANEN et al. 2012).

The red deer (*Cervus elaphus*) and the white-tailed deer (*Odocoileus virginianus*) are studied for a multitude of reasons like quantifying human influence (DECHEN QUINN et al. 2013, DROLET et al. 2016) or the effects of climate change (RIVRUD et al. 2010). These problems are however not restricted to those species. It could be that the cervids are used as a readily available model species for large herbivores in general (RIVRUD et al. 2010).

Wood mice (*Apodemus sylvaticus*) are studied as they inhabit agricultural land (TEW et al. 2000, TATTERSALL et al. 2001, ROSALINO et al. 2011) Their influence on pastures and their possible role as indicator species for habitat quality therefore has to be studied (TATTERSALL et al. 2001).

While fish and amphibians did not have a species with five or more publications, the species with the highest numbers of publications (*Micropterus salmoides*, *Salmo salar*, and *Salvelinus namaycush* for fish and *Bufo viridis* and *Lithobates sylvaticus* for amphibians) are also species widely found in Europe and North America (IUCN 2020). The aforementioned fish species are also commercially important fish, which might further contribute to the interest in them (FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS 2005).

Some of the reasons stated within the publications coincide with our assumptions on what could make an order interesting to study, but it also further proves that assessments like these are best done on species level.

Allocation of topics within publications

The main topics of home range and habitat selection studies over all classes are conservation/human influence, intraspecific differences, and home range shifts and exploratory behaviour while population density, reproductive behaviour, territoriality/aggression and interspecific interactions are studied less.

Across all taxa, conservation and human influence are always important study subjects, as they constitute the bridge between theoretical interest in these animals and applications important to economy, politics, and other branches outside science. These studies focus on the evaluation and development of concrete conservation applications. In turn, these studies can have access to more funding possibilities than purely theoretical studies (LAUDEL 2006) further contributing to their popularity. This hypothesis is further supported by the fact that even publications without specific goals in that regard often argue for the importance of their data in developing future conservation plans.

The concern with home range shifts and temporary leaving of the home range is also important when studying conservation efforts, because they can give insights on habitat requirements, dispersal capabilities and home range fidelity. Northern watersnakes (*Nerodia sipedon*), for example, have been reported to increase side fidelity in urban areas, presumably because exploratory behaviour is discouraged by human-related hazards (PATTISHALL & CUNDALL 2008). Home range shifts and temporary leaving of the home range also stand in direct relation to conservation efforts because of the way that animals translocated or released due to conservational efforts have to go through a phase of dispersal in which finding a new home range is at risk of failing (KNOX et al. 2017). In 2017, KNOX et al. for example studied the effects of translocation techniques on post-release dispersal of jeweled geckos (*Naultinus gemmeus*) and highlighted the importance of knowing and optimizing species dispersal capabilities for the successful translocation of populations. Furthermore, studying causes not directly related to active conservation measures or human influence assessment can also give valuable insights on animal habitat requirements and willingness to take risks. Female roe deer (*Capreolus capreolus*), for instance, have been shown to temporarily leave their home range in search for new mating opportunities (DEBEFFE et al. 2014). It is noteworthy that interest is reduced in birds and mammals when compared to lower vertebrates. One possible reason being that terrestrial lower vertebrates usually have more limited home ranges and are less mobile than birds and mammals. Therefore, habitat shifts are often more prominent and easier to study in these clades. In the case of birds, seasonal habitat shifts like overwintering migrations can span several continents. Even though migrations are in a strict sense home range shifts, causes and effects of migrations are usually considered far above home range scale (GUAN et al. 2013).

Intraspecific differences are also often considered. The simplest forms of studying intraspecific differences, to compare males and females, or adults and juveniles, are also most common in the list of publications. Sex and age determination can be achieved rather easily in many species by identifying sexual dimorphism or examining genitalia when marking the animals for relocations or applying transmitters. As long as the sample sizes for the different intraspecific groups are large enough, splitting the data set into subsets and comparing them is usually not an issue and easily done. In mammals, differences between males and females can be interesting for numerous reasons. On one hand, pregnant females or females rearing young could have very different habitat requirements than males in terms of energy intake or safety. This has been shown repeatedly for roe deer (*Capreolus capreolus*) (e.g., TUFTO et al. 1996, SAÏD et al. 2009). On the other hand, males could show very different behaviour from females when searching or courting for females (FERNANDO et al. 2008). The number of studies on intraspecific differences is highest in reptiles perhaps because studies focusing on lizards can have larger sample sizes in a set radius, as lizard home ranges tend to be small (as discussed above).

Population density might be less studied because in order to assess population density, there is no need to study home range or habitat selection (see e.g., KREBS 1989, GAILLARD et al. 1993, THOMAS et al. 2010). Even though space use and population density can be combined, studies focusing mainly on population density might choose those other ways. Reproductive behaviour is also less studied in most clades except in birds, where it is studied more. This can be explained by the fact that bird parents, providing for their offspring, actively forage food and therefore, optimal use of home range and habitat - with possible shifts during nesting and brood care - is critical to species survival (GARZA et al. 2005, BELTRAN et al. 2010, WILLIAMS et al. 2016). There is lower interest in mammals in this regard, even though they, too, care for their young, which can be explained due to advantages linked to lactating, saving them the effort of finding suitable food sources for them.

The publication of studies on interspecific interactions could be hampered by the requirement to study multiple species. This increases the workload because an apparent interaction or influence of one species on the home range and habitat selection behaviour of another must be shown. The most common examples are competition for resources (INDERMAUR et al. 2009, STAKĖNAS et al. 2013, BRAMLEY 2014, MOLSHER et al. 2017) and predation (e.g., MOLSHER et al. 2017).

The rarity of reviews on the topic can be allocated to two reasons. First of all, reviews are always rare, as it is their aim is to sum up the existing literature on a topic. Therefore, reviews on the same topic are not necessarily needed in quick succession. Reviews on entire clades or communities can be very broad and often focus on specific questions like the ecological effect of roads (TROMBULAK & FRISSELL 2000) or the effectiveness of marine reserves (KRAMER & CHAPMAN 1999). There are, of course, helpful reviews on the subject for specific species as well as for groups of species. DOHERTY et al. reviewed habitat use of feral cats in 2015, in order to better manage potentially harmful populations. The ecology of mountain gorillas, including their space use has been reviewed by WATTS in 1998. Red-cockaded woodpecker foraging habitat has also been reviewed in 2002 by WALTERS et al. while CLEMENS et al. reviewed shorebird home range boundaries in 2014.

Conclusion

As suspected, the proportion of home range and habitat selection studies between orders seems to be independent of species richness, relatedness, or amount of threatened species. There are however other reasons for the observed allocation pattern not studied here. We suspect however, that most of these causes act mainly on the level of smaller taxonomic units as orders are too diverse to generalize factors like body size, mobility, ecology or popularity over an entire order. We expect these factors to work mainly on species level. The short list of most studied species we did look at supports this hypothesis in the reasons mentioned by the studies themselves, however it is way to small of a sample to prove it. To properly assess the representation of vertebrate biodiversity within home range studies, multiple reviews executed based on smaller taxonomic units, rather than orders, would be necessary. However, this review gives first insights and clues towards the allocation of publications towards taxonomic groups and might prompt researchers to review certain smaller taxonomic groups in order to more accurately identify groups needing further research. The same can be said about fields of research and foci of home range and habitat use studies. Conservation, intraspecific differences, and home range shifts seem to be the most popular research topics to be studied alongside home range and habitat selection. The applicability of certain foci to certain taxa as well as the benefits drawn from these studies might mostly be assessable on species level, but the review has identified key trend differences between major groups. In both cases, the justification of the allocation of studies should be questioned and possible reasons should be explored to properly identify research gaps on a finer scale. Even though this study does not claim that the Web of Science search it is based on delivers a complete record of home range and habitat studies made in the last 38 years, it assumes the search results to be a fitting approximation.

This review serves as a first broad look across the field of vertebrate space use studies and a first step in assessing the completeness of the field. As research power is limited, there are bound to be gaps in our understanding of these topics but a broad view allows the scientific community to identify potentially interesting and important subjects for further research. We proposed possible reasons why certain clades or topics have received more or less attention. If we were to identify gaps in knowledge and propose taxa to which more attention should be directed, we would suggest to identify gaps not simply by species richness but by richness of at risk species as those taxa are in more immediate need of habitat use assessment studies. Some of them like Proboscidea, Ceratodontiformes, Caudata, Primates, Lamniformes and many more have so far been severely overlooked despite the large portion of endangered species making up these orders. In our opinion, those species are definitely worth considering when choosing a study subject as understanding their spatial use can help to prevent the loss of entire orders currently threatened to disappear. We acknowledge however, that this study did not explore all the possible reasons for the observed allocation pattern and therefore cannot give a definitive statement on the appropriateness of the distribution. In the end, we see the responsibility in the scientific community itself to decide whether gaps are worth filling.

Acknowledgements

We would like to thank MARC CLEMENT for his input and helpful comments as well as the staff and researchers of the ZFMK for their helpful discussions and access to their library of literature.

Part B

An ecological profile of *Lacerta agilis* LINNAEUS, 1758 - Spatio-tempoal patterns, weather preferences, habitat selection, and home range.

This illustration was made by MANUEL SCHUMACHER and commissioned by the author of this thesis. The artist consented to the inclusion and publication of the illustration.

Chapter 2

Spatiotemporal patterns of habitat use by the sand lizard (*Lacerta agilis* LINNAEUS, 1758): Effects of climatic seasonality?

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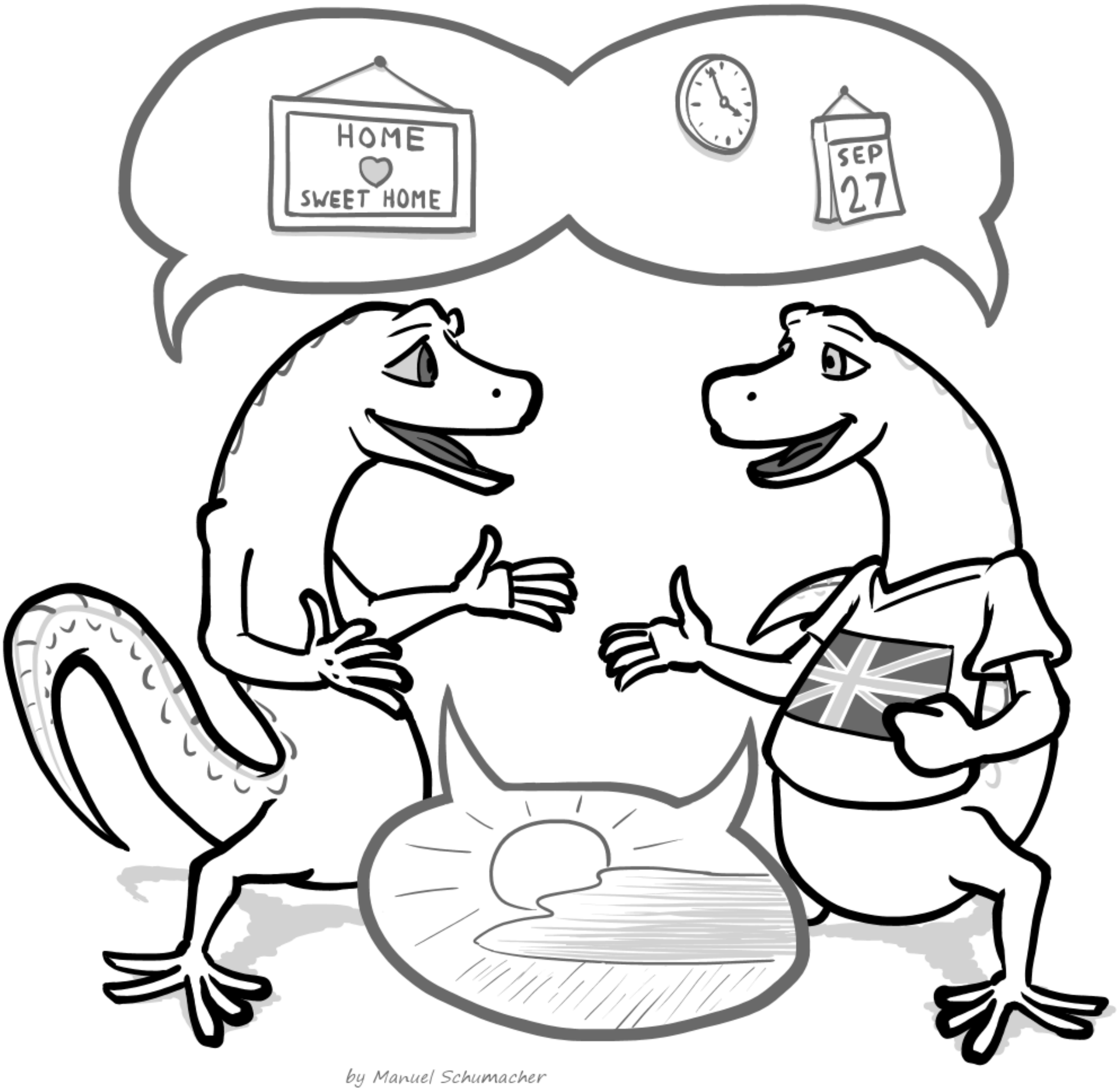

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Preface summary and author contributions

This chapter has been published in the journal Salamandra as:

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All authors consented to the inclusion of this publication into this doctoral thesis. As copyright holder, the journal was asked to allow the inclusion as well to which they consented.

As preface, I first give a summary of the publication's background, contents, results, and conclusions and highlight my contributions to the work that went into this publication. The original publication can be found in the appendix under the name Publication_S2. Please note that numbers of figures and tables were changed from the original publication to fit the structure of the thesis. Additionally, spelling mistakes that slipped through proof-reading in the publication may have been corrected.

A species' ecology dictates its distribution and occurrence within its habitat. Therefore, successful monitoring and hence conservation requires close investigation on which factors influence a species interaction with its environment. These interactions can however differ between populations, especially in widespread species. In conservation, where we often work on population level, results that stem from the concerned species but from far away localities can be at risk of misleading conservationists into sub-optimal measures. The sand lizard, *Lacerta agilis* LINNAEUS, 1758 is such a widespread species which has been studied extensively in the periphery of its distribution. As such, seasonal changes as well as size and sex specific differences in habitat use have been reported from the species' range edges. In this study, we investigate patterns in habitat use of *L. agilis* in western Germany which lies at a more central part of its range in order to verify trends reported from the periphery of the species' range. We used generalized linear models, hypervolumes, density estimations and Chi-squared tests to check for seasonal changes and differences between males and females and subadults and adults. We created a categorical habitat map in order to summarize habitat choice. We used finding points during visual encounter studies and calculated distance data between each finding point and the closest area corresponding to each habitat. We also used weather data at the time of sightings and collected data of microhabitat and microclimate. The resulting variables within these four categories were summarized separately using multiple principal component analyses. The resulting principal components were then investigated. With the help of generalized linear models, we tested whether distance to habitat structures depends on time, weather, microhabitat structures or microclimatic conditions and whether microhabitat choice depends on sampling time and/or microclimatic conditions. With density plots and pairwise permutation tests between morning, midday, and afternoon, we tested whether the data differed between those time periods. Finally, multidimensional hypervolumes were calculated with the principal components to assess differences in niches between sexes and ontogenetic stages. The results of our general linear models suggest, that sand lizards' movement in their habitat is independent of time, weather, microhabitat structures and microclimatic conditions. Density estimation plots and pairwise permutation tests revealed that in the morning, lizards kept a higher distance to the open habitats sand and grass, presumably because in the morning lizards stay closer to their hiding spaces in denser vegetation. Hypervolume analysis shows slight deviations in the niches of subadults versus those of adults which could be due to filial cannibalism, competition with the adults, smaller lizards being able to hide in smaller vegetation, or differences in thermoregulation. All in all, differences remain slight however and results are not in accord with reports from the periphery of the lizards' distribution where these differences were reported to be very pronounced. This means that in this central population lizards follow a eurybiontic lifestyle contrary to the stenobiontic lifestyle confirmed for populations at the edges of the distribution. We therefore conclude, that for the conservation of local populations, we need to rely on local data. This publication was meant to show the differences between populations and hence the usefulness of our remaining data for the conservation of local populations despite the seeming frequency with which *L. agilis* is studied.

As co-author I contributed mostly to the conceptualisation, data collection and review of the final manuscript. I was managing and leading the fieldwork in form of visual encounter studies in the years 2018 and 2019 including instructing LISA M. SCHMITZ who adopted the field work in 2020. The collection of weather data from the DWD and the construction of a categorical habitat map was done by LISA M. SCHMITZ based on previous work done by me, which I introduced to her (see chapters 3 and 4 whose studies were done chronologically earlier). Throughout the study I took on a mentoring role alongside DENNIS RÖDDER for LISA M. SCHMITZ and assisted for questions and revised the first draft of the manuscript and gave input leading to the final manuscript which was submitted.

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.

Keywords. 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 to 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 a species itself (GRINNELL 1917, HUTCHINSON 1957, 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 1983b, 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 the 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, VAN 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 1983b, 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 periphal 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 of 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 – 59m 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 (Figure 2.1). 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 survesy see Supplementary Material, Figure S2.1). 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 duration (hours), and precipitation duration (minutes), 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 a random samples.

Field data was 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 in borders of transects and numbers of random points were necessary.

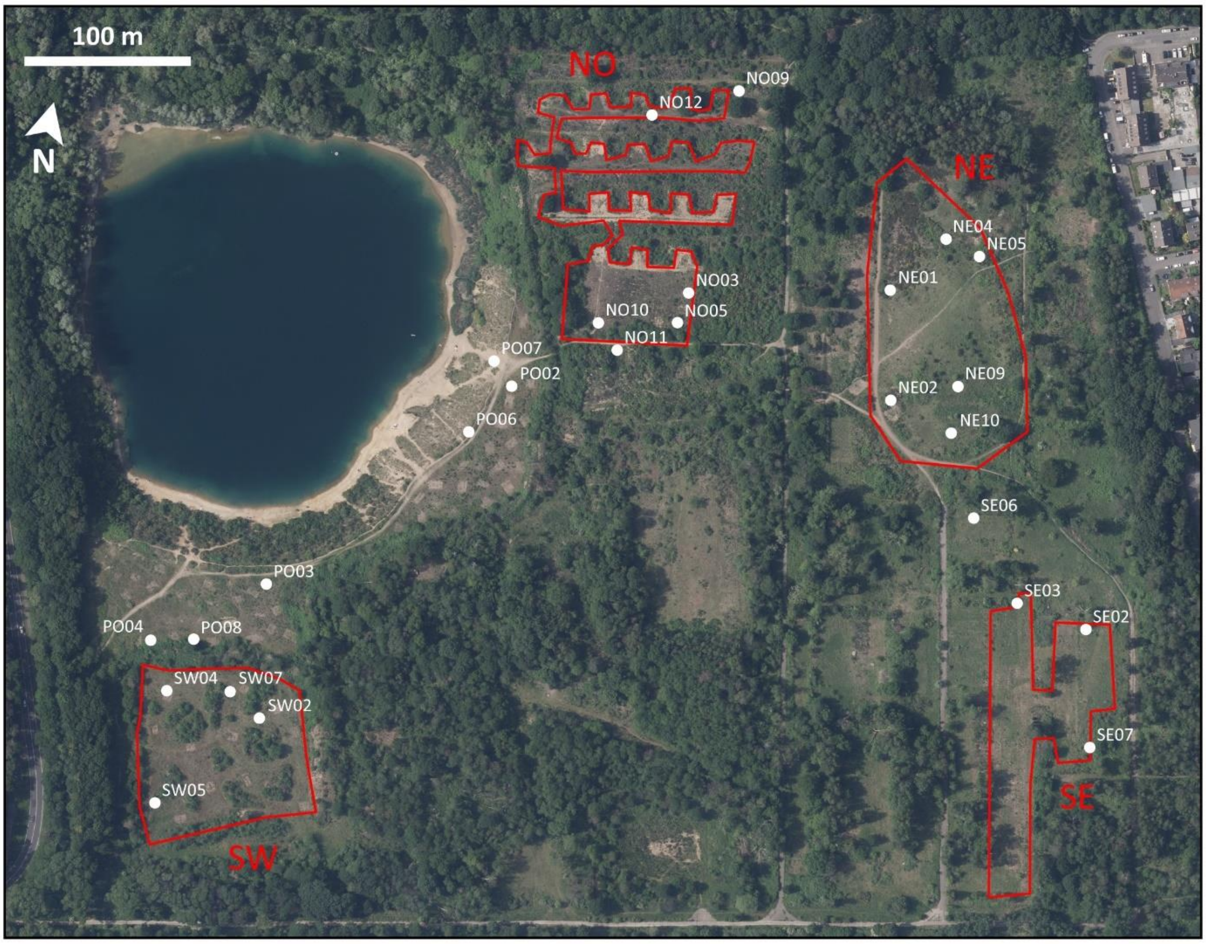

Figure 2.1: Aerial imagery of the study area Dellbrücker Heide. Red lines indicate transect locations. Red abbreviations serve as identification of the different transects after compass directions. White dots indicate random point locations with abbreviations as individual identifier of each point.

All transects and random points were visited equally alternating at different time intervals, at least once in the morning from approximately 9:00 h to 12:00 h, at midday from approximately 12:00 h 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 was 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 Material, Table S2.1), cloud cover in three categories 0 = 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 the brightness of light at the sampling spot (categorized as sunny [spot fully exposed to the sun], half-shaded [shaded with insolated or sunny with shaded patches] or shaded). Microhabitat structure data were assessed within a 5-m radius, including the vegetation and the 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 minutes), solar irradiance (in joule), hours of sunshine (in hours), 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 Material, Table S2.2, 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 them 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. 2017a; for details, see below), as well as the geographic information system QGIS version 3.14.16 (QGIS DEVELOPMENT TEAM 2020), and the statistics program R version 4.0.5 (R CORE TEAM 2020). 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. 2017a, WALDEN-SCHREINER et al. 2017, XU et al. 2019). In a next step, using R (R CORE TEAM 2020), 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 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 x 50 cm per pixel using the nearest neighbour approach with the function resample() from the raster package (HIJMANS 2020a). Based on the land cover mosaic map, distance maps quantifying the distance of every grid cell to all seven habitat categories were created (HIJMANS 2020a).

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 minutes), solar irradiance (in joule), hours of sunshine, 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 thebrightness of light the encounter spot (sun =1, half-shade = 2, shade = 3). Microhabitat structure contains eight variables, slopeing in the microhabitat (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 higher than 500 cm above ground (present = 1, not present = 0), substrate type (sand, gravel, soil and combinations) and the type of location (substrate =1, grass = 2, litter = 3, wood = 4, moss = 5, heath = 6, blackberry = 7, or shrub = 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, 2020). 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 2020), 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 dial 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 defininės 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 which 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 2020) 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 2.1) 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.

Table 2.1. Results of habitat classification calculated with Maxent.

class	**training samples**	**averaged AUC_{Test} ± sd**	**threshold**	**band 1 contri-bution**	**band 2 contri-bution**	**band 3 contri-bution**
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
shrub	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

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 (Figure 2.2). 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 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 (Figure 2.2).

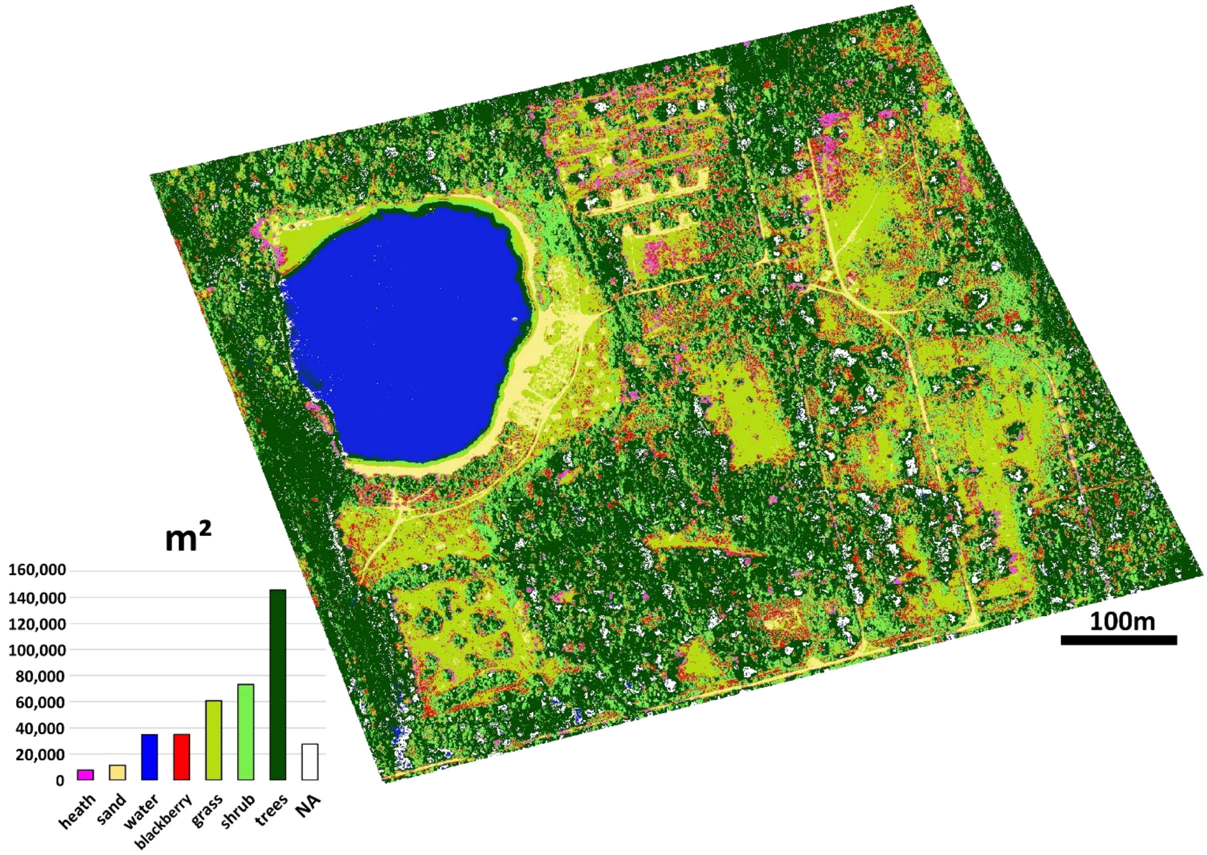

Figure 2.2: Land cover mosaic map depicting the seven habitat categories and the area covered by each in square meters (m^2) with a resolution of one pixel corresponding to 50 x 50 cm area.

Principal component analysis (PCA), generalized linear models (GLMs) and density estimations

The PCA based on weather conditions produced six PCs with eigenvalues > 1 (Table 2.2). The PCA based on distances to habitat features produced five PCs with eigenvalues > 1

(Table 2.3). The distances to water as represented by a large lake was neglected because it had a very coarse gradient and was not directly present in 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 2.4), and the PCA based on microhabitat structures produced three PCs with eigenvalues > 1 (Table 2.5).

Table 2.2: Summary of the Principal Component Analysis 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
global radiation (joule)	0.96	-0.27	-0.04	0.01	0.01	0.00
duration of sunshine (hours)	0.83	-0.08	-0.01	-0.15	-0.06	0.01
duration of precipitation (minutes)	-0.37	-0.05	-0.12	0.33	-0.03	-0.86
precipitation height (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 2.3: Summary of the Principal Component Analysis 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 shrub	-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 2.4: Summary of the Principal Component Analysis of microclimate, showing factor loadings for each predictor, eigenvalues, explained variance, and the cumulative sums of the explained variance. “ifr” = measured with an infrared thermometer.

variable	PC1	PC2
clouds	0.48	0.58
temperature of substrate (ifr)	-0.79	0.00
temperature of the air	-0.71	0.51
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 2.5: 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
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
found location	-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

GLMs for some of the combinations produced significant p-values ($p < 0.05$) (Supplementary Material, Table S2.3 and Table S2.4), but when repeating the models with the significant terms R^2 values were always lower than 0.07 (Supplementary Material, Tables S2.5 and S2.6), 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 (Figure 2.3). 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 ($p < 0.001$) (Figure 2.3).

As for microclimate, the density plot of PC1 shows slight differences between the time groups morning and midday and midday and afternoon respectively (Figure 2.3). 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 (Figure 2.3), proving that densities at midday differ from those in the morning and in the afternoon.

For microhabitat structure, we only found differences depending on the time interval for PC2 showing a lower density in the morning, and in midday and afternoon the density is slightly higher (Figure 2.3). Microhabitat structure PC2 mainly contains 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; Figure 2.3). Pairwise permutation tests of all other PCs were not significant.

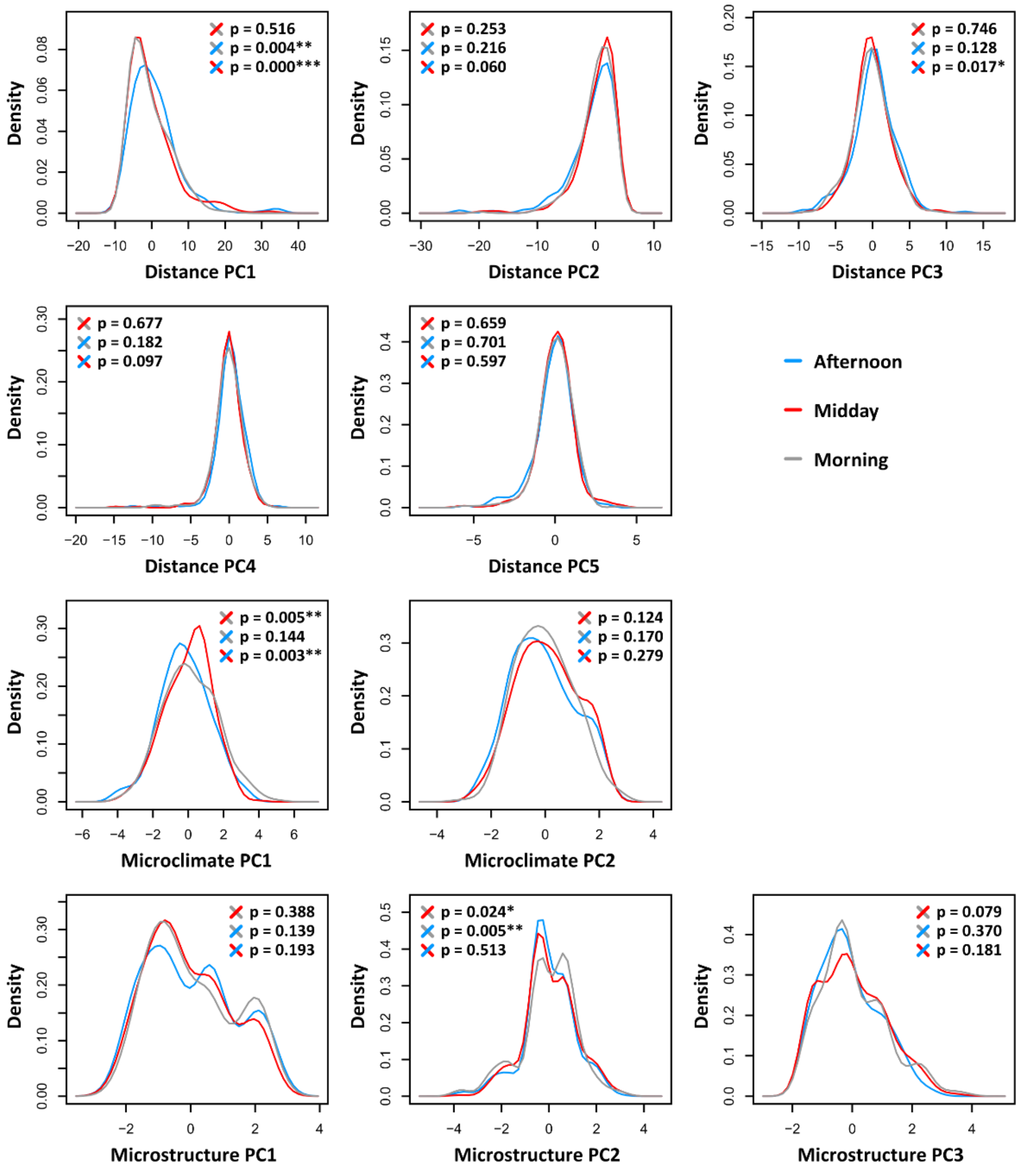

Figure 2.3: Density estimation plots for microclimate, distance, and microhabitat structure after time interval (morning/midday/afternoon), with p-values of pairwise permutation test of equality. * p < 0.05, ** p < 0.01 and *** p < 0.005.

Hypervolumes and density estimation

The overlap statistics of the hypervolumes (HVs) for pairwise comparisons of females, males and subadults are provided in Table 2.6. For distances, both similarity indices of all pairwise comparisons are 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, showing 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%).

Table 2.6: 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

Density estimation plots for the sexes reveal an extremely high density of data points in a very small range especially for distance, which do not differ between specific sexes (Figure 2.4). 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 irridiance and hours of sunshine and minimum temperature 5 cm above the ground (Table 2.2). 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 meinly minimum and maximum wind speeds (Table 2.2), the density plot shows small differences between sex classes (Figure 2.4). 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 the total variance of the weather variables the significant p-values were neglected.

For microclimate PC1 mainly including the variable light condition at spot and microclimate PC2 mainly containing light condition at the finding spot, cloudiness, and temperature of the air, density estimation plots show that females have a lower density then males and subadults (Figure 2.4). Permutation tests for microclimate do not show 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 (Figure 2.4). 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.

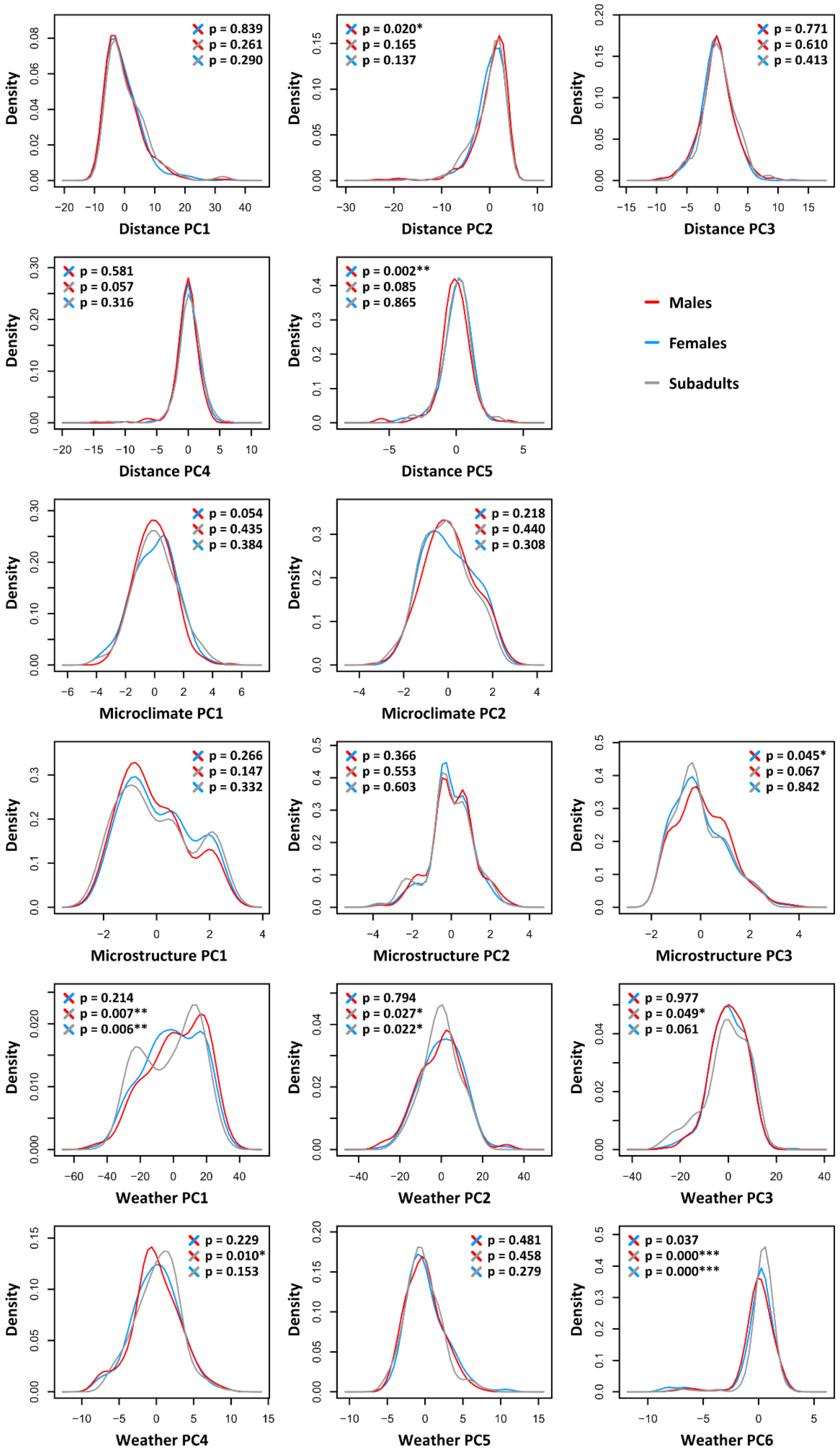

Figure 2.4: Density estimation plots for weather, microclimate, distance, and microhabitat structure per sex group with p-values of pairwise permutation test of equality. * p < 0.05, ** p < 0.01 and *** p < 0.005.

Density estimation plots for the weather conditions on the sampling days (Figure 2.5) illustrate that a broad range of different values are represented for every weather variable. Permutation tests between sampling days and non-sampling days reflect this in the shape of significant differences for all weather variables (maximum temperature $p < 0.001$, relative humidity $p < 0.001$, mean wind speed = 0.03, sunshine duration $p < 0.001$, precipitation duration $p = 0.000$).

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.

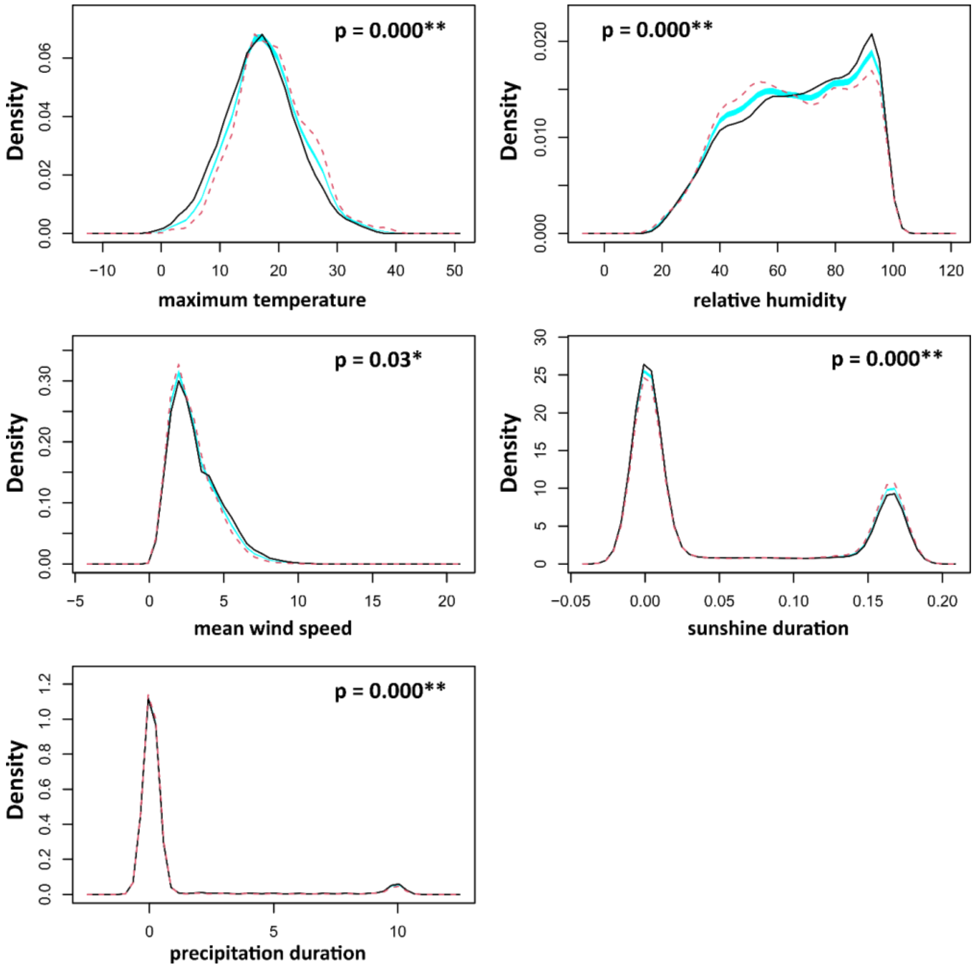

Figure 2.5: Density estimation plots for maximum temperature (°C), relative humidity (%), mean wind speed (m/s), sunshine duration (hours), and precipitation duration (minutes) (measured for every ten minutes), compared for all sampling days with p-values of permutation test of equality. * $p < 0.05$ and ** $p < 0.01$. Black lines indicate sampling days, red, dotted lines indicate non-sampling days and blue lines indicate confidence intervals.

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 1983b, AMAT et al. 2003, NEMES et al. 2006, CEIRÂNS 2007, GROZDANOV 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 proven 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 on 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 Material, Figure S2.1) 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 hroups (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. 1979, 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 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 extend the habitats occupied also by adult males and femalest, which is not surprising due to them being young males and females, but they also partly use other habitats to a smaller extent. This deviation could possibly be due to possible 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 amall 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 and 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 in after hibernation in early spring and continues until July (Glandt & Bischoff 1988, Blanke & Fearnley 2015). Female home ranges are cited as often much smaller 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 pattern can be expected as mate guarding and home range defence is well known from the males of this species (Olsson 1993, Olsson 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 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 columes 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 yet 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 the its distributional range, from which differences were reported to be very pronounced and influenced by various habitat characteristics (JACKSON 1978, HOUSE & SPELLERBERG 1983b, 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 srage, 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 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 a 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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Chapter 3

Weather-related detection probability of *Lacerta agilis* LINNAEUS, 1758 within the core range in western Germany.

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Preface summary and author contributions

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All authors consented to the inclusion of this publication into this doctoral thesis. As copyright holder, the journal was asked to allow the inclusion as well to which they consented.

As preface, I first give a summary of the publication's background, contents, results, and conclusions and highlight my contributions to the work that went into this publication. The original publication can be found in the appendix under the name Publication_S3. Please note that numbers of figures and tables were changed from the original publication to fit the structure of the thesis. Additionally, spelling mistakes that slipped through proof-reading in the publication may have been corrected.

Weather conditions play an important role in the day-to-day life of animals. Weather can influence animal behaviour and activity either directly or by dictating the availability of certain resources. Ectothermic animals are especially influenced by weather conditions as their body temperature and physiology are more dependent on external factors than endothermic animals. The sand lizard (*Lacerta agilis* LINNAEUS, 1758) is often the subject of environmental impact assessments and compensation measures due to it favouring human altered landscape structures. As such undertakings are often time and cost sensitive, it is important to know when to expect the lizards to be most active. As discussed in the previous chapter, the extensive investigation of *L. agilis* at the edges of its distribution do not necessarily apply to all local populations. This is also true for weather preferences of *L. agilis*. In this study, we use encounter rate as an estimation of activity and identify the weather conditions that best explain the observed encounter rates collected over 238 sampling intervals over 156 days of fieldwork. We do this by using a Bayesian model framework to identify the weather variables, that best explain the observed encounter rate out of 86 weather variables including variables describing the conditions 3/6/12/24 hours before the sampling interval. We identified maximum temperature 6 hours prior to sampling, mean wind speed during sampling, precipitation duration 24 hours before sampling, relative humidity during sampling and sunshine duration 3 hours before sampling as the best explaining variables. Maximum temperature had a squared relationship with detection probability that peaked around 20°C while mean wind speed and relative humidity had a negative linear relationship with detection probability and precipitation duration and sunshine duration had a positive linear relationship with detection probability. Bayesian model frameworks are a great way to identify best explaining variables but struggle to display in a simple and easy to understand manner the relationship between said variables. This is, however, where regression tree models come in. We used regression tree models with the best explaining variables to display an unpruned tree highlighting which detection probabilities have been found at which combination of conditions. The tree showed results in accordance with the Bayesian model framework. The methods shown in this study allow conservationists to use pre-existing weather and encounter data and deduce the optimal weather conditions in an easy-to-read decision tree. We think this method and results will be helpful in the conservation and long-term monitoring of not just *L. agilis* but also other small sized ectotherms.

In this chapter I, as author, contributed on all parts. I conceptualised the idea together with DENNIS RÖDDER and we both worked closely together with JULIA EDANACKAPARAMPIL on developing the methods. DENNIS RÖDDER concentrated his main efforts on the Bayesian model framework while JULIA EDANACKAPARAMPIL and I worked on preparing the weather data and on the regression tree model. Both sides gave regular input into each other's work and developed the final methods together. Field work was led by myself with RIEKE SCHLUCKEBIER, LISA M.SCHMITZ and JULIA EDANACKAPARAMPIL joining in at different times for the first two years while the fieldwork in 2020 was led and conducted by LISA M. SCHMITZ. I wrote the first draft of the work and with input from all other authors finalized the work for publication.

Abstract

Weather conditions are important factors determining the activity, and consequently detection probability, of animals. Especially in ectotherms from temperate habitats, activity can vary strongly depending on weather. The sand lizard *Lacerta agilis* is a wide-ranging lizard that is often subject to environmental impact assessments due to its proximity to humans and prevalence as a candidate for compensatory measures according to the Flora and Fauna Habitat Directive of the European Union. *Lacerta agilis* has been studied extensively at certain edges of its distribution, but studies focusing on the core range have been rare. We use Bayesian models in order to identify the best explaining weather variables out of a large variety of available variables for a population of *Lacerta agilis* in western Germany. We furthermore depict their interactions with an easy-to-understand regression tree model. Sand lizards have shown to be more active during dry conditions with low windspeeds. They further are best found after sunny weather with temperatures around 20°C. Rainfall in the previous 24 hours also increases the detection probability. An unpruned regression tree reaffirms the results while giving concrete variable values and exploring how the values influence each other. Overall, the method delivers a decision tree based on easy to obtain weather variables that allows for post- survey analysis and for determination of the best survey conditions.

Keywords. Bayesian model, Lacertidae, CART model, activity pattern, thermal ecology, European lizard

Introduction

Weather conditions play an important role on every ecological scale. The effects of climate change and global warming have been shown to affect ecological communities on large scales (e.g., GILMAN et al. 2010, KORDAS et al. 2011), while local weather fluctuations can, for example, affect ecology and phenotype of individuals (e.g., VANNINI et al. 2021, WINTER & SHIELDS 2021). The influence of weather conditions on animal populations and communities is an important subject in the study of ecology and the practice of conservation as weather conditions can influence population dynamics in numerous ways. Weather conditions can influence the phenotype of individuals in a population. Western diamond back rattlesnakes (*Crotalus atrox*) in Arizona have been shown to become larger in colder, wetter environments than in dry and hot environments, presumably because hotter weather limits foraging time for the animals (AMARELLO et al. 2010). Similarly, weather can influence prey availability as has been shown for frog eating keelbacks (*Tropidonophis mairii*), which have more reproductive success in hot and wet years, when frogs are more abundant (BROWN & SHINE 2002, BROWN & SHINE 2007). It has also been shown that weather conditions can directly influence movement patterns of lizards like western green lizards (*Lacerta bilineata*) (SOUND & VEITH 2000) and Cuban brown anole (*Anolis sagrei*) (LOPEZ-DARIAS et al. 2012) as well as influence fecundity and survival rate (ADOLPH & PORTER 1993). So especially for ectothermic species, day to day weather plays an important role.

Consequently, weather conditions also have a strong influence on encounter rates during any type of field study involving ectotherms (e.g., ADOLPH & PORTER 1993, BROWN & SHINE 2002, SPENCE-BAILEY et al. 2010). Be it general ecological field work or targeted environmental impact assessments made in advance of a large developmental project, many fieldwork studies on animals require visual encounter surveys or procedures otherwise dependent on the animal activity at the time of field work. For example, according to §16 of the UVPG (Gesetz für die Umweltverträglichkeitsprüfung/Law for the environmental impact assessment) of the Federal Republic of Germany, part of an environmental impact assessment is the inventory and assessment of concerned species. It is therefore important to consider detection probability at the time of the surveys to correctly estimate population size. Furthermore, knowing detection probability within a population in advance can help schedule surveys on days at which conditions suggest detection probability is highest and thus maximize sample size. Existing literature on activity periods and detection probability of a species cannot be expected to accurately predict the phenology of particular populations. Phenology, and therefore detection probability, are likely to differ among populations especially in wide ranged species (KÜHNELT 1965). For those species, unless a study has been conducted specifically in the target area, previously reported activity patterns give no more than a rough idea at best.

Lacerta agilis LINNAEUS, 1758 is one of such widespread ectothermic species occurring in vast parts of the Palaearctic (EDGAR & BIRD 2006). It is listed as “Least Concern” internationally in the IUCN red list but is locally threatened especially in its north-western range (IUCN 2020). As a synanthropic species, this mid-sized member of the Lacertidae often lives near humans as it benefits from the open, bushy habitats humans create (HOUSE & SPELLERBERG 1983b, DENT & SPELLERBERG 1987, BISCHOFF 1988, NEMES et al. 2006). However due to its proximity to humans it is also often victim of developmental expansion and therefore subject to environmental impact assessments and subsequent compensatory measures after Appendix IV of the FFH Guidelines of the Natura2000 Project (RÖDDER et al. 2016). It is therefore a likely candidate to be subject to numerous visual encounter surveys in a variety of drastically different areas.

Even though activity patterns of *Lacerta agilis* have been studied in the past, many of those studies focus on the edges of their distribution, where *Lacerta agilis* is restricted to montane areas (AMAT et al. 2003) or sand dunes (HOUSE et al. 1979, HOUSE & SPELLERBERG 1983b, DENT & SPELLERBERG 1987, EDGAR & BIRD 2006), providing little insight into its ecological potency within the core range. For the closely related *Lacerta viridis*, it has already been shown that populations at the core and periphery of its distribution range differ in their realized niches (PRIETO-RAMIREZ et al. 2018).

To summarize known weather preferences, *Lacerta agilis* within the mountainous habitats in the Pyrenees favour air temperatures between 17°C and 20°C (AMAT et al. 2003), while an activity peak at 31°C-32°C has been reported for populations in Hungary near Budapest albeit here, temperatures 5 cm above ground level were measured (HELTAI et al. 2015). In Latvia, warm and dry habitat has been reported as the most important factor (ČEIRÂNS 2006) as well. Sand lizards in lower Saxony, Germany, have been reported to be most active around 20°C (BLANKE 1999). Sand lizards in a South-West Siberian coniferous forest are mainly dependent on low humidity and sunshine, while temperature only plays a role if it fluctuates strongly (KURANOVA et al. 2003). However, populations from southern England are by far the most extensively studied. Here, it was reported that temperatures have to reach 18°C before sand lizards come out and start basking (HOUSE et al. 1979, EDGAR & BIRD 2006, FEARNLEY 2009). At 23°C, basking is greatly reduced and lizards tend to retreat into burrows (HOUSE et al. 1979, EDGAR & BIRD 2006, FEARNLEY 2009) and *Lacerta agilis* retreat into their burrows at night at 19°C (HOUSE et al. 1979). Sand lizards have a bimodal activity pattern, hiding during the hot hours at noon but they can switch to a unimodal pattern on colder days (HOUSE et al. 1979). Sand lizards are generally more thermophilic than sympatrically occurring lacertids like *Zootaca vivipara*, *Anguis fragilis* or *Podarcis muralis* (HOUSE et al. 1979, LITVINOV & GANSHCHUK 2003, HELTAI et al. 2015). Furthermore, sand lizards have been shown on multiple occasions to be heliothermic (FEARNLEY 2009) and usually bask either by radiation alone, or by radiation and convection (SAINT GIRONS 1976). To that end, *Lacerta agilis* usually bask in full sunlight, sheltered from the wind (EDGAR & BIRD 2006), and favour high heat capacity spots for basking (HOUSE et al. 1979). Furthermore, activity declines when conditions are overcast or raining (HOUSE et al. 1979).

FEARNLEY (2009) suggests that there are shifts in weather variable importance before, during, and after breeding season. Over time, temperature, sunshine intensity and duration and humidity seem to play a role for sand lizards (FEARNLEY 2009) which are the variables, we see reoccurring in other studies.

In this study, we assess weather dependent detection probabilities that identify key weather contributors. These can be used before a study to maximize encounter rates as well as after or during a study to set encounter rates into context. We combine visual encounter surveys with the weather data of a nearby weather station to identify weather components influencing the activity pattern of a population of *Lacerta agilis* in the Dellbrücker Heide in Northeast Cologne, Germany. We use a Bayesian model framework to identify the influence of the most important weather variables. Knowing the best explaining terms, we also compute a CART model, a decision tree that can be used to determine the best overall weather conditions for high encounter rates. CART models use these explanatory variables to split data into more homogenous groups (DE'ATH & FABRICIUS 2000). In this case, the CART model groups subsets of similar encounter rates, based on weather variables. Based on what is known on weather dependent activity patterns of sand lizards elsewhere, we expect that important factors will be temperature, sunshine duration and intensity, humidity and rainfall. We expect that ideal temperatures to be similar to other parts of Europe between 17°C and 23°C and we expect detection probability to be highest when sunshine duration and intensity are strongest, and conditions are dry.

Materials and methods

Data collection

Data on the activity of *L. agilis* was collected in the Dellbrücker Heide, a heathland nature reserve in northeast Cologne (approximate corners in WGS 84: NW: 50.9836°N, 7.0514°E; NE: 50.9848°N, 7.0611°E; SE: 50.9808°N, 7.0646°E; SW: 50.9788°N, 7.0541°E). Data was collected from the 02.05.2018 to the 26.09.2018, from the 14.04.2019 to the 03.09.2019, and from the 07.06.2020 to the 11.09.2020. The same population was studied in two further papers which characterize the population (CLEMENT et al. 2022, SCHMITZ et al. 2022). The area was split into three parts of roughly equal size (Figure 3.1A). We randomly generated 100 points in ArcMap 10.6 (ESRI 2018) and went to the field to check them for accessibility, and potential suitability for *L. agilis*. We chose 10 points in each third that were accessible and suitable for sand lizards (Figure 3.1A). One random point became inaccessible in the central area as the area was fenced off as a pasture for goats and sheep. Afterwards, it was

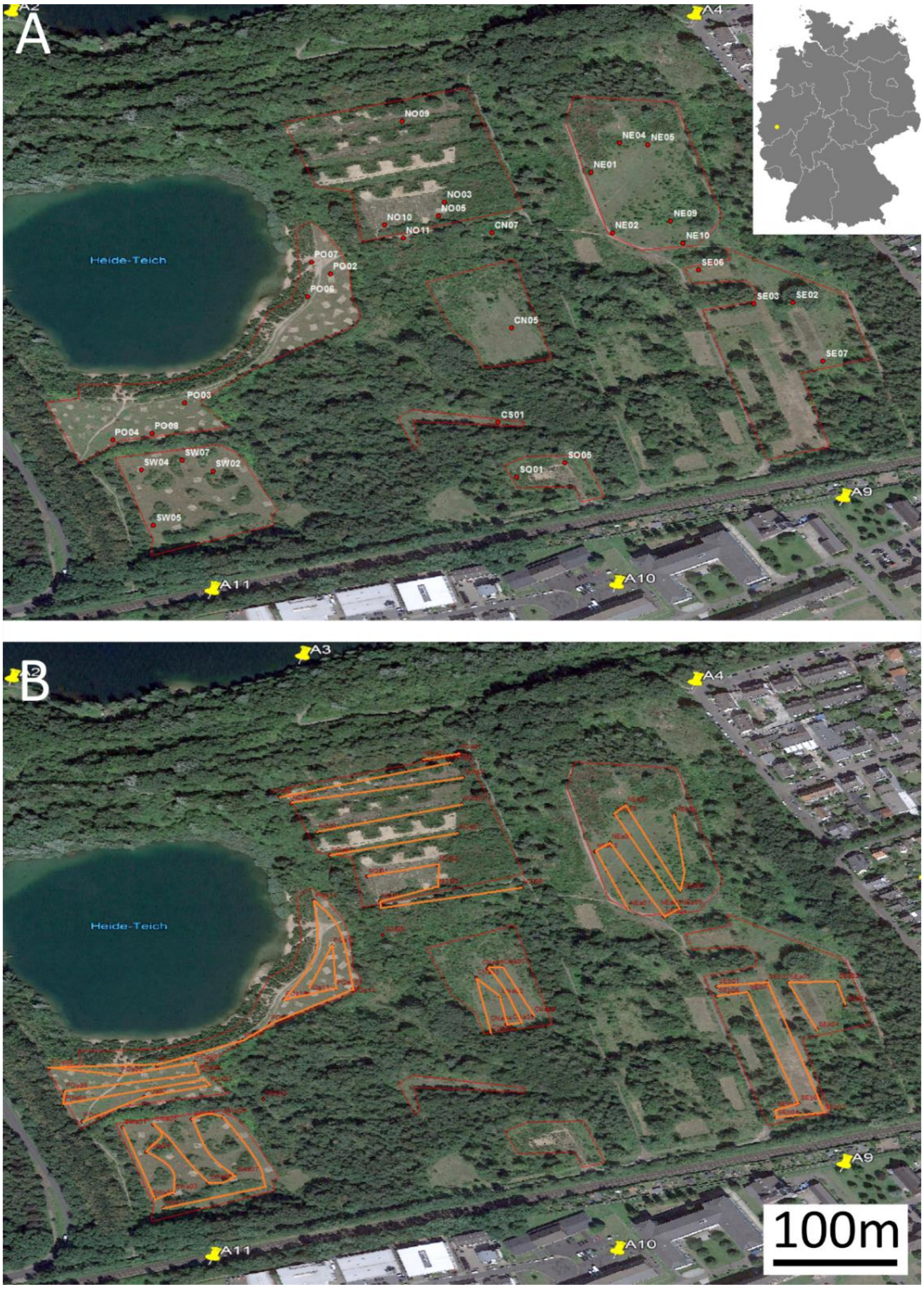

Figure 3.1: Study area in the Dellbrücker Heide with marked sampling points (A) and transects (B). Yellow pins were used to georeference the footage. Satellite photo taken with Google Earth. Top right shows the location within Germany. Map provided by https://simplemaps.com

largely stripped of the needed vegetation and hence discarded. Within each week, each area was visited once, and lizards were registered around every point in a 10m – 20m radius depending on vegetation density. One to two people spent around 15 minutes at a point. Areas were visited either in the morning (09:00 – 12:00), during midday (12:00 – 15:00), or in the afternoon (15:00 – 18:00). Within the framework of another study (SCHMITZ et al. 2022), lizards were registered along transects 65 times as well to assess distribution across the area (Figure 3.1B). Time to traverse the transects was taken and paused whenever a lizard was located. On average, one transect took 20-30 minutes to complete without the stopping. Once a lizard was detected, date and time were noted as well as the time interval for the sampling interval (morning, midday, or afternoon). GPS Coordinates were recorded with the "My GPS Coordinates" app by GPS Tools. Relocations on the same day were avoided by keeping an eye on lizards recorded in close proximity and making special notice of striking features or particular back patterns. If there was uncertainty about a lizard already being recorded on that day, it was not recorded to avoid pseudorecplications. Usually, sampling was not initiated on rainy days but was continued if it started to rain during sampling. Each encounter was assigned with a unique ID. Overall, we recorded 1115 encounters (679 on random points and 436 on transects) over a course of 205 days.

Weather data for the time period was acquired from the Deutscher Wetterdienst (DWD). We used weather data recorded by the weather station "Köln-Bonn" (ID2667), which is situated at 50°51'N and 7°09'E and is hence the closest weather station to the study area only being about 16km away. Table 3.1 shows a description of used weather variables as well as their respective units. Weather data was recorded every 10 minutes and all variables can be found in the electronic supplement (Table S3.1).

Table 3.1: Explanation of weather variables used with units.

Variable Name	**Description**	**Unit**
max_temp	Highest temperature recorded at 1m above ground within the last 10 minutes	°C
min_temp	Lowest temperature recorded at 1m above ground within the last 10 minutes	°C
min_temp_5cm	Lowest temperature recorded at 5cm above ground within the last 10 minutes	°C
air_press	Mean air pressure recorded at 1m above ground within the last 10 minutes	hPa
air_temp	Air temperature recorded at 1m above ground at that moment	°C
air_temp_5cm	Air temperature recorded at 5cm above ground at that moment	°C
rel_humidity	relative humidity recorded at 2m above ground at that moment	%
Tau_temp	Dew point at that moment	°C
diffuse_radiation	diffuse radiation at that moment	J/cm^2
global_rad	global radiation at that moment	J/cm^2
sunshine_duration	duration during which the sun shone unblocked within the last 10 minutes.	hour
precip_duration	duration during which it rained within the last 10 minutes.	minute
precip_height	Sum of precipitation height of the last 10 minutes.	mm
max_wind_speed	Highest wind speed within the last 10 minutes	m/s
min_wind_speed	lowest wind speed within the last 10 minutes	m/s
mean_max_wind_speed	highest 10-minute average wind speed within the last 10 minutes.	m/s
mean_wind_speed	mean wind speed within the last 10 minutes	m/s

Data processing

We estimated the relationship between temporal and environmental variables and the detection probability of sand lizards in a sampling interval using binomial generalized linear models in a Bayesian framework. The general workflow follows FALASCHI (2021), with the following refinements: As environmental predictors, we used the local weather data obtained from the DWD (Figure 3.2A). As we expect time lags between some of the weather events such as rain or windspeed, we calculated the average of all values during the observation interval and during the three, six, twelve, and twenty-four hours prior to the beginning of the interval, identified by the suffixes _int (for averages during the observation interval), _3h, _6h, _12h, _24h (for averages in the 3/6/12/24 hours prior to the beginning of the observation interval) (Figure 3.2A→B). Hence, the total set of predictors comprised 85 variables as well as the Julian date, which was added as temporal variable to include the possibility, that lizards are influenced by length of day or show seasonal shifts in their activity patterns, which may change over the year (Figure 3.2B). To estimate the distribution of likely coefficients of each term, the original variables were standardized using the bestNormalize function of the bestNormalize package for R (PETERSON & CAVANAUGH 2020, PETERSON 2021), automatically selecting the optimal settings to reduce skewness and to scale the variables to a mean of zero and a standard deviation of one.

As a first step, we analyzed the explanative power of each candidate term separately, by estimating the coefficients (a-d) for each variable (x) of Bayesian model with the following structure (Figure 3.2B→C):

y = intercept + a * x + b * x2 + c * x * julian date + d * x2 * julian date.

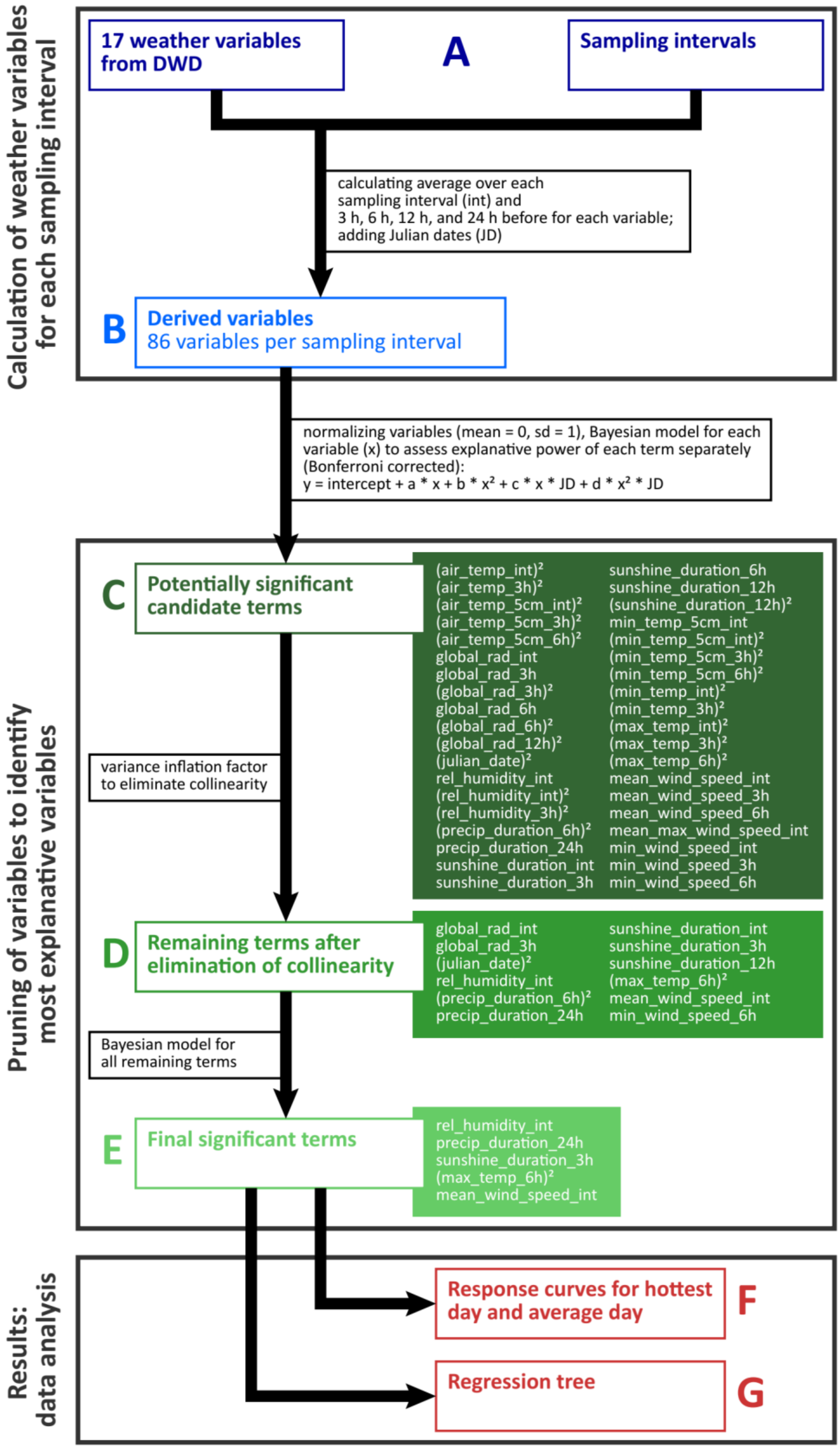

Figure 3.2: Workflow of methods, processing raw weather data into the final most significant terms. First by calculating average weather data for every sampling interval, then pruning the data by eliminating insignificant terms and eliminating collinearity and finally examining the most explanatory terms

The priors of the regression coefficients were set to uniform, ranging from -10 to 10, and three chains were run (each 20,000 interactions, discarding the first 10,000 as burn-in) following (FALASCHI 2021). Convergence was checked visually and by assessing Rhat values (<1.01 for each parameter). Significance of each term per variable was assessed by evaluating the region of practical equivalence (ROPE) and pd (≥ 0.99) parameters and the associated p-values using the bayestestR package (MAKOWSKI et al. 2019), which were corrected for potential alpha-error inflation using a Bonferroni correction ($p < 0.05$). ROPE represents a null hypothesis to test if a parameter is significant, i.e., important enough to be included in the final model. The proportion of the whole posterior distribution that does not lie within the ROPE interval can then be used to assess significance in terms of p-values (MAKOWSKI et al. 2019). The final set of terms comprised 38 potential candidates (Figure 3.2C). To further reduce the number of candidates, we used the variance inflation factor with a cut-off of 10 to select the best suitable subset to compute the final model (Figure 3.2C→D), as we expected some collinearity issues among the temporal subsets of the potential terms. The final set comprised 12 candidate terms (Figure 3.2D), which were used to build a new binomial generalized linear model with the following structure (Figure 3.2E):

y = intercept + a*global_rad_3h + b*global_rad_int + c*mean_wind_speed_int + d*min_wind_speed_6h + e*precip_duration_24h + f*rel_humidity_int + g*sunshine_duration_12h + h*sunshine_duration_3h + i*sunshine_duration_int + j*(julian_date)^2 + k*(max_temp_6h)^2 +l*(precip_duration_6h)^2.

This was analyzed in the same Bayesian framework as explained above, and only significant terms were further analyzed (Figure 3.2E→F and Figure 3.2E→G). All analyses were conducted in R (R CORE TEAM 2020) using adapted scripts provided by FALASCHI (2021) and the package R2jags (SU & YAJIMA 2015). The package bayestestR was used to assess significances (MAKOWSKI et al. 2019). Results were visualized via response curves, plotting detection probability as a function of one variable while keeping all other variables at their averages (Figure 3.2F). Resulting terms were also visualized in a descriptive graph as to represent the weather conditions during the study period (Figure S3.1).

Additionally, using these remaining significant terms, a regression tree was constructed in R using the function rpart from the package rpart (THERNEAU et al. 2019, Figure 3.2G). This allows for an easy-to-follow decision process predicting expected detection probability based on the best explaining variables only. We left trees unpruned to examine activity patterns in relation to the five terms resulted from the Bayesian model (TREILIBS et al. 2016).

Results

Overall, 238 sampling intervals were conducted over 156 days. All sampling points with coordinates as well as time and date of sighting, and the duration of the sampling intervals can be found in the supplementary material (Table S3.2). Furthermore, weather conditions during the sampling intervals can also be found in the supplementary material Figure S3.1.

Weather conditions throughout the months of the sampling intervals are for the most part quite similar. The general trends are similar between the years (Figure S3.1).

Pruning of variables

Pruning of variables revealed 38 candidate terms with significant influence on the number of lizards found during a survey trip after conducting the multiple, Bonferroni corrected Bayesian models for every set of variables. The resulting potentially significant candidate terms are found as a list in Figure 3.2C and details are provided in Table 3.2. Complete results of the Bayesian models can be found in the appendix (Table S3.3, terms with significant influence on number of lizards found are identified by the first column). After calculating the variance inflation factor to eliminate collinearity in the independent variables (Figure 3.2C→D), twelve final variables were left for the refined Bayesian model, which are listed in Figure 3.2D.

Model analysis

Using the 12 variables in combination (Figure 3.2D→E), only five remained significant which had a strong effect on detection probability (Figure 3.2E and Figure 3.3). These terms are the 10 minute averages of relative humidity during the observation interval (rel_humidity_int), precipitation duration within the 24 hours before the observation interval (precip_duration_24h), sunshine duration within the 3 hours before the observation interval (sunshine_duration 3h), the square of the maximum temperature within the 6 hours before the observation interval [$(\text{max\_temp\_6h})^2$], and mean wind speed during the observation interval (mean_wind_speed_int). The final formula for the model equation is:

$y = -2.902 - 0.011 * \text{global\_rad\_3h} + 0.054 * \text{global\_rad\_int} - 0.140 * \text{mean\_wind\_speed\_int} + 0.012 * \text{min\_wind\_speed\_6h} + 0.269 * \text{precip\_duration\_24h} - 0.135 * \text{rel\_humidity\_int} + 0.118 * \text{sunshine\_duration\_12h} + 0.263 * \text{sunshine\_duration\_3h} - 0.183 * \text{sunshine\_duration\_int} + 0.031 * (\text{julian\_date})^2 - 0.113 * (\text{max\_temp\_6h})^2 - 0.058 * (\text{precip\_duration\_6h})^2$.

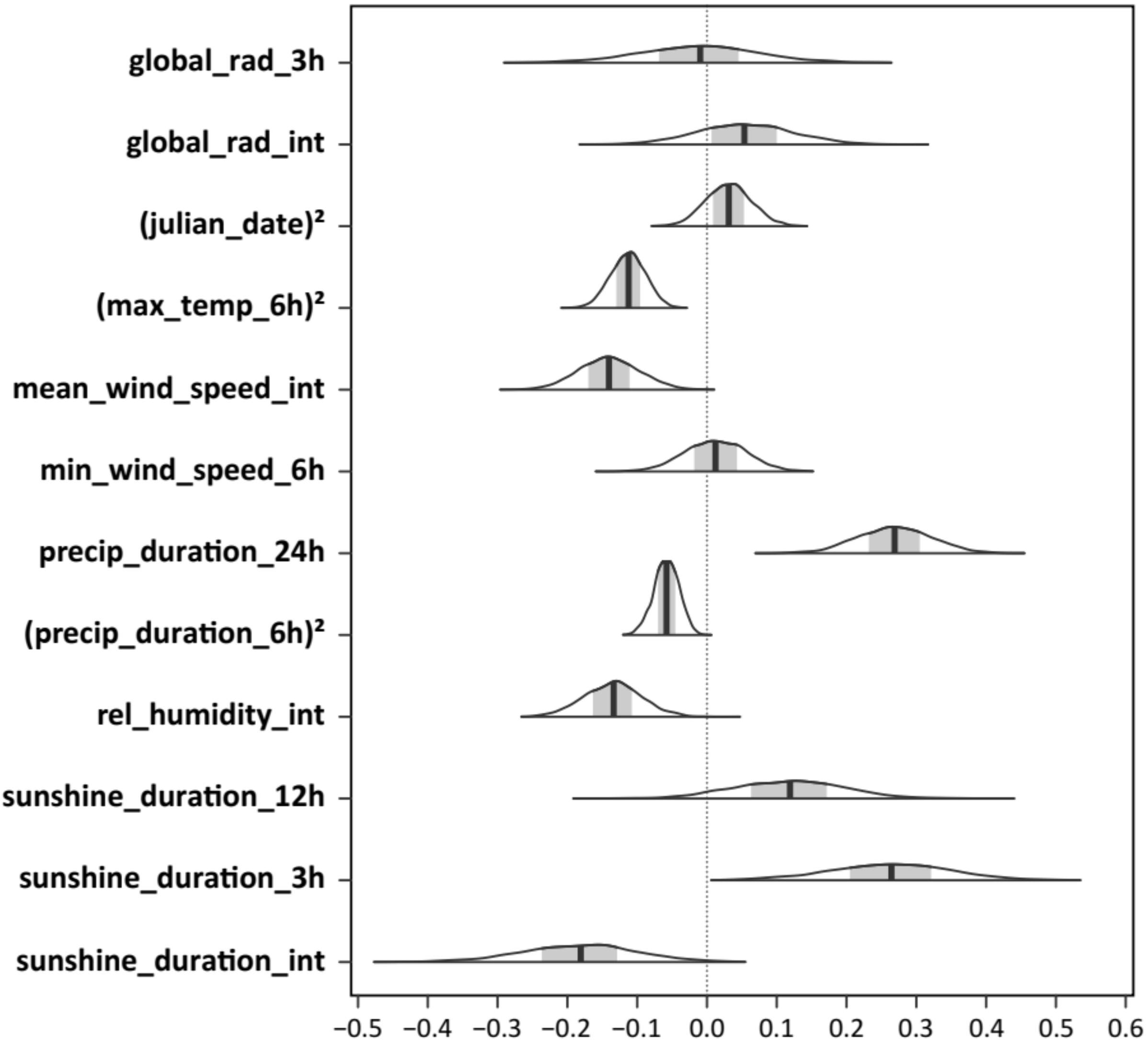

Figure 3.3: Density plots of the posterior distribution for the terms of the final Bayesian Model. Thick vertical lines represent the median estimated effect for each term, shaded areas represent the 80% confidence interval.

The terms that best explain detection probability are (max_temp_6h)^2, mean_wind_speed_int, precip_duration_24h, rel_humidity_int, and sunshine_duration_3h. Average 10-minute maximum temperature in the six hours before sampling (meaning the average of the maximum temperature within 10 minute intervals over the 6 hours prior to sampling) showed a squared relationship with detection probability with the probability being highest at 20°C (Figure 3.4). Mean wind speed and relative humidity during the sampling interval show a negative relationship with detection probability while precipitation duration in the 24 hours preceding the sampling interval and average 10-minute sunshine duration in the 3 hours preceding the sampling interval (meaning the average time the sun shone during 10-minute intervals over the 3 hours prior to sampling) show a positive relationship (Figure 3.4). This suggests that lizards are less likely to be found in humid and windy conditions while rainy weather the day before and sunny weather immediately preceding the collecting period increase the encounter rate.

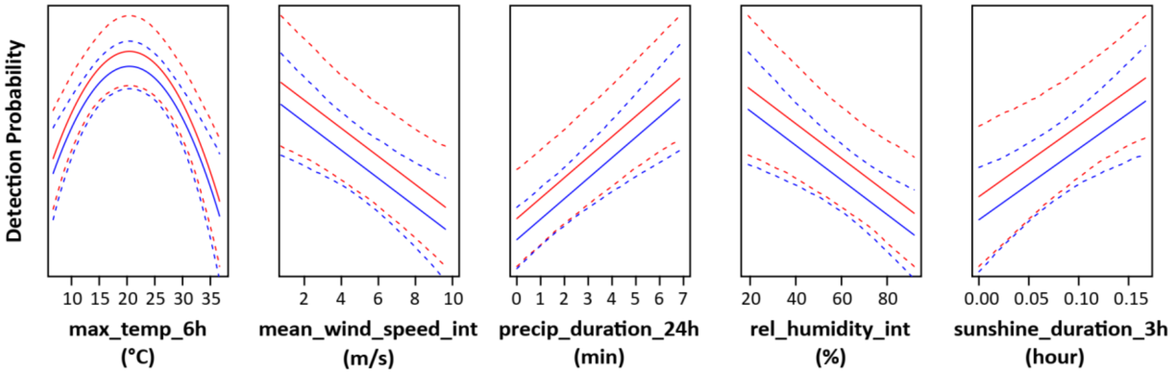

Figure 3.4: Response curves showing the detection probability as a function of one term if all other terms are kept to the average. Dotted lines represent the 95% confidence intervals. Red lines indicate the hottest day (julian day 268) and blue lines for an average temperature day (julian day 183).

Table 3.2. Summary statistics of significant candidate variables and terms obtained from Bayesian modeling. Model status indicates if the respective candidate variable entered the final model (final), while significance in the final model is indicated as bold. For each candidate, the term structure is indicated as linear or quadratic and the probability of direction (pd) and the Bonferroni corrected significance level are provided (p_ROPE_bf).

Variable	Model status	term	estimate	std.error	pd	p_ROPE_bf
global_rad_3h	final	linear	0.46	0.06	1	<0.001
global_rad_int	final	linear	0.30	0.05	1	<0.001
julian_date	final	squared	-7.39	1.83	1	<0.001
max_temp_6h	**final**	squared	-0.28	0.05	1	<0.001
mean_wind_speed_int	**final**	linear	-0.29	0.05	1	<0.001
min_wind_speed_6h	final	linear	-0.30	0.05	1	<0.001
precip_duration_24h	**final**	linear	0.40	0.08	1	<0.001
precip_duration_6h	final	squared	-0.39	0.08	1	<0.001
rel_humidity_int	**final**	linear	-0.52	0.06	1	<0.001
sunshine_duration_12h	final	linear	0.35	0.06	1	<0.001
sunshine_duration_3h	**final**	linear	0.44	0.06	1	<0.001
sunshine_duration_int	final	linear	0.39	0.06	1	<0.001
air_temp_3h	canditate	squared	-0.33	0.06	1	<0.001
air_temp_5cm_3h	canditate	squared	-0.45	0.06	1	<0.001
air_temp_5cm_6h	canditate	squared	-0.41	0.06	1	<0.001
air_temp_5cm_int	canditate	squared	-0.27	0.05	1	<0.001
air_temp_int	canditate	squared	-0.32	0.06	1	<0.001
global_rad_12h	canditate	squared	-0.42	0.06	1	<0.001
global_rad_3h	canditate	squared	-0.37	0.06	1	<0.001
global_rad_6h	canditate	linear	0.35	0.06	1	<0.001
global_rad_6h	canditate	squared	-0.39	0.06	1	<0.001
max_temp_3h	canditate	squared	-0.40	0.06	1	<0.001
max_temp_int	canditate	squared	-0.28	0.05	1	<0.001
mean_max_wind_speed_int	canditate	linear	-0.27	0.05	1	<0.001
mean_wind_speed_3h	canditate	linear	-0.27	0.04	1	<0.001
mean_wind_speed_6h	canditate	linear	-0.27	0.04	1	<0.001
min_temp_3h	canditate	squared	-0.32	0.05	1	<0.001
min_temp_5cm_3h	canditate	squared	-0.49	0.06	1	<0.001
min_temp_5cm_6h	canditate	squared	-0.37	0.06	1	<0.001
min_temp_5cm_int	canditate	linear	0.34	0.07	1	<0.001
min_temp_5cm_int	canditate	squared	-0.24	0.05	1	<0.001
min_temp_int	canditate	squared	-0.28	0.05	1	<0.001
min_wind_speed_3h	canditate	linear	-0.36	0.04	1	<0.001
min_wind_speed_int	canditate	linear	-0.36	0.05	1	<0.001
rel_humidity_3h	canditate	squared	-0.39	0.06	1	<0.001
rel_humidity_int	canditate	squared	-0.44	0.06	1	<0.001
sunshine_duration_12h	canditate	squared	-0.35	0.05	1	<0.001
sunshine_duration_6h	canditate	linear	0.42	0.06	1	<0.001

Regression tree analysis

The regression tree (Figure 3.5) suggests that over the course of the experiment, encounter rate was lowest when relative humidity during the sampling interval was above or equal to 63.7% (Node 2). Contrary, encounter rate was among the highest recorded, albeit with lots of variance, when relative humidity during sampling interval was below 63.7%, mean wind speed during sampling interval was smaller than 2.2 m/s, mean sunshine duration per 10 minutes in the 3 hours before sampling was above 0.086 hours (meaning on average, the sun shone during 5.16 minutes out of 10 minutes during those 3 hours), and mean wind speed was larger or equal to 1.8 m/s (Node 19). Compared to that path in the tree, encounter rate is somewhat reduced when mean wind speed was instead smaller than 1.8 m/s (Node 18), while it was greatly reduced when average sunshine duration in 10 minutes during the 3 hours prior was smaller than 0.086 hours (Node 16). It was still possible to get high encounter rates if mean wind speed was larger than 2.2 m/s as long as relative humidity during the sampling interval remained below 63.7%. For this, 10-minute average maximum temperature during the six hours preceding the sampling interval had to remain below 21.1°C and relative humidity during the sampling interval had to be below 35.5% (Node 14). If the 10-minute average maximum temperature was higher or equal to 21.1°C, encounter rate was low (Node 5). If the 10-minute average maximum temperature remained below 21.1°C but relative humidity was above or equal to 35.5% there were three possibilities depending on sunshine duration. If 10-minute average sunshine duration was below 0.011 hours, encounter rate was low (Node 8) while for a 10-minute average sunshine duration between 0.011 hours and 0.038 hours, encounter rate was higher (Node 13). For a 10-minute average sunshine duration above 0.038 hours, encounter rate was higher, when the average maximum temperature during 10 minutes for the 6 hours prior to the sampling interval was higher or equal to 20.6°C (Node 12) and low when it is below that threshold (Node 11).

As a regression tree partitions data according to the recorded variables, it is important to note, that encounter rate outside the recorded range of these variables, can be inferred but has not been considered by the model. Therefore, an expression like > X for any variable really means a value between X and the largest recorded value for the tree. To identify the values, where the model ends and speculation begins, the range of the variables used for the model have to be considered (Table 3.3) (Complete summary of the regression tree can be found in the supplementary material Text S3.1).

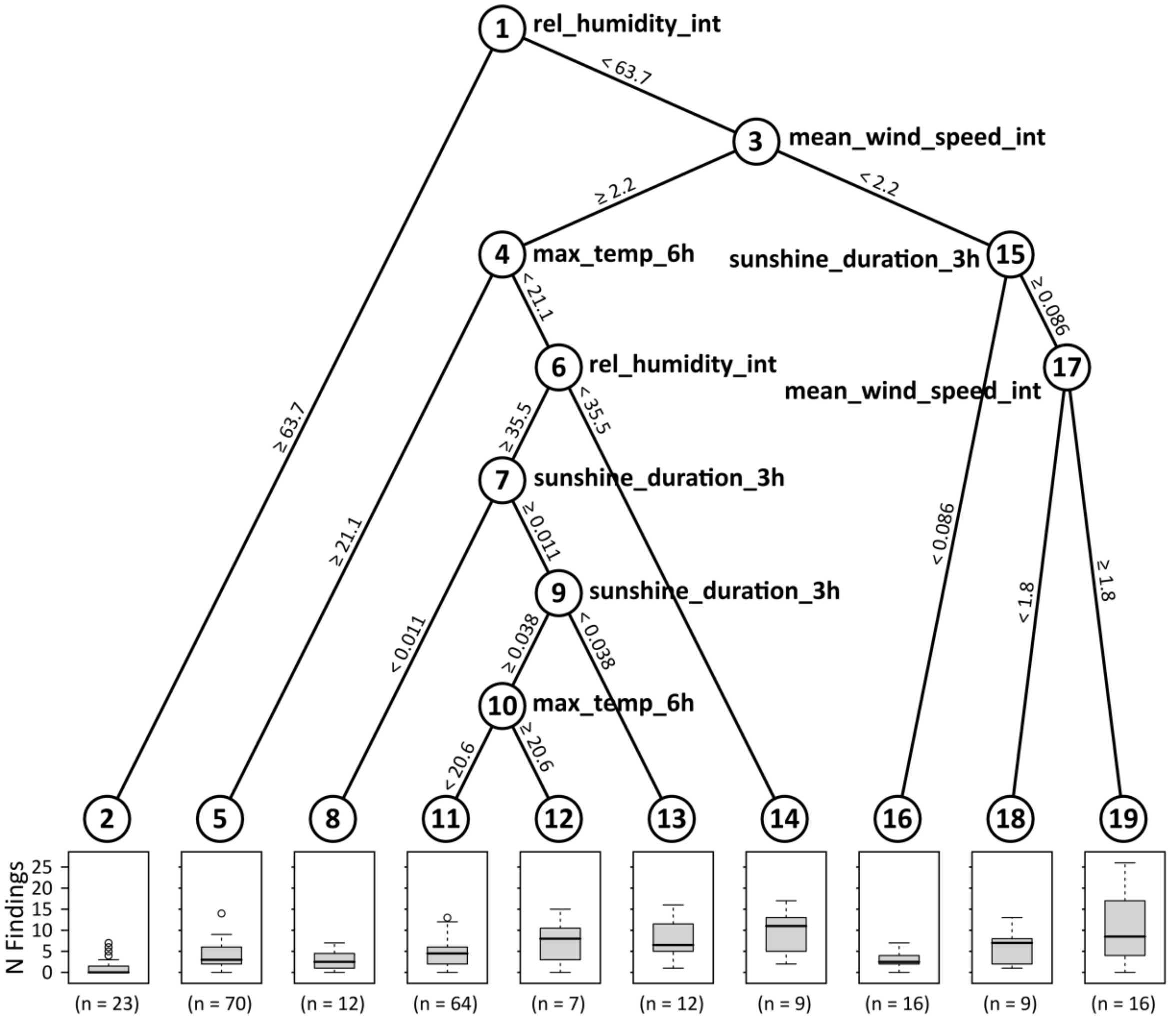

Figure 3.5: Regression tree for encounter rate of *L. agilis*. Data are partitioned by the five weather variables with the highest explanatory effect. Non-terminal nodes are numbered in boxes above the variable names. Terminal nodes are numbered above the boxplots. Terminal nodes are labelled with the number of sampling intervals for the corresponding conditions, and display the distribution of lizard counts in a boxplot. Variables have the same units as shown in figure.

Table 3.3: Ranges of the five terms best explaining the detection probability.

Interval	**maximum**	**minimum**	**unit**
rel_humidity_int	91.9	19.1	%
precip_duration_24h	6.8	0.0	min
sunshine_duration_3h	0.167	0.000	h
max_temp_6h	36.7	6.7	°C
mean_wind_speed_int	9.6	1.1	m/s

Discussion

Interpreting the best explanatory terms

The step by step pruning of variables revealed that the majority of *L. agilis'* detection probability can be explained by five weather variables: average maximum temperature six hours prior to the sampling interval, mean wind speed and relative humidity during the sampling interval, mean precipitation duration in the 24 hours before the sampling interval and sunshine duration in the three hours prior to the sampling interval. Temperature has a squared relationship with detection probability, peaking around 20°C, while wind speed and relative humidity have a negative linear relationship and precipitation duration and sunshine duration have a positive linear relationship with detection probability.

The 10-minute average of max temperature over the six hours before the sampling period shows, that temperatures deviating too much from 20°C in either direction can lead to reduced detection probability and hence, reduced activity in *L. agilis*. *Lacerta agilis* has been shown to avoid temperatures below 17°C while spending prolonged periods of temperatures above 23°C whether active in the shade under dense vegetation or inactive in hiding, leading to decreased detection probability (HOUSE et al. 1979, EDGAR & BIRD 2006, FEARNLEY 2009). Sand lizards consequently have a bimodal activity pattern which can on colder days become unimodial (SAINT GIRONS 1976, HOUSE et al. 1979) sharing this pattern with many other European reptiles (BÖHME 1984, GRIMM et al. 2014, GRIMM et al. 2015). However, we found maximum temperature in the six hours proceeding the sampling interval to be a better indicator than temperature during the sampling interval. We can assume a time lag between temperature fluctuations and lizard behaviour. According to BLANKE (1999), *L. agilis* in lower Saxony, Germany start basking at temperatures near 20°C. While basking, lizards remain largely immobile making them harder to detect explaining the increased detection rate due to higher activity some hours after temperatures reached that point. Lizards in hiding could especially need some time to become active as temperature fluctuations might take some time to reach hiding spots.

The negative linear relationship between detection probability and mean wind speed and humidity during the sampling interval are what is to be expected for a small heliophile lizard (FEARNLEY 2009). Increased humidity is correlated with increased wetness in the environment and is also related to rain probability. A wet environment reduces basking capabilities by convection as evaporation cooling of surfaces and the skin of the lizard occurs. Meanwhile overcast or rainy skies reduce basking capabilities by radiation as clouds block the sun. As sand lizards are known to bask via those two mechanisms, the negative correlation of humidity to detection probability appears to be reasonable. It is possible, that lizards use the opportunity to hydrate but forego prolonged periods of activity due to the aforementioned reasons, making them in turn hard to detect. Sand lizards have been shown on multiple occasions to be mostly active when conditions are dry (HOUSE et al. 1979, KURANOVA et al. 2003, ČEIRÂNS 2006). Lower activity during humid and overcast conditions distinguishes *L. agilis* from the sometimes sympatrically occurring *Zootaca vivipara* which is more tolerant of those conditions (HOUSE et al. 1979, KURANOVA et al. 2003). Wind on the other hand, is rarely mentioned as a contributor to lizard activity in other studies. It has even been cited specifically as avoidable by the lizards (EDGAR & BIRD 2006). However, high wind speed can make life hard for small animals as bushes are rattled, alarming sounds are masked, and air temperature tends to sink. As higher wind speeds increase convective heat transfer (PORTER et al. 1973), the animals cool down faster in windy conditions leading to more time spend basking or hiding. This is especially true in wet conditions due to the aforementioned cooling effects of evaporation. Additionally, fewer insects might be found during higher wind speeds (WILLIAMS 1961). High wind speeds have been shown to be avoided by another lacertid, *Podarcis guadarramae* in spring, autumn and winter (ORTEGA & PÉREZ-MELLADO 2016). There is also a possibility, that lizards are not affected by wind speeds directly but instead, detection capabilities of researchers could be impacted as lizards were best detected by the rustling sound of their movements.

The importance of sunshine duration three hours prior the surveys can be explained by the heliothermic nature of *L. agilis* (AVERY 1979, FEARNLEY 2009). The more the sun shines, the better for thermoregulation, as surfaces heat up, while long periods of shaded conditions could lead to the lizards cooling out faster and taking more breaks to bask and taking longer to heat up (HOUSE et al. 1979). Both ways, sand lizards' basking is directly reliant on sunlight as both basking by radiation and basking by convection need sunlight to heat up the lizard or the surfaces it basks on. Sand lizards have been observed to have shorter activity periods on overcast days, possibly not even emerging at all (HOUSE et al. 1979). As with temperature, there is a time lag between achievement of optimal conditions and increase of detection probability as lizards need time to heat up. The time lag is smaller for sunshine than for temperature, possibly hinting at the importance of sunshine in the activity of the heliophile lizard. *Lacerta agilis* has been shown to be more reliant on sunlight than *Zootoca vivipara* who often occurs in the same areas (HOUSE et al. 1979, KURANOVA et al. 2003).

Finally, the positive relationship of detection probability and precipitation duration 24 hours prior to the sampling interval might seem contradictory to our interpretations of relative humidity thus far but can be explained by lower physiological performance during rainy days. It has been shown that during rain, lizards rarely appear (HOUSE et al. 1979, ČEIRÂNS 2006). So, after the rains stopped, lizards could be inclined to venture out even in conditions they would normally deem sub-optimal to make up for lost time. Increased activity after rainfall in the 24 hours prior has been shown for *Podarcis muralis* by (FALASCHI 2021), who also hypothesised the animals making up for lost time or suggested, that prey insects could be more abundant after rainfall according to WILLIAMS (1951).

Regression tree analysis

Analysis of the regression tree shows that lizard activity is not dependent on a single variable but rather can be dependent on multiple variables. While CART models can deal with a large number of covariates and can therefore stand on their own (TREILIBS et al. 2016), they are helpful in visualising the complex relationship between the best explaining variables resulting from a data-reduction technique.

An overall important factor for detection probability of *Lacerta agilis* is relative humidity remaining below 63% as higher humidity leads to the lowest encounter rate in the study (Figure 6 Node 2). Humidity being a limiting factor for sand lizard activity has been proven in the past as discussed above (HOUSE et al. 1979, KURANOVA et al. 2003). Whenever humidity remained below that threshold, most lizards were encountered on sunny days with very light breezes. Under these conditions, detection probability is highest, but also shows high variance (Node 19). Alternatively, comparatively high encounter rates are also found on more windy days as long as temperature was below 21°C six hours prior to sampling and either very dry during the sampling or at least moderately sunny three hours before. The tree reinforces the results of the Bayesian model that sunny and dry conditions overall increase encounter rates. While encounter rates are best during low wind speeds, it is possible to encounter lots of lizards when wind speeds are higher. This may suggest, that the negative effects of wind might be offset by especially low humidity or sunny weather further reinforcing the importance of dry, sunny weather for sand lizards. Evaporation cooling, which was discussed above as one adverse effect of high wind speeds when combined with humid conditions would not be a problem in dry, sunny weather. As *Lacerta agilis* spends a considerable amount of time basking, dry surfaces heated up by sunlight are important for the animals to finish basking quickly (GLANDT 1979, HOUSE et al. 1979, HEYM et al. 2013). Furthermore, by basking in spots sheltered from the wind, sand lizards can offset high wind speeds while wet or overcast weather is much harder to escape. Temperatures diverging too far from 20-21°C in the six hours prior to the sampling interval led to lower encounter rates again reinforcing the results of the Bayesian model.

In conclusion, the relations from the Bayesian model are reflected overall in the CART model but might diverge in the cases of wind speed and sunshine duration later in the tree when the algorithm was already trained with a subset of the data the Bayesian model used. These subsets might have different relationships towards encounter rate than the original complete set of encounters. The absence of precipitation duration during the preceding 24 hours from the tree suggests, that although the positive effect of rainfall the preceding day has been shown, other variables might have a more immediate effect on lizard activity as discussed above. If lizards are making up for lost time as proposed by FALASCHI (2021), it is possible that rainfall duration in the past 24 hours might be more of an additional encouragement for lizards while other factors could impact the lizard’s performance more directly, for example through basking efficiency. The CART model is not only a comprehensive decision-making tool but it also highlights interactions between the best explaining variables in a way the Bayesian model could not.

Conclusion

Overall, our results suggest that *L. agilis* in the Dellbrücker Heide prefer dry and sunny weather conditions with temperatures around 20°C prior to their activity phase and low wind speeds. Additionally, lizards are even more exposed if it rained a lot in the 24 hours prior. Our hypotheses concerning temperature, sunshine duration and humidity were confirmed although we did not expect windspeed to play a defining role and did not find sunshine intensity among the best explaining variables. Our results are in line with other studies especially in northern and central Europe suggesting weather dependent activity of *Lacerta agilis* is similar. Bayesian models are a great tool to identify the terms that best explain encounter rate but fail to comprehensibly depict the complex relationship of these related weather variables. Regression trees therefore complement the Bayesian model by delivering an easy-to-understand depiction of which relationships lead to which encounter rates. Regression trees of variables that can realistically be predicted by consulting weather forecasts can be a great help in finding optimal conditions for field studies or predict encounter rate within a population. Aside from the post field work analytical aspects, this method can also be an enormous help in studies involving field work, especially if field work opportunities are limited. The combination of methods between the Bayesian model framework and the CART tree are computationally fairly straightforward and rely solely on the number of encounters during fieldwork and the availability of weather data for the corresponding time periods. The method is also not species or habitat specific and works with any visual encounter survey, even post-survey. We therefore think it is of great value in conservation, monitoring, and wildlife management. While the big disadvantage to the method is, that it needs a rather large sample size, it can be helpful for populations that are regularly checked on or studied over a long period of time for example in the context of long-term monitoring projects.

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Chapter 4

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

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This illustration was made by MANUEL SCHUMACHER and commissioned by the author of this thesis. The artist consented to the inclusion and publication of the illustration.

Preface summary and author contributions

This chapter has been published in the journal Salamandra s:

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All authors consented to the inclusion of this publication into this doctoral thesis. As copyright holder, the journal was asked to allow the inclusion as well to which they consented.

As preface, I first give a summary of the publication's background, contents, results, and conclusions and highlight my contributions to the work that went into this publication. The original publication can be found in the appendix under the name Publication_S4. Please note that numbers of figures and tables were changed from the original publication to fit the structure of the thesis. Additionally, spelling mistakes that slipped through proof-reading in the publication may have been corrected.

Effective conservation and management of animal populations requires an in depth understanding of animal space use. Many aspects of conservation require knowledge on how animals select their habitat and how they determine their home range. Among them are studies investigating how animals would react to anthropogenic alterations in their environment as well as practical applications like relocations, habitat management or compensation measures. Radio-telemetry and satellite imagery provide a possibility to monitor both an animal's movements and the environment in which said movements take place. However, small animals present challenges to radio-telemetry and satellite imagery in that they require tags small and light enough to not hinder them and require fine scale habitat assessment which is not always possible or affordable with satellite imagery. In this study we use radio-telemetry to determine the home range of a German population of sand lizards (*Lacerta agilis* LINNAEUS, 1758). We were among the first to attach transmitters to lizards of this size and present a new version of a previously successful attachment method, modified for *L. agilis* and lizards of similar size and build. Furthermore, we use an unmanned aerial vehicle (UAV) to record the environment in high resolution. For *L. agilis*, habitat and microhabitat choice happen on the scale of singular bushes or patches of bare soil often only several centimetres across. Our method provided high resolution habitat maps where 1 pixel corresponded to 3.6cm x 3.6cm of ground surface. We used a Maxent algorithm to make every pixel correspond to a habitat category and thus create a categorical habitat map in which we plotted the home ranges received through radio-telemetry. We used old and new approaches to home range calculation as to keep comparability with older studies while also incorporating newer methods. We used JACOBS' electivity index (JACOBS 1974) to determine which habitat categories the lizards preferred, avoided, and used according to availability. We conclude therefore that the blackberry bushes in the area (which remain under 1m height) present desirable structures possibly due to their openness combined with the protection they provide due to their thorns. Lizards might avoid open sand since they only need small areas for basking close to cover and larger areas of open sand risk exposing them to predators. Lizards might also avoid high vegetation as trees and some bushes do not provide much cover from predators but cast a lot of shade making finding basking spots significantly more difficult for no additional value compared to lower vegetation. We furthermore investigated whether the preference/avoidance for certain habitats correlated with each other or with home range size. Our results indicate that sand lizards in this central population favour including blackberry bushes into their home range while avoiding high vegetation and sand and use grass and low vegetation according to individual preferences. JACOBS' electivity indices were not correlated but certain home range sizes were positively correlated with a preference for high vegetation, sand, and grass indicating that those lesser favoured habitat structures might constitute lesser used areas that are only incorporated into the home range as travelling routes. This study provides good insights into the home range and habitat selection of *L. agilis* in the Dellbrücker Heide and presents methods useful for conservation as they can be done within a short time frame and provide more control over the habitat maps than satellite images. The paper also provides a method for attaching radio transmitters to lizards.

This study was the first idea, that sparked the rest of this thesis and as such, I have been happily involved a lot in working on it. Conceptualisation and methods were worked out by myself in collaboration with DENNIS RÖDDER. I did extensive research and practice on radio-telemetry together with the BAFF (Bonner Arbeitskreis für Fledermausschutz) and WERNER DRECKMANN including a seminar and multiple sessions where I built an antenna together with WERNER DRECKMANN. I also took part in a course on operating the UAV together with DENNIS RÖDDER. The Maxent algorithm and further statistical methods were worked out by myself and RIEKE SCHLUCKEBIER with input from DENNIS RÖDDER. I also led the radio-telemetry field work with the help of RIEKE SCHLUCKEBIER. I wrote the first draft of the publication and finished the final manuscript with the helpful input of both co-authors.

Abstract

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

Keywords. Home range, *Lacerta agilis*, high spatial resolution, unmanned aerial vehicles, microhabitat selection, categorical map, Maxent algorithm.

Introduction

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

Unmanned aerial vehicles (UAVs) can be a powerful tool to monitor the environment. UAVs already find frequent application in agriculture where they facilitate the mapping of crops (BERNI et al. 2009, KANEKO & NOHARA 2014, LIU et al. 2020). Lately, the use of unmanned aerial vehicles has been adopted in biological fields and expanded to answer a multitude of questions. Biological fields benefit from broad vegetation analysis via remote sensing in the case of postfire vegetation survey for instance (FERNÁNDEZ-GUISURAGA et al. 2018), or studies ascertaining the influence of animals on vegetation structure and composition (QIN et al. 2020). Further applications include the surveying of large to mid-sized mammals over great distances, at night, or in hard-to-reach locations with thermal image capturing (BUSHAW et al. 2019, HE et al. 2020) or identification of specific plant species as habitat for specialized arthropods (HABEL et al. 2016). As the technology becomes more and more affordable, new applications will be developed and larger areas will be able to be surveyed. Its ability to deliver high resolution information on vegetation is also useful when assessing microhabitat selection in animals with small home ranges as the high resolution allows for distinction of small-scale structural differences (see HABEL et al. 2016).

One animal that is of particular interest in terms of microhabitat selection due to its proximity to humans and anthropogenically altered landscapes is the sand lizard (*Lacerta agilis* LINNAEUS, 1758). *Lacerta agilis* is an on average 18cm – 25cm long insectivorous lacertid native to large parts of the southern half of the Palaearctic (EDGAR & BIRD 2006). It is diurnal with activity times from spring to early autumn while hibernating the remaining months of the year (VAN NULAND & STRIJBOSCH 1981, EDGAR & BIRD 2006). *Lacerta agilis* favour open canopy with occasional shrubs over densely vegetated areas and therefore thrive in heathlands or marginal vegetation (HOUSE & SPELLERBERG 1983b, DENT & SPELLERBERG 1987, NEMES et al. 2006). On the northern edges of their distribution, they are restricted to sandy dune vegetation while on the southern edges they prefer montane areas (BISCHOFF 1988). They have benefited from anthropogenic influences such as forest clearings and farmland creation since medieval times as it opens new areas with suitable habitat for them (BISCHOFF 1988). Due to their long history as a synanthropic species, populations of *L. agilis* often live near humans and are therefore easily accessible. However, they also often fall victim to developmental expansions, and subsequently become the subjects of compensation measures. This, in combination with the declining numbers of *L. agilis* (IUCN 2020) make it a fitting species for our study as it could be a main beneficiary.

In this study, we combine high resolution vegetation analysis via unmanned aerial vehicle and radio-telemetry-assisted home range assessment in order to calculate and quantify the habitat and microhabitat selection of the sand lizard, *L. agilis*. We use an unmanned aerial vehicle to record high resolution images of the habitat and tag individuals within the habitat with transmitters to determine the size, limits and variation of the home ranges via frequent relocation of the individuals. We then analyse habitat composition and preference within the home range in order to identify important structures on a microhabitat level. This approach yields a wide range of applications for conservation agencies and environmental compatibility assessments. Environmental compatibility assessments are conducted to test the impact of a planned developmental project on the environment and to integrate appropriate compensatory measures to the project plan. As described in §16 of the UVPG (Gesetz für die Umweltverträglichkeitsprüfung / Law for the environmental compatibility assessment) of the Federal Republic of Germany for instance, environmental compatibility assessments require, among other things, a description of the environment in the area (RÖDDER et al. 2016). This includes inventory and assessment of concerned species. Our method allows the inclusion of microhabitat requirements of affected species in the description of the environment and makes it easier to provide correct microhabitat structure in compensatory measures.

Material and methods

Data collection

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

In order to find lizards often enough to assess their home ranges, individuals were equipped with radio transmitters to relocate them. We used V1 tags offered by Telemetrie-Service-Dessau with slight modifications. Signal intensity was reduced such that the direction of the signal was still detectable in close proximity and in order to extend battery life. The sensors weighed 0.35g and operated at 200µW. As evidenced by another study conducted in the same area (SCHMITZ et al. 2022) the average adult lizard body weight within the population during August and September was 10.5g meaning sensors on average were 3.3% of the weight of averagely sized lizards. Small individuals were avoided. The transmitters had an estimated lifetime of 30 days. We used a 4 element Yagi antenna provided by Telemetrie-Service-Dessau, optimized towards frequencies at 150Mhz as well as a self-made 5 element Yagi antenna constructed together with WERNER DRECKMANN of the BAFF (Bonner Arbeitskreis für Fledermausschutz / Working group for bat protection Bonn) according to an instruction article (Praxisheft 27 für Amateurfunk und Elektronik in der Schule und Freizeit, p. 131-133). The self-made antenna was optimized towards determining the direction of incoming signals by having a narrower cone of detection. As a receiver, we used the ICOM IC-R30 which was also provided by Telemetrie-Service-Dessau.

Radio-telemetry was carried out between August 19 and 28, 2019, after the breeding season (EDGAR & BIRD 2006) so as to avoid interference with copulations or male-male interactions. Adult lizards were captured by hand in order to attach radio transmitters. The latter were attached after WARNER et al. (2006) with modifications in order to accommodate the different body plan of *Lacerta agilis* compared to *Amphibolurus muricatus* studied by WARNER et al. (2006) The attachment procedure is detailed in Figure 4.1. Nylon mesh from a fly screen was cut in a “V” shape with a flatter angle and the tag was glued to the bottom of the “V” with the antenna pointing away from the arms. We used super glue (Pattex Sekundenkleber Flüssig, cyanoacrylate) to attach the tag to the nylon mesh and to later attach the tag to the animal. Cyanoacrylate glue is commonly used on reptile skin (PRICE-REES & SHINE 2011, VAN WINKEL & JI 2014, HANSEN et al. 2020) without any adverse effects observed as the glue is inert when hardened (HOSER 2019). The resulting harness was only attached to lizards when the glue connecting the tag and the mesh were completely dried intending to avoid attaching the transmitter to the skin directly. The previous step was therefore done a day before going out into the field. After lizards were caught, the harness was placed on their backs with the antenna pointing caudally (Figure 4.1A). The arms of the harness were then drawn over the lizards’ shoulder and crossed at the chest (Figure 4.1B). The arms were then drawn through the axillae towards the transmitter and tied into a knot above the transmitter (Figure 4.1C). The harness was secured with a drop of superglue ahead of the shoulders, behind the axillae, and at the cross over the chest (Figure 4.1D). Additionally, the knot was secured with superglue and glued to the transmitter while the rest of the mesh arms were cut off (Figure 4.1D). The lizard was then held as calmly as possible with its front legs spread so it would not touch the glue behind its legs before it was completely dried, as this would have glued the legs to its flank. During the procedure, special attention was paid to make sure the lizards’ shoulder joints were not restricted and the mesh was tight enough to prevent escaping but not too tight, so that the animal would not be harmed. The drops of glue in front and behind the shoulders are important as lizards would otherwise have been able to push their front limbs under the mesh, resulting in a much faster loss of the harness. The harness was deliberately only glued on key points, allowing the glue to come off easily at the next moulting of the animal and cover as little skin as possible. Forgoing the use of glue to secure the tag to the skin directly was also deliberate, as the tag could be removed by cutting the mesh anytime without hurting the animal in case severe mobility issues were observed. Suitability of the method was assessed by lizard mobility immediately after the attachment and every consecutive relocation. In total, 15 animals (seven females and eight males) were tagged over a period of 1.5 weeks but never more than 10 at a time due to permit restrictions. If one animal lost its tag, a new one was caught and got a new tag to avoid stressing a single animal too much. Animals were observed for 1.5 weeks (19-28 August 2019) daily from 9 a.m. to 4-6 p.m. via visual encounters by the experimenters. Animals were located via radio-telemetry and their coordinates were noted. An animal was considered located when visual confirmation was given regardless whether the animal had moved since its last relocation. Due to the tags wearing numbers on their backs for frequency allocation, animals were easy to identify even among other tagged individuals. After each animal was relocated once, a 30-minute period without disturbance was given to the animals. After this time span, relocation began anew. Since relocation itself took 20-30 minutes this effectively resulted in every animal being relocated once every 50-60 minutes. The aim was to achieve at least 19 relocations per individual to calculate home range (after ROSE 1982) but if the tag stayed attached, relocations were continued. Six lizards lost their tags before 19 relocations could have been achieved. A detailed history of relocations for every individual can be found in the electronic supplement Supplementary Material Table S4.1.

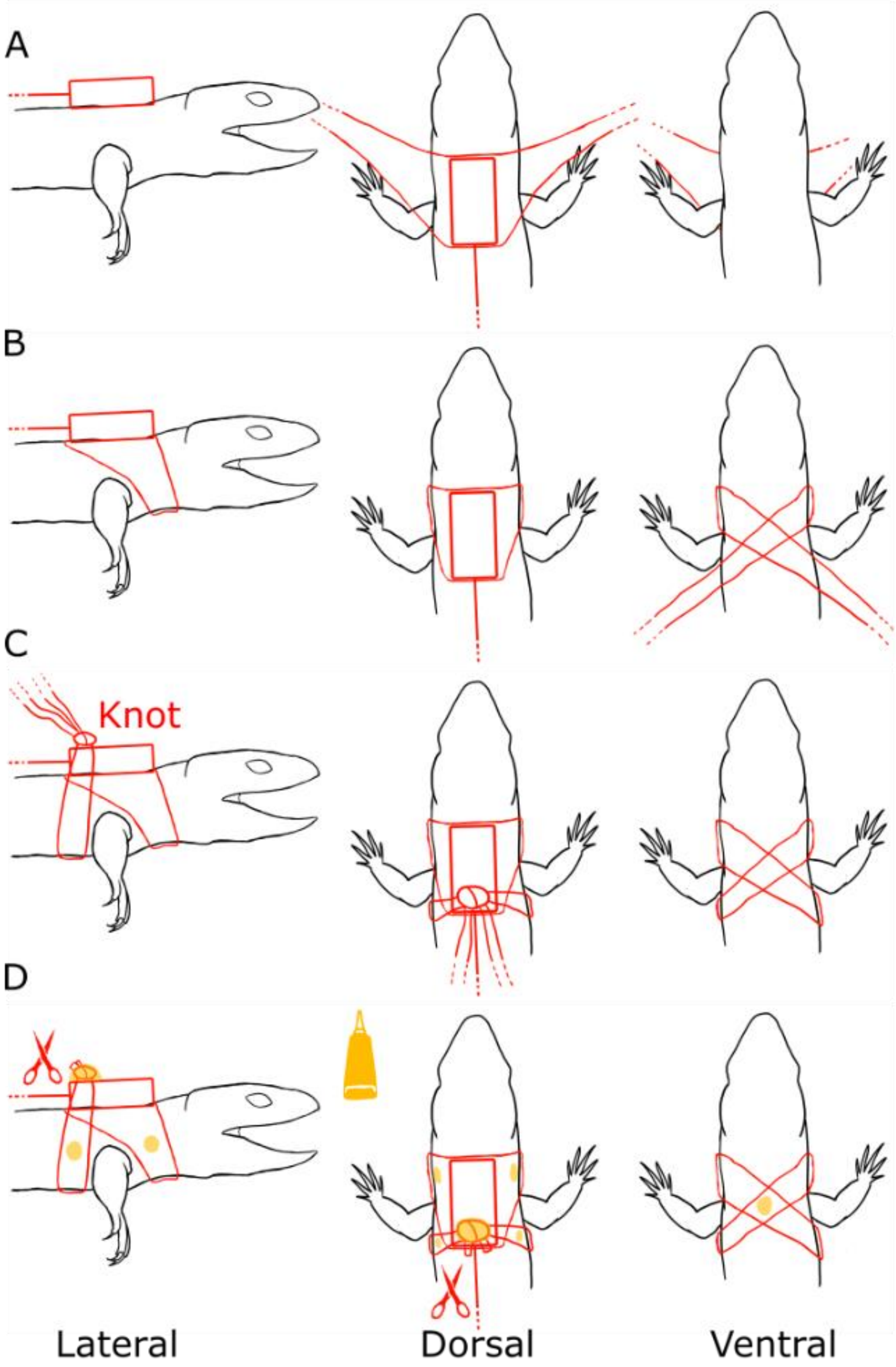

Figure 4.1: Attachment procedure of the radio transmitters (red rectangle) to the lizard via mesh backpack. Read from A to D. Lateral, dorsal and ventral views provided for each step. Yellow spots mark glue drops.

Mapping of the area

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

Starting and landing periods were removed by cutting video footage or deleting corresponding pictures. We used the software Pix4DMapper 4.5 (PIX4D SA 2019) in order to mosaic the images (or video frames) and to compute the maps. Pix4DMapper was also used to calculate a normalized difference vegetation index (NDVI) and a digital surface model from the mosaiced maps and display it as additional maps. The NDVI is calculated by comparing the near-infrared channel and the red channel and provides an index on the amount of photosynthetically active vegetation.

While the images from the multispectral camera and the resulting map were georeferenced already, the high definition RGB map had to be georeferenced as well. The map was georeferenced in ArcMap 10.6 (ESRI 2018) using the Sequoia maps for reference. Using R 3.6.1 (R CORE TEAM 2020) the RGB map was resampled to the grid of the multispectral maps and divided into its red, green and blue band and saved as separate *.asc files along with the multispectral maps. We performed spearman rank correlation to test for correlation between the maps. In case two maps were highly correlated ($r > 0.75$), one of them was excluded from further analysis. The remaining maps were stacked together with a mask to exclude large no data areas at the edges. The channels of the RBG map were recombined into a black and white image (since the channels were strongly correlated) by summation. The stack was loaded into ArcGIS again and 10,000 randomly generated training points were plotted onto the stack. Out of these, 9891 remained after the points that lacked data had been eliminated. The training points were then manually assigned to habitat classes based on experience from the field. The real-life habitat served as point of reference to make sure classes were distinguished properly. The classes were sand, blackberry bushes, grass, trees (and high bushes), slope vegetation (vegetation at the northern slope towards the beach) and low vegetation (bushes of 1 m or lower). The different training points for each class were saved as separate excel files. In DIVA-GIS (HIJMANS et al. 2001), points were then transformed into masks and compared against each other in case one point would have been counted towards two classes.

The Maxent algorithm (PHILLIPS et al. 2004, PHILLIPS et al. 2006, PHILLIPS et al. 2017b) was used to calculate habitat classes using the training points of the different classes as samples and the maps as environmental layers in order to examine the likelihood of each pixel belonging to a certain class based on the colour values of the pixel on the different maps. Replications for the model were set to 100 and the test percentage was 20 using a bootstrap approach. The analysis resulted in likelihood maps (cloglog format) for each class, depicting the chance of every pixel belonging to a specific land cover class. The algorithm was first trained with sand as it was the most uniquely coloured microhabitat. The resulting map of sand was then incorporated as environmental layer for the other classes. A threshold-independent evaluation (ROC analysis) was performed. The receiver operating characteristic curve (ROC) evaluates the prediction accuracy of the model (SWETS 1988, XU et al. 2019). This analysis is a commonly used method to test the utility of a model, whereby the area under the ROC curve (AUC) provides a threshold-independent measure of model performance, since it has an intuitive interpretation that random positive instances and random negative instances are correctly ordered by the classifier (PHILLIPS et al. 2004, PHILLIPS et al. 2006, NA et al. 2018, XU et al. 2019). The accuracy of a model performance is proportional to AUC value, thus AUC ≥ 0.9 indicates that the model performance is excellent (WALDEN-SCHREINER et al. 2017, XU et al. 2019). Additionally, we performed a threshold-dependent analysis in DIVA-GIS, for which everything below the 10-percentile training presence cloglog threshold calculated by Maxent was reclassified as no data while everything above the threshold was resampled to values between 0 and 1 based on the likelihood of each pixel to correspond to the class in question. The 10-percentile training presence cloglog threshold is one of the most commonly used thresholds in Maxent analysis (ZARZO-ARIAS et al. 2019). It predicts unsuitable habitat for 10% of the most extreme training points, assuming that 90% of the training points are classified correctly (KADEJ et al. 2017, ZARZO-ARIAS et al. 2019). The results of the Maxent analysis are provided in the electronic supplements Supplementary Material Table S4.2 for the sand analysis and Table S4.3 for the following analysis. After the Maxent analysis, trees and slope vegetation (which consisted mostly of high bushes and small trees) were combined to high vegetation. This step was necessary as we observed a lack of differentiation between these categories, and that slope vegetation was the only class defined by its position rather than its properties. The combined class "high vegetation" on the other hand is defined by its properties. It has been shown for *L. agilis* that vegetation structure is the most important factor when determining habitat preference (HOUSE & SPELLERBERG 1983b). While this could be an argument for the merging of blackberry bushes with low vegetation as well, we decided against it. Blackberry is structurally distinct from average low vegetation in the area and could therefore be used to see if one species differs from the general low vegetation in terms of preference, potentially hinting at structural preferences of *L. agilis* within the class of low vegetation. The likelihood maps were then stacked into one map with the highest likelihood value for each pixel at the top resulting in a map displaying the most likely habitat class for every pixel effectively showing the distribution of the aforementioned habitat classes.

Calculation of home range

Home ranges were calculated using R and the packages adehabitatHR (CALENGE 2006), sp (PEBESMA & BIVAND 2005, BIVAND et al. 2008), rgdal (KEITT 2010), and raster (HIJMANS 2020b). Home range was calculated for every individual with at least 19 locations. We calculated 95% minimum convex polygon home range in the following abbreviated MCP (MOHR 1947) and 95% and 50% kernel density estimation home range with bivariate normal kernels in the following abbreviated K95 and K50 respectively (WORTON 1989). The ad hoc method for the bivariate normal kernel for estimating the smoothing parameter h was used (see kernelUD function in the adehabitatHR package CALENGE 2006). The resulting smoothing parameters were 8.987 for ID04, 3.795 for ID05, 7.763 for ID06, 5.628 for ID11, 4.083 for ID14, 4.407 for ID22, 3.232 for ID23, 6.403 for ID24, and 4.289 for ID25. Both kernel density estimation and minimum convex polygon methods have been shown to have limitations in the study of lizard home range despite being the most frequently used methods. Kernel density estimations have been shown to require many relocations and tend to overestimate home range drastically depending on the smoothing parameter chosen (ROW & BLOUIN-DEMERS 2006). Lately, they have been deemed inappropriate for lizard home range by some authors (e.g., ROW & BLOUIN-DEMERS 2006, GETZ et al. 2007, LAVER & KELLY 2008, SILLERO et al. 2021). While minimum convex polygon estimations are more predictable, they are incapable of displaying unused areas within their home range due to their convex nature. Additionally, they display no information about utilization distribution within the area. A solution to this was proposed by SILLERO et al. 2021, in which small scale ecological niche models (ENMs) with individual lizards were calculated within MCP home ranges to subtract unsuitable areas. We recreated this, by using the variables (without the DSM map) and method used previously to calculate the categorical habitat map with the relocations of an individual lizard to establish a distribution model. We added a mask encompassing all of the individuals' home range areas in order to facilitate modelling. We excluded areas below the 10-percentile training cloglog threshold from the home range as unused areas. We then added the resulting home ranges to our calculated home ranges with the suffix _ENM, in the following called ENM home ranges as opposed to non-ENM home ranges, which are the home range estimations without preceding distribution model. We chose to keep the old home ranges despite discussed flaws to keep comparability with other studies. A Kruskal-Wallis-test was conducted for all home range types to determine the differences between males and females, as the data did not fulfil the assumptions for an AN(C)OVA. Additionally, Spearman's rank correlation coefficient was calculated, in order to check for a link between the number of relocations and home range size. In both cases, p-values were adjusted with the false discovery rate (FDR) transformation to account for multiple tests.

Habitat use, preference and avoidance

Animal movements were approximated by connecting relocation points in chronological order with straight lines. Using R, and the packages adehabitatLT (CALENGE 2006), adehabitatHR (CALENGE 2006), maptools (BIVAND et al. 2008), raster (HIJMANS 2020b), SDMTools (VANDERWAL et al. 2014), and splancs (ROWLINGSON & DIGGLE 2017) we simulated 100 movements according to the distances and movement angles observed in the actual home ranges but randomized. We calculated new non-ENM home ranges from the resulting points (95% minimum convex polygon, 95% kernel density estimation and 50% kernel density estimation), following similar movement patterns but ignoring habitat. We calculated JACOBS' electivity index for each habitat type sand, blackberry bushes, grass, high vegetation (trees and bushes of 1m or higher) and low vegetation in the observed home ranges and the randomly generated home ranges using R. Jacobs' index (JACOBS 1974) was originally designed to study food preferences when food was available in different abundances (JACOBS 1974). The calculation can also be used for other resources like habitat, however. The index is then written as follows:

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

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

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

Results

Radio-telemetry

In total, 15 animals (seven females and eight males) were tagged wherein six specimens lost their transmitters before 19 relocations could have been obtained (see electronic supplement Supplementary Material Table S4.1). Consequently, nine specimens (five females and four males) kept their tag long enough for sufficient relocations. These animals were called ID04, ID05, ID06, ID11, ID14, ID22, ID23, ID24 and ID25. ID05, ID11, ID22, ID23, and ID25 were female, while ID04, ID06, ID14, and ID24 were male. Animals were mobile and could traverse dense vegetation with the tag within the first minute after releasing. Only one animal got lost with the tag during the trial as it left the area for very dense vegetation. Every other tag was successfully retrieved. Of the observed animals, none fell to predation for the entire time the tag was attached and only one had to be cut free from the tag after it entangled a foot in the nylon mesh but had been observed untangled 30 minutes prior.

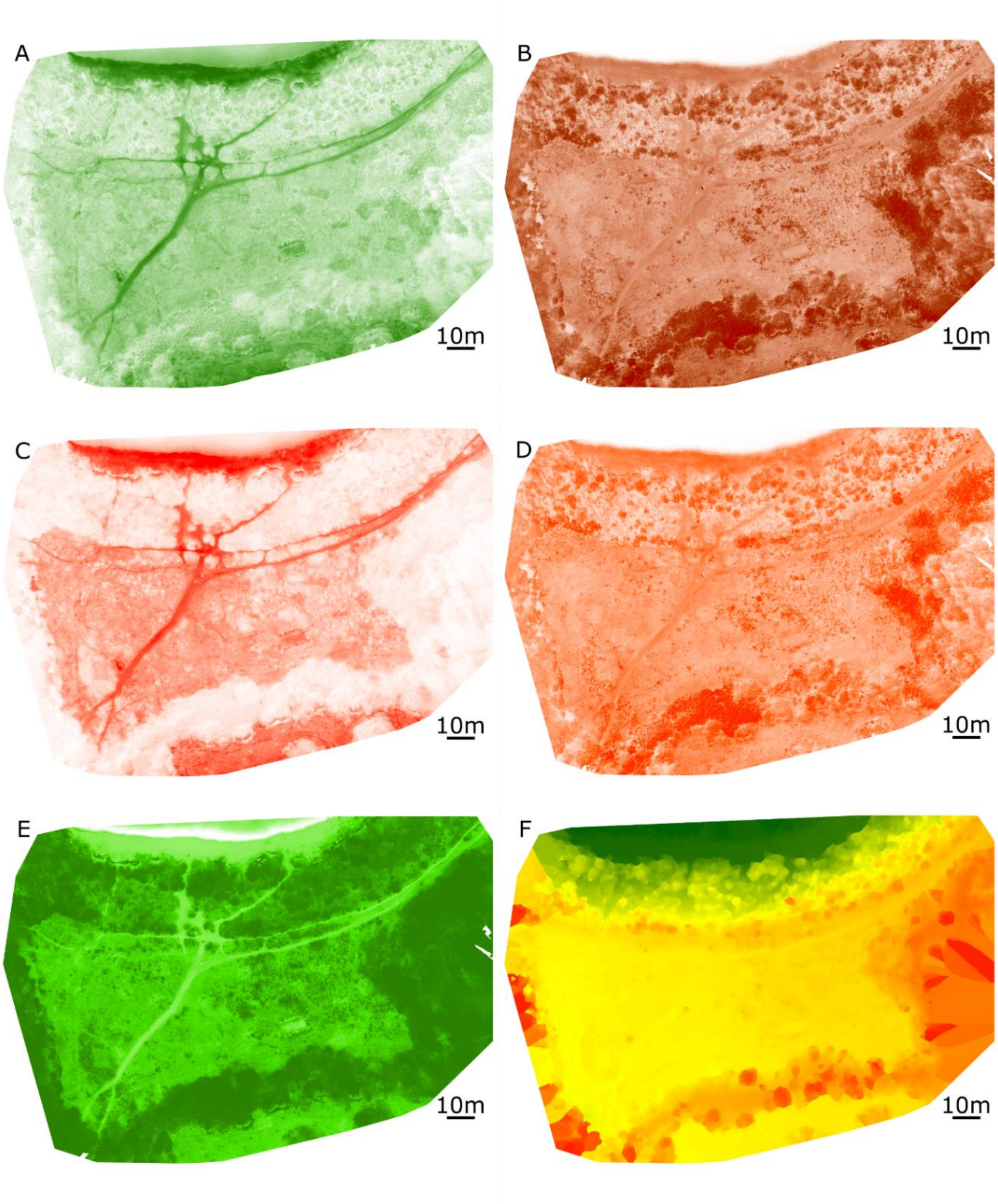

Figure 4.2: Mosaiced maps from the sequoia and calculated NDVI map. Shown are the green channel (A), the near-infrared channel (B), the red channel (C), the red edge channel (D), the NDVI (E) and the DSM (F). Scales go from low reflection (white) to high reflection (colourful) except for the DSM map, which goes from low altitude (green) to high altitude (red).

Mapping of the area and Maxent analysis

In order to create a categorical map showing different habitats within the study area, the mosaic maps recorded by the multispectral camera (green channel, near-infrared channel, red channel and red edge channel) (Figure 4.2); the maps directly calculated by Pix4D as a result of the recorded maps (NDVI and DSM) (Figure 4.2); as well as the RGB map patched together from the video recorded by the 4k RGB camera (Figure 4.3) were used. Before the analysis, Spearman's correlation coefficient was calculated to eliminate repetitive data (Table 4.1). The RGB map was split up into its three channels, but since all parts of the RGB map were highly correlated, we only used the sum of all channels in the Maxent analysis. Furthermore, the Sequoia red map correlated with both the NDVI and Sequoia green maps. Since the latter two did not strongly correlate with each other, we discarded the Sequoia red map. The Sequoia red edge map correlated with the Sequoia NIR map of which the NIR map was kept and the red edge map was discarded.

The AUC values of the Maxent analysis for accuracy of the classification of training points (Table 4.2) show that all model performances are of high quality (SWETS 1988, WALDEN-SCHREINER et al. 2017, XU et al. 2019). Mean Test AUC values for all classes vary between 0.804 for trees and 0.886 for blackberry. Furthermore, the mean value for sand is 0.930. The classes “slope” and “trees” were combined into the class “high vegetation” since slope vegetation and trees in the area were both high vegetation and it was preferable to define the categories by structure rather than position.

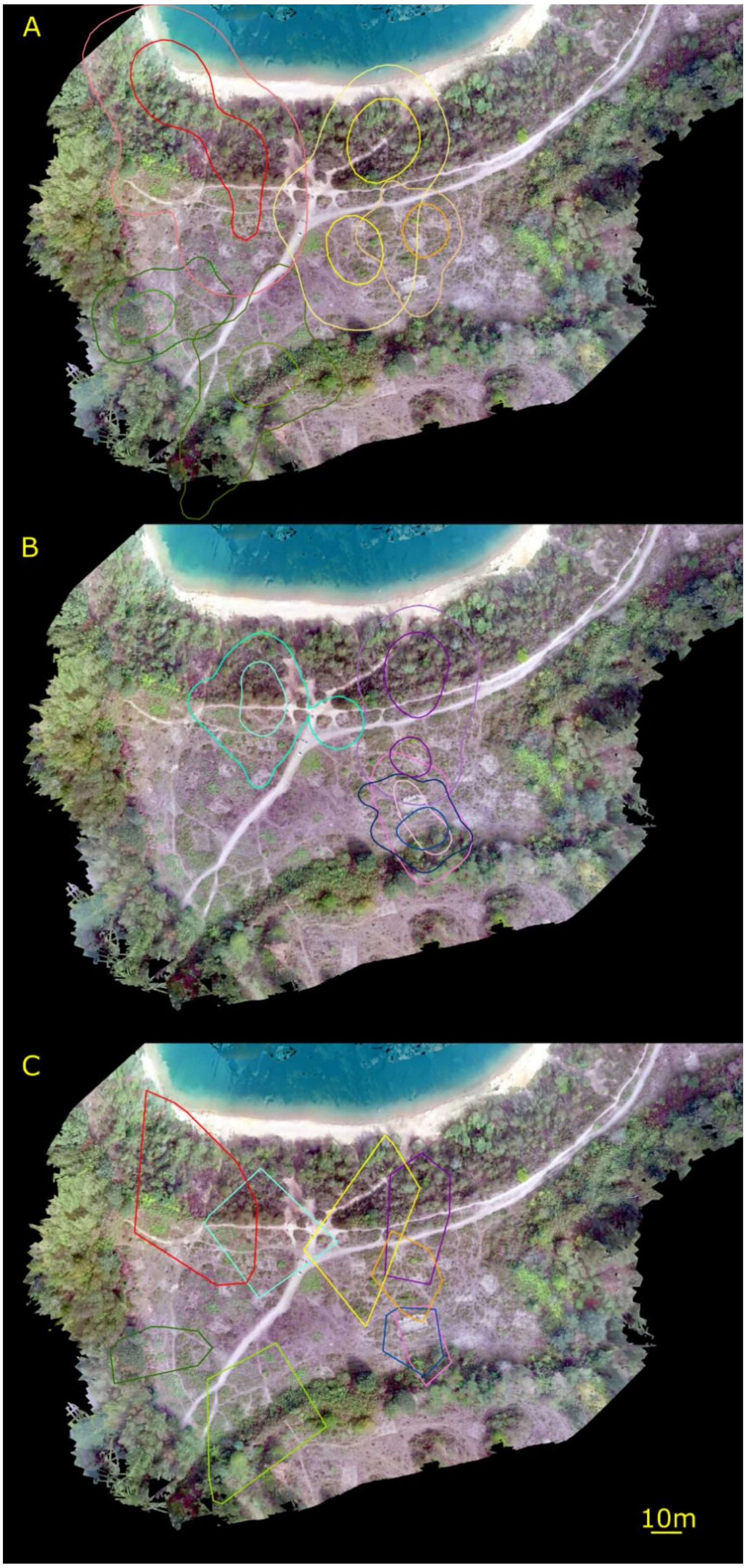

Figure 4.3: High resolution RGB map with 95% and 50% kernel density estimation home ranges for all individuals (A+B) and MCP home ranges for all individuals (C). ID04 (red), ID05 (orange), ID06 (yellow), ID11 (light green), ID14 (dark green), ID22 (turquoise), ID23 (dark blue), ID24 (purple), and ID25 (pink).

Table 4.1: Spearman correlation coefficient between multispectral maps (Sequoia…), digital surface model (dsm), NDVI, 4K RGB map (SumRGB) and its blue, green and red channels. Strongly correlated pairings are marked by *.

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

The categorical map (Figure 4.4) has a high resolution with 1 pixel corresponding to a 3.6cm x 3.6cm area. White areas indicate the absence of data. High vegetation mostly frames the area, while grass, blackberry and low vegetation are mostly found in the centre. Bare sand is mostly restricted to the beach area in the north, and the pathways. High vegetation (43.19%) takes up the highest amount of landcover, whereas sand (9.04%) takes up the lowest (Figure 4.4). Blackberry (15.89%), grass (14.77%), and low vegetation (17.12%) are distributed in similar proportions (Figure 4.4).

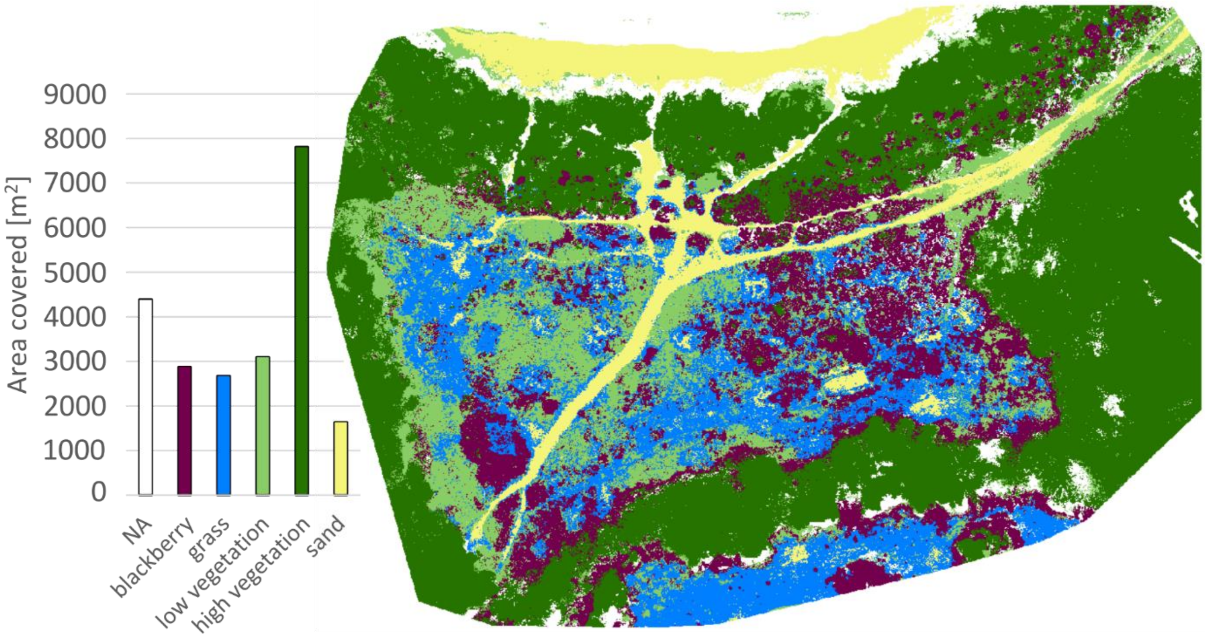

Figure 4.4: Microhabitat map depicting the five final microhabitat categories and the area covered by each in m^2.

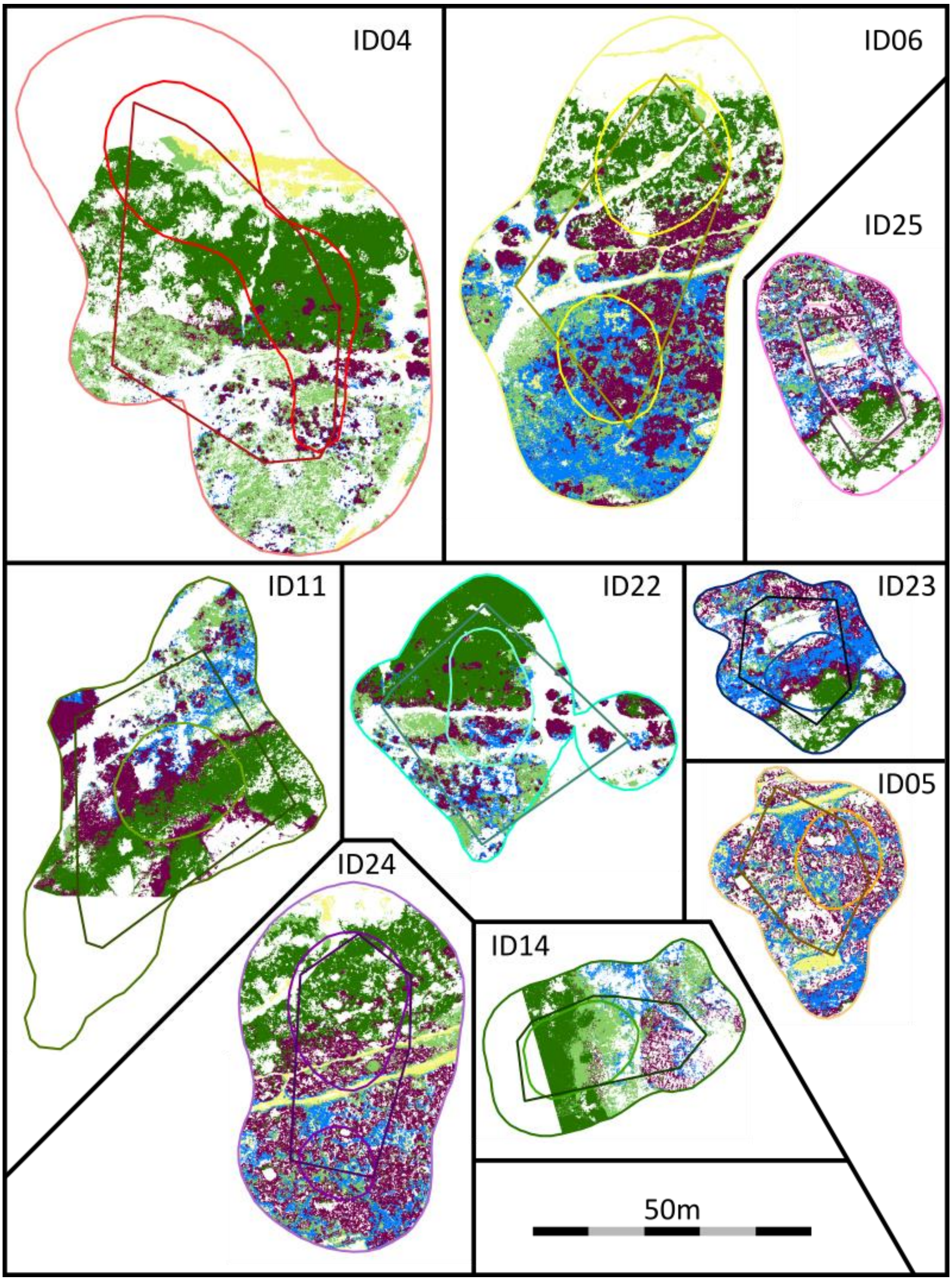

Figure 4.5: ENM home ranges of K95 (outer borders), K50 (inner round borders) and MCP (darker, polygon borders) home ranges. White areas are excluded from the home range either by missing data or the ENM. Habitat colours show purple for blackberry, blue for grass, light green for low vegetation, dark green for high vegetation and yellow for sand.

Table 4.2: Training samples, test AUC and standard deviation, 10% training presence cloglog threshold, and map contributions resulting from the Maxent analyses to make the categorical map. Training samples are training points, which were assigned to each class to define classes.

Class	**Training samples**	**Test AUC ± SD**	**10-percentile training presence cloglog threshold**	**SeqoiarGreen contribution**	**SumRGB contribution**	**dsm contribution**	**ndvi contribution**	**sand_mask contribution**	**seqoiarNIR contribution**
Blackberry	297	0.886 ± 0.014	0.317	17.13	3.702	34.387	44.015	0	0.765
Grass	524	0.880 ± 0.009	0.414	2.093	5.635	19.224	71.58	0	1.469
Low Vegetation	129	0.848 ± 0.037	0.294	15.324	2.648	21.259	32.115	0	28.654
Slope	1090	0.848 ± 0.008	0.378	27.94	4.532	41.039	24.496	0	1.992
Trees	1628	0.804 ± 0.007	0.411	1.223	0.806	27.376	69.952	0	0.644

Table 4.3: Training samples, test AUC and standard deviation, 10% training presence cloglog threshold, and map contributions resulting from the Maxent analyses for getting the ecological niche models. Training samples are taken from the relocations of the individuals.

Individual	**Training samples**	**Test AUC ± SD**	**10-percentile training presence cloglog**	**SeqoiarGreen contribution**	**SumRGB contribution**	**ndvi contribution**	**seqoiarNIR contribution**	**mask contribution**
ID04	35	0.702 ± 0.084	0.378	12.17	39.43	33.498	14.901	0
ID05	30	0.655 ± 0.094	0.455	26.787	23.553	38.631	11.029	0
ID06	40	0.600 ± 0.085	0.4849	25.92	17.503	33.354	23.223	0
ID11	37	0.680 ± 0.081	0.366	43.682	8.479	37.635	10.205	0
ID14	22	0.638 ± 0.096	0.501	19.996	18.342	54.627	7.034	0
ID22	40	0.648 ± 0.079	0.445	7.454	22.784	54.137	15.625	0
ID23	28	0.592 ± 0.101	0.477	30.423	14.179	34.29	21.109	0
ID24	23	0.595 ± 0.108	0.512	11.514	44.966	23.611	19.91	0
ID25	16	0.650 ± 0.123	0.467	18.568	23.366	29.889	28.177	0

Home ranges

Overall, there were nine specimens who had been relocated often enough to calculate home ranges (Figures. 4.3, 4.5). In total four males and five females were suitable with ID25 being the least (19) and ID11 and ID22 the mostly often relocated one (59). The data used for the Maxent models, as well as the contributions of the maps can be found in table 4.3. The 10-percentile cloglog training thresholds, which were used to cut unused habitat out of the home range, can also be found in table 4.3. Overall, test AUC was not quite as good as for the categorical map but still deemed sufficient (range: 0.592 ± 0.101 to 0.702 ± 0.084).

Overall, home ranges differ in size quite drastically (Figure 4.6), with ID04 having the largest non-ENM K95 home range (4057.116 m^2), and ID23 having the smallest (781.815 m^2). While ID23 also has the smallest K95_ENM home range (523.968m^2), the largest K95_ENM home range belongs to ID06 (2315.242 m^2). For the core area, ID04 has the largest (non-ENM: 1126.074 m^2, ENM: 697.733 m^2) while ID23 has the smallest non-ENM (174.518 m^2) and ID05 has the smallest K50_ENM (143.324 m^2). ID04 also has the largest MCP home range (non-ENM: 1757.085 m^2, ENM: 1029.755 m^2) but the smallest MCP home range belongs to ID25 (non-ENM: 295.110 m^2, ENM: 170.430 m^2). Other home range sizes range in between these numbers (Figure 4.6). On average for non-ENM home ranges, K95 home ranges are 1853.263 m^2 in size. The average size of K50 and MCP home ranges is 457.053 m^2 and 808.084 m^2 respectively. For ENM home ranges, average home range sizes were 1141.341 m^2 for K95_ENM, 326.134m2 for K50_ENM and 531.721m^2 for MCP_ENM. Home range size was not significantly correlated the with the number of relocations in any home range (Spearman rank test for K95 home range: $\rho = 0.36$, $q = 0.342$, for K95_ENM home range: $\rho = 0.377$, $q = 0.342$, for K50 home range: $\rho = 0.36$, $q = 0.342$, for K50_ENM home range: $\rho = 0.443$, $q = 0.342$, for MCP home range: $\rho = 0.72$, $q = 0.114$, for MCP_ENM home range: $\rho = 0.694$, $q = 0.114$). Similarly, home range size between males and females did not differ significantly (Kruskal-Wallis-test for K95: $\chi^2 = 2.16$, df = 1, $q = 0.212$, for K95_ENM: $\chi^2 = 2.16$, df = 1, $q = 0.212$, for K50: $\chi^2 = 2.94$, df = 1, $q = 0.212$, for K50_ENM: $\chi^2 = 3.84$, df = 1, $q = 0.212$, for MCP: $\chi^2 = 0.96$, df = 1, $q = 0.327$, for MCP_ENM: $\chi^2 = 1.5$, df = 1, $q = 0.265$).

Table 4.4: Mean and standard deviation of land cover across home range types. Home ranges with preceding species distribution model are annotated with _ENM.

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

Concerning the proportional coverage of the studied microhabitat (Table 4.4), blackberry and high vegetation make up the largest parts of the home ranges, with each of them covering on average roughly a quarter of the entire home range, if not more. Grass and low vegetation follow, each making up 13-21% of the area in different home ranges. Lastly, sand covers up the least amount of area in all home ranges ranging from 2-9%. Sand coverage is especially low in ENM home ranges where it is highest in K95_ENM home ranges with 3.27%. This is lower than the lowest land cover in the non-ENM home ranges. Standard deviations range from +- 3-15% being highest in blackberry and high vegetation, and lowest in sand.

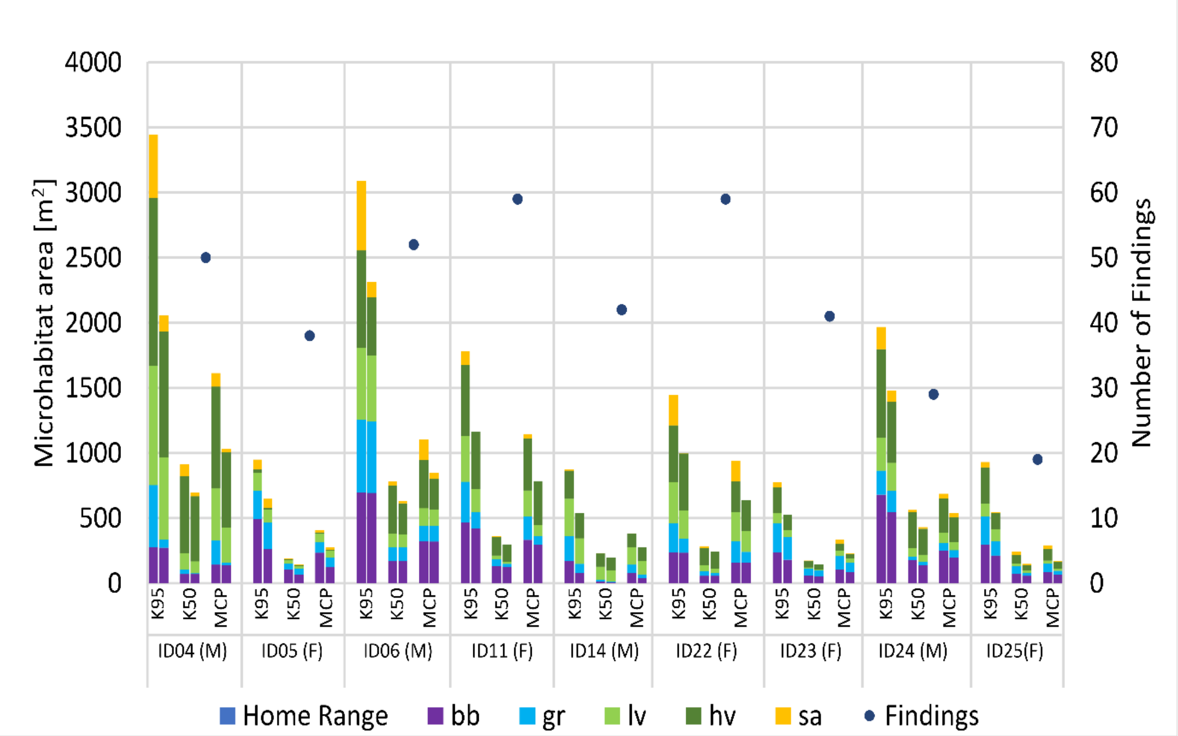

Figure 4.6: Microhabitat area (bars), total microhabitat area (sum of bars) and number of findings (points) for every individual for each of the three calculated home range types without preceding ENM (left of the pairs) and with preceding ENM (right of the pairs) Area depicted in m2. Sex is marked next to the ID names of the lizards as M for males and F for females.

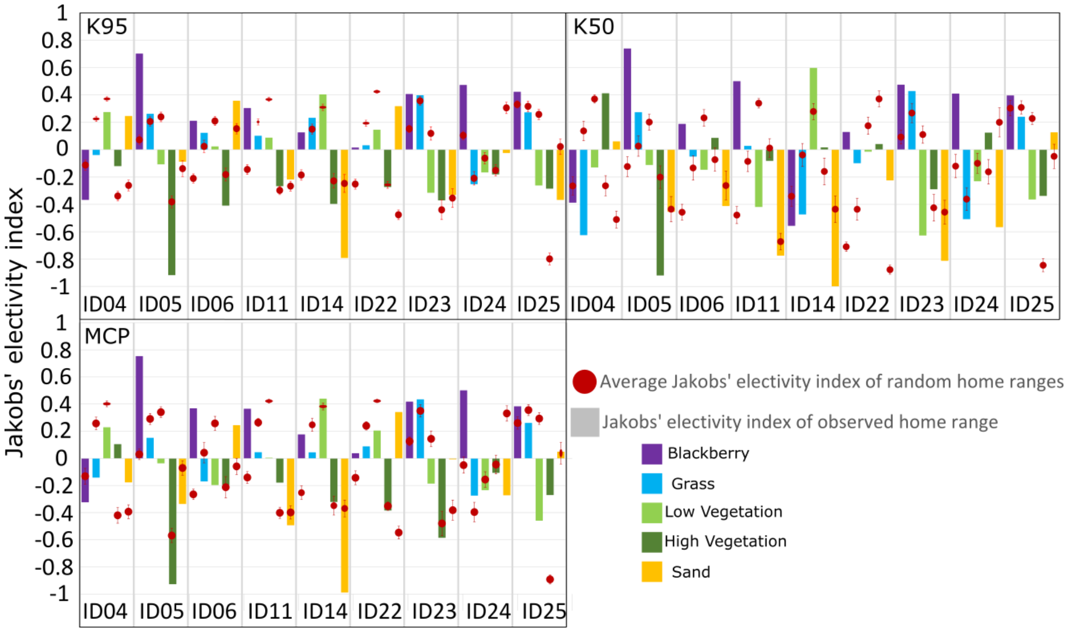

Figure 4.7: JACOBS' electivity index for blackberry, grass, low vegetation, high vegetation, and sand within the K95, K50 and MCP home ranges of studied individuals. Tips of the bars represent the JACOBS' electivity indices for the observed home ranges while red dots show the averages of simulated home ranges with 95% confidence intervals. For small confidence intervals, red dots have been replaced with red ellipses in order for the confidence intervals to still be visible.

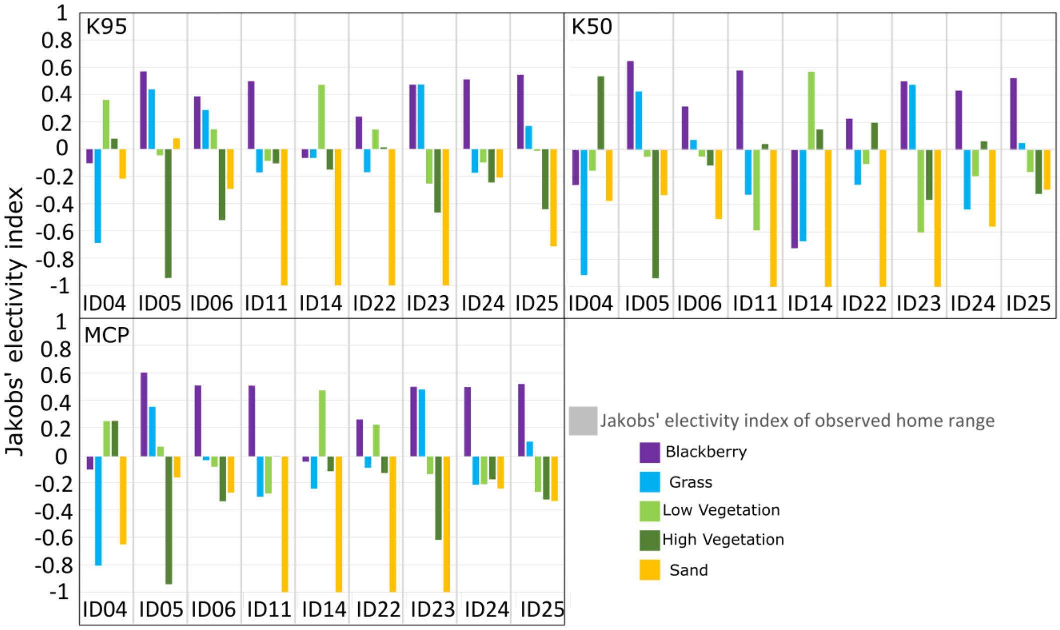

Figure 4.8: JACOBS' electivity index for blackberry, grass, low vegetation, high vegetation, and sand within the K95, K50 and MCP home ranges with preceding ENM. Tips of the bars represent the JAKOB'S electivity indices for the observed home ranges.

Habitat use, preference, and avoidance

We calculated the electivity indices for blackberry (bb), grass (gr), low vegetation (lv), high vegetation (hv), and sand (sa) for every individual inside their different home ranges (Figure 4.7 for non-ENM home ranges, Figure 4.8 for ENM home ranges), as well as the confidence intervals calculated from the simulated non-ENM home ranges (Figure 4.7) in order to ascertain whether the electivity index is within the confidence interval. Most electivity indices are outside the confidence interval – meaning that the electivity index of the chosen habitat structure in the home range is significantly different from that of random habitat composition meaning it is likely that the lizards actively choose the composition of their home ranges thus. However, there are 13 instances, where the observed electivity index is within the confidence interval of the randomly generated home ranges. Thus, in these cases, the observed electivity is not significantly different from random chance. These instances are exclusively found for sand, high vegetation, and grass. The electivity index for sand is within the confidence interval in the K95 home range and the K50 home range of individual ID05, in the K95 home range of specimen ID23, and in the MCP home range of individual ID25. The electivity index for grass is within the confidence interval in the K50 home range of individual ID06 and the K95 home range of individual ID23. The electivity index for high vegetation is within the confidence interval in the K95 home ranges of individuals ID11, ID22, ID23 and ID24 and in the MCP home ranges of individuals ID06, ID14, and ID24.

Table 4.5: Spearman's correlation coefficients for all pairings of JACOBS' electivity indices within the home ranges across all individuals. No pairings were significantly correlated after p-value adjustment by FDR. Home ranges with preceding species distribution model are annotated with _ENM.

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

Overall, our results suggest seven cases of an electivity index being within the confidence interval in the K95 home ranges, two cases in the K50 home ranges and four cases in the MCP home ranges. After adjustment of p-values for multiple correlation tests, no electivity indices correlate with each other within home ranges (Table 4.5).

In the K95 home ranges (Figure 4.7), an overall preference for blackberry can be observed with only ID04 avoiding blackberry bushes and ID14 and ID22 using them according to their availability. In K95_ENM home ranges (Figure 4.8), preferences for blackberry increase overall compared to K95 home ranges, except in ID05 and ID14. Electivity indices of grass are overall close to zero with most animals having a slight preference for grass, or using it as available, except ID23 and ID25 in their non-ENM home ranges and ID05 and ID23 in their K95_ENM home ranges. Here the preference is stronger. Additionally, ID24 slightly avoids grass and ID04 strongly avoids grass in its K95_ENM home range - which is a drastic difference compared to its non-ENM home range. In non-ENM home ranges, low vegetation is avoided by ID23, ID24, and ID25 but sought out by ID04, ID14, and ID22 - while ID05, ID06 and ID11 seem to have little preference or avoidance. Meanwhile, in their ENM home ranges, low vegetation is avoided by ID23, preferred by ID05 and ID14, and used as available by the rest. High vegetation is universally avoided, safe for ID04, which uses it according to availability in both its K95 home ranges, as well as ID11, ID14 and ID22 which use high vegetation according to availability in their ENM home ranges. Sand is avoided by ID11, ID14, ID23, and ID25, while it is preferred by ID04, ID06, and ID22. ID05 and ID24 show little avoidance or preference for sand in non-ENM home ranges, while sand is almost universally strongly avoided in K95_ENM home ranges, except for ID04, ID05, and ID24, who use it close to availability. On average, blackberry bushes are favoured while sand is avoided. High vegetation is avoided in K95 and MCP home ranges. Grass and low vegetation are on average used according to availability. Electivity indices of sand also show the highest spread of values, and sand is especially avoided in ENM home ranges (Figure 4.9). MCP indices are very similar to their K95 counterparts in both ENM and non-ENM home range types and show mostly similar preferences and avoidances.

In the core areas of both home range types, blackberry is almost universally preferred except for ID04 and ID14, which avoid it in both ENM (Figure 4.8) and non-ENM (Figure 4.7) home ranges. Grass is avoided by ID04, ID14 and ID24 in both their K50 home ranges. ID11 and ID22 avoid grass in their K50_ENM home ranges but use it according to availability in their K50 home ranges. Additionally, grass is used according to its availability by ID06 in both home range types and by ID25 in its non-ENM home range. Grass is sought out by ID05 and ID23 in both home ranges and by ID25 in its non-ENM home range. Low vegetation is preferred or avoided similarly between non-ENM and ENM home ranges in the core area with only ID14 showing a strong preference. ID11 and ID23, on the other hand, show an avoidance while the rest uses grass close to availability. ID25 avoids grass a little more in its K50 home range compared to its K50_ENM home range, where it is used closer to availability. Similarly, high vegetation use is more or less constant between non-ENM and ENM home ranges in any individuals. ID04 prefers high vegetation, while ID04 and ID25 avoid it. The rest uses high vegetation more or less according to availability. Sand is universally avoided in ENM home ranges, while it is almost universally avoided in non-ENM home ranges, with ID04, ID22 and ID25 showing an index around zero. Overall, differences between ENM and non-ENM home ranges are less drastic and less frequent in core areas. However, in core areas, variation between individuals is higher than in K95 and MCP home ranges. On average, blackberry is preferred within the core area, while sand is avoided and the rest average out to no preference or avoidance (Figure 4.9). In the core area, the difference in indices for sand between non-ENM and ENM home ranges is smaller due to the already lowered index in non-ENM home ranges.

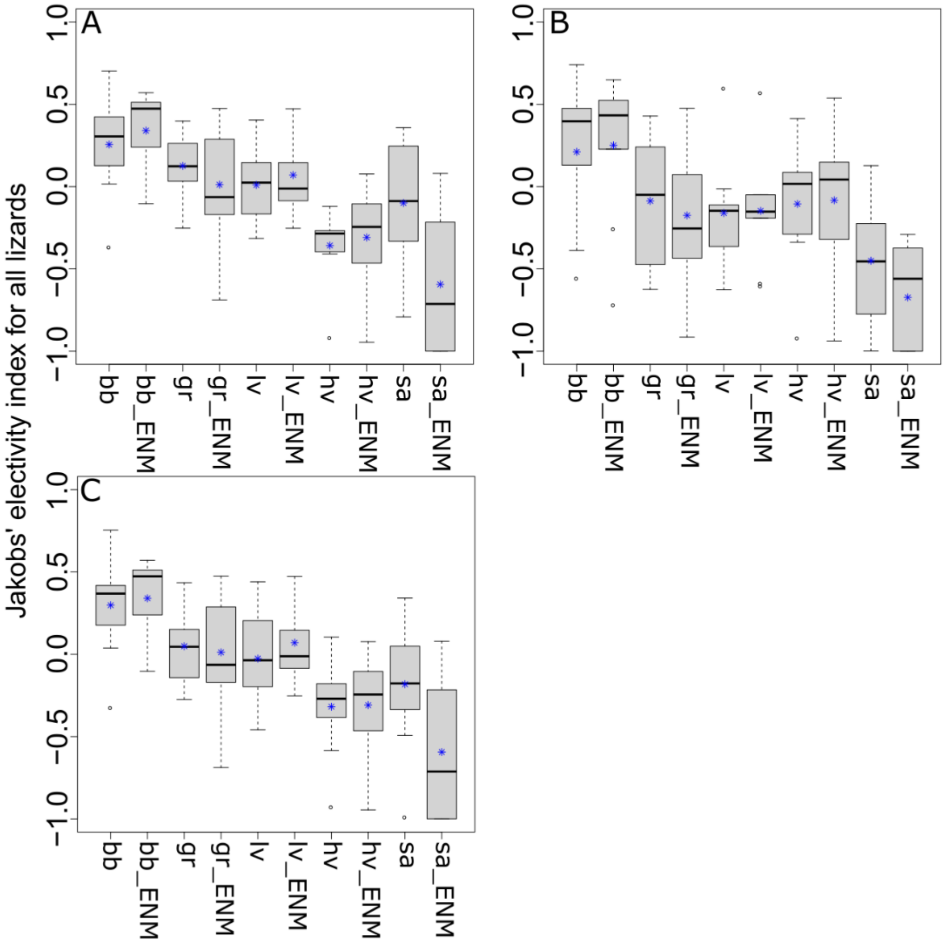

Figure 4.9: Boxplots showing the average (blue) and median electivity indices for blackberry (bb), grass (gr), low vegetation (lv) high vegetation (hv), and sand (sa) over all individuals across their 95% kernel density estimation home ranges (A), their 50% kernel density estimation home ranges (B) and their minimum convex polygon home ranges (C) with and without preceding ENM.

Home range size and electivity index

The electivity index of grass shows strong negative correlation with home range size while the electivity index for sand is strongly positively correlated with home range size in the K95 home range. Neither correlation is found in the K95_ENM home range (Table 4.6). In the non-ENM K50 home range, the electivity index of high vegetation is strongly positively correlated with home range size but not in the ENM K50 home range (Table 4.6).

Table 4.6: Spearman's correlation coefficients for all electivity indices with the size of their home ranges. Significantly correlated pairings are marked with *.

Class	K95	K95_ENM	K50	K50_ENM	MCP	MCP_ENM
bb	-0.317	-0.2	-0.367	-0.517	-0.533	-0.333
gr	-0.8*	-0.55	-0.733	-0.633	-0.617	-0.633
lv	0.333	0.233	0.05	0.067	0.4	0.2
hv	0.483	0.217	0.833*	0.7	0.617	0.5
sa	0.783*	0.385	0.45	0	0	0.05

Discussion

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

Radio-telemetry

The number of tagged individuals is comparable to similar studies (WARRICK et al. 1998, REFSNIDER et al. 2015, WIECZOREK et al. 2020, CLEMENT & RÖDDER 2021). The observed mobility and near-complete absence of entanglement and predation suggests that the method, originally described by WARNER et al. (2006), can also be used for *Lacerta agilis* given the herein-made modifications. Although formal testing has yet to be conducted, as of now, suitability is based on observations. As WARNER et al. have described, frequent observations are beneficial to reduce accidental mortality, as entangled lizards can be easy targets for predators and are prone to overheating. The one instance in which a lizard's foot became entangled was promptly resolved, since the lizard was observed unentangled 30 minutes prior. Yet, the possibility of entanglement is certainly there, and we strongly advise to regularly check on individuals when using this method, to also check for entangled vegetation or body parts whenever a lizard is located, in order to avoid any form of impairment, stress or mortality. The method can be improved and adjusted. For example, in their publication in 2015 REFSNIDER et al. proposed to paint the transmitters with acrylic paint, to match the lizard's dorsal coloration and thus reduce detectability by predators. The same method has also been adjusted for the more cylindrical bodyshape of Scincidae (PRICE-REES & SHINE 2011). Different materials for the harnesses have been tried out like Co-Flex® (Andover Healthcare Inc.), or the rubber of inner bicycle tires (VAN WINKEL & JI 2014). However, VAN WINKEL & JI (2014) observed abrasions and skin lesions when using rubber harnesses on geckos after a few weeks, hence discouraging their use in transmitter attachment. Co-Flex® did not have the same adverse effects according to this study.

Mapping of the area and Maxent analysis

The generated maps shown in Figures 4.2 and 4.3 are all accurate representations of the study area when compared to on-site experience. There are some small merging problems, occuring mainly on the edges of the map, outside of the actual study area. It is therefore important to include a wide margin during the recording. Recording of images via UAV proved to be a successful way of capturing maps of small areas. UAVs can hence be a powerful tool to bring large-scale, satellite-based ecological procedures to smaller scales and finer resolutions. Satellite-based maps often fail due to insufficient resolution or varying temporal resolution (HABEL et al. 2016). The ability to generate maps from exactly the required place at exactly the required time will be a big contributor towards more accurate ecological assessments. It also enables novel methods in the assessment of space use, like using ecological niche models to assess home ranges (SILLERO et al. 2021). The method is limited by the size of monitorable area. However, additional loaded battery packs, an on-site loading station or more advanced UAVs can drastically increase the size the of coverable area, should the means for purchase be available. In conclusion, UAV-assisted habitat recording is a fast and efficient way to get high resolution habitat maps. It can be limited by flight time which is dependent on the budget. Although first-time costs can be comparatively high, once acquired, UAV-assisted habitat recording becomes a very time and cost-effective method when used regularly.

Maps were tested for correlation to reduce data size and eliminate redundant data. This resulted in the channels of the RGB map, the Sequoia red, and the Sequoia red edge maps being discarded as it led to the highest variety of non-redundant maps. The AUC values for all classes of the Maxent analysis indicate good model performance (WALDEN-SCHREINER et al. 2017, XU et al. 2019). The map resulting from the Maxent analysis (Figure 4.4) has a resolution of 1 pixel corresponding to a 3.6 x 3.6 cm area. This level of detail is hard to achieve by satellite images (PURNAMASAYANGSUKASIH et al. 2016, LIU et al. 2020). The distribution of habitat structures shows that high vegetation covers roughly three times the area that blackberry, grass and low vegetation do. Sand covers even less ground. Aside from the fact that, from above, higher structures cover up lower structures, the large amount of high vegetation is also explained by the growth surrounding the study area. We estimate that all chosen habitat classes are covering enough land to be viewed as relevant to *L. agilis*. The high amount of missing data has several reasons. First, the water of the pond area has not been classified due to it being irrelevant for non-aquatic *L. agilis*. Second, mistakes in stitching the images together occurring at the edges of the map create areas of no data within the high vegetation outside the study area. Third, it is possible that uniquely coloured patches of vegetation have not been recognised by the model. Inspection of the categorical map (Figure 4.4) shows that those spots are mostly restricted to the high vegetation surrounding the area. Most relevant is the observation that the transition from high vegetation to sand in the northern parts of the study area and at the beach did not work out well. The mistake is probably due to the model not recognising shaded sand as such. This could be improved by adjustment of flight time to eliminate shade in that area, or the inclusion of more shaded areas into the training points for sand in the Maxent analysis. We therefore strongly advise a conscious effort to include shaded areas in training points.

Home ranges

The observed home ranges are larger than most home ranges of sand lizards reported in literature. *Lacerta agilis* home ranges have been calculated all over Europe. Even when looking only at a small subset of studies, results vary greatly and range from as small as 13.6 m^2 (HEYM et al. 2013) to over 1000 m^2 (NICHOLSON & SPELLERBERG 1989). In all cases, average home range size was larger for males, although significance was not always confirmed. We did not find any significant differences between males and females. The lack of difference is, in our opinion, at least partially due to the small sample size of four males versus five females. It remains that the average home ranges in this study are much larger than in other recordings. This has been partially remedied by adding an ecological niche model to the home range calculation and cutting out unused habitat from the home ranges. ENM home ranges are closer to traditional estimates and more accurately portray the habitat actually used (SILLERO et al. 2021). Furthermore, TURNER et al. (1969) tested the relationship between lizard weight and home range size across many lizard species and came to the conclusion that $A = 171.4W^{0.95}$ (A = home range area in m^2 and W = lizard body weight in g) is the best-fitting equation for a rough home range size estimation in lizards. Assuming a weight of 10g for *L. agilis*, we come to a predicted home range size of 1527.604 m^2. Most K95 home range sizes are around that prediction, while MCP home ranges fall below it, and are therefore closer to older predictions. It is noteworthy that with a K95 home range size over 3000 m^2, ID04 and ID06 have home ranges twice as large as TURNER at al. predict. In general, we assume the calculated home ranges to be plausible, but we acknowledge the differences between our recordings and past publications. Many older calculations have used the MCP method or an offshoot of this method, which, as evidenced here as well, result in smaller home range estimates even with the same data set (see also e.g., HANSTEEN et al. 1997, BARG et al. 2005, BÖRGER et al. 2006). Additionally, habitat quality/abundance of key resources can have an inverse effect on home range size, as lower densities of food and other necessities like egg laying sites, hides or basking areas potentially require lizards to move larger distances to satisfy their needs (ROSE 1982). Finally, the number of records has shown to be a strong influence on estimations (NICHOLSON & SPELLERBERG 1989) though no such connection has been found in this case - possibly due to the small sample size. Disturbances by humans, such as the ones observed in our study area, could also lead to larger home ranges, as lizards would need access to resources even whilst avoiding potential human passers-by. Moreover, frequent passing of humans could also affect microhabitat structure. It is possible that disturbance during relocations would lead individuals to move further distances in order to avoid the scientists. Increased activity after handling and observation has been shown in the lizard *Tiliqua rugosa* (KERR et al. 2004). However, in this study, the risk was deemed unavoidable and if this had an effect, some lizards were clearly more affected than others. In future studies, telemetry stations (e.g., GOTTWALD et al. 2019) could be installed, using triangulation to locate tagged lizards within the area without the need for interference as long as the method of attachment was proven good enough not to risk entanglement without regular check-ups.

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

Significance of JACOBS' electivity index

In most cases, JACOBS' Electivity Indices of habitat classes within lizard home ranges are significantly different from Electivity Indices of randomly generated home ranges. Since JACOBS' electivity index calculates the use of resources relative to their availability (JACOBS 1974), this means the individual in question elects to use its surroundings differently from the average of 1000 simulated individuals that have similar mobility but no regard for habitat structure. Therefore, it can be assumed that in most cases, lizard habitat use is non-random.

This is to be expected since habitat composition within the home range is specific to the animal’s needs (BURT 1943). On the other hand, in cases where the observed electivity index is within the confidence intervals of the randomly generated indices, random use of a microhabitat cannot be ruled out. In case of smaller home ranges like ID05, ID14, ID23 and ID25, or fewer relocations like ID25, the method of generating random home ranges could lead to home ranges closer to the observed ones as less options of recombination are available.

Structural preferences and avoidances

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

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

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

Home range size and electivity index

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

Conclusion

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

Overall, *L. agilis* in this population tend to actively incorporate blackberry bushes in their home ranges while on average avoiding high vegetation and sand while grass and low vegetation differ from individual to individual but average out around having no preference.

Most preferences show high individual variation which are most likely based on unexplored characteristics. Overall, we hypothesise that high vegetation and sand are largely unsuitable and incorporated mainly as travel routes between resources with two exceptions: one being that some grass and sand are needed for basking but never anywhere near in the quantities provided, the second exception being that high vegetation does not seem to be avoided in core areas. Overall, preferences in core areas show higher individual variance then in K95 or MCP home ranges suggesting that habitat composition might play a secondary role when determining core activity area.

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

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General Discussion

This illustration was made by Manuel Schumacher and commissioned by the author of this thesis. The artist consented to the inclusion and publication of the illustration.

Combining the results

Aim of this thesis was to establish an ecological profile of a central population of *Lacerta agilis* in the Dellbrücker Heide in Cologne by providing spatiotemporal patterns, weather dependent detection probability, home range, and habitat selection. In addition, I investigated allocation of focus of previous works concerned with home range and habitat selection. The data presented is not only of interest to the local conservation agencies but adds to the overall knowledge on the ecology of *Lacerta agilis* in the centre of its distribution, an area, which has been studied less compared to the range's edges. Additionally, I combined new and established methods with conservation work in mind. Hence, the methods presented herein can be adjusted for many small sized animals as an effort has been made, to keep them general enough to apply to a multitude of situations.

In previous studies, home range and habitat selection have been studied in numerous contexts and on many vertebrate orders. I have summarized the efforts and highlighted the focus in part A of the thesis. For most orders, proportion of studies is higher than proportion of species within the order. I found no evidence for the observed biases being related to relatedness between orders or number of vulnerable species within orders. I recognise however that particularly species rich or species poor orders are almost impossible not to under or overrepresent respectively. As possible causes to explore in the future, I suggest looking into animal size, mobility, accessibility, lifestyle, popularity amongst the public, importance within their ecosystem, or impact on or usefulness to humans. Many orders have not been represented in the sample at all but most of them were species poor or difficult to track or even access. Investigating the most studied species, I found that Testudines and Carnivora, specifically marine turtles and mesocarnivores were among the most studied species. Possible reasons for the focus on sea turtles are, that sea turtles are endangered animals, that are easy to tag with tracking hardware and whose lifestyle and travelling behaviour is still widely unknown to us (e.g., MAKOWSKI et al. 2006, HAWKES et al. 2011, HOENNER et al. 2012, CHRISTIANSEN et al. 2017). Meanwhile studies on mesocarnivores (and the black bear) often focus on intraguild competition and influence on humans (e.g., ARJO & PELTSCHER 2004, GEHRT & PRANGE 2007, GEHRT et al. 2013, MOLSHER et al. 2017). The exception being studies on domestic cats which focus a lot on impact of cats on local biodiversity (HALL et al. 2000, FERREIRA et al. 2011). A closer look at the allocation of focus on topics studied together with home range and habitat selection reveals, that conservation and human influence, intraspecific differences and home range shifts/exploratory behaviour are most often studied in concordance with home range and habitat selection.

Summarizing, the review gives first insights into allocation of focus in orders and topics between vertebrate groups but could not detect any apparent connection between attention allocated to a group and its diversity or relatedness to other groups. Nevertheless, identifying gaps and the reasons behind them is important with regards to the fast decline of global biodiversity (BROOKE et al. 2014). In several publications (e.g., AMORI & GIPPOLITI 2000, BONNET et al. 2002, CLARK & MAY 2002, LAWLER et al. 2006), the presence of bias for certain groups is assessed on very large scales but not on order level across all vertebrates as discussed here. I hope this review prompts researchers to investigate smaller groups and look for explanations on lower scales as for example done by (BROOKE et al. 2014), who found that body size and range size had a positive effect on allocation of focus in carnivores while omnivory reduced interest. They concluded and criticised, that the need for conservation had no significant influence on popularity of a species as a research topic. Meanwhile, BONNET et al. (2002) highlighted that researchers are often most interested in papers on their own study subjects, which could lead to a cascading effect in which papers based on model organisms or commonly studied organisms are viewed more sympathetically during peer review and editorial decisions than publications on more obscure species. Scientists should not aspire to focus on everything equally, as differences in urgency and importance definitely exist between groups and topics (MASTER 1991, BROOKE et al. 2014). Instead, I call for a critical analysis of the distribution of attention in order to identify gaps in knowledge as a first step, with the following steps being the determination and evaluation of possible reasons for the observed gaps and assessment of importance to fill them. In 2002, CLARK & MAY argued, that conservation is often limited to focus on charismatic species like birds and mammals in order to retain public support and corresponding funding. This shows potential reasons for allocation of focus to sometimes come from external pressures rather than a lack of interest of researchers themselves. Finding, evaluating and, if necessary, working on abolishing these reasons are an important step in ecological studies. However, knowing the current distribution is prerequisite for identifying the areas, where the acquisition of more information is most urgent. The rest of my thesis concerns itself mainly with *Lacerta agilis*, its home range and habitat selection as well as its thermal ecology and spatiotemporal patterns with a focus on conservation questions. With that, I focus on the same topic as many before us with an animal, belonging to a group that might be considered slightly understudied. This again highlights the importance of also considering the species and not just the order when choosing a study subject. The decline of *Lacerta agilis* and its proximity to humans and subsequent prominence as subject of compensatory measures in the centre of its distribution warrants a closer inspection of its ecology.

In part B, the main goal of the thesis is to establish an ecological profile of *Lacerta agilis* in the Dellbrücker Heide in Cologne. In chapter 2, together with others, I assessed, if central populations of *Lacerta agilis* have different spatio-temporal patterns in habitat choice than much studied populations at their range's edges. If central populations are different from populations at the periphery, it is important to consider local populations for conservation and not rely on literature from far away populations. In this chapter, we showed, that lizard space use cannot be explained by a combination of season, weather or microclimate. While lizards may show variation in distance to habitat structures and microclimate choice during the day, those variations are small. We discuss that the broad niche and independence between space use, weather/microclimate conditions and seasonality of the studied population is a stark contrast to populations at the range's edges where *L. agilis* is reported to be more specialized (e.g., JACKSON 1978, HOUSE & SPELLERBERG 1983b, AMAT et al. 2003, NEMES et al. 2006, ČEIRÂNS 2007, GROZDANOV et al. 2014, WOODFINE et al. 2017, PRIETO-RAMIREZ et al. 2018). Overall, in this population, *L. agilis* occupies a broad climatic niche independent of sex and only slightly different for subadults. They also show broad habitat niches with subadults again showing slightly narrower niches. Differences between subadults and adults are very small but hypothesised to be due to the smaller size of subadults, making them inferior competitors or potential prey to the adults and leading to the need for subadults to thermoregulate at different frequencies and conditions than adults. Only a few slight differences in microhabitat and distance data have been found between males and females which are hypothesised to be due to male wandering behaviour during the breeding season. As described, according to our observations, lizard space use cannot be explained by a combination of microhabitat, weather, microclimate and seasonality. Therefore, the slight differences in microhabitat choice and weather preferences between time of day, sex and ontogenetic stage are better explained by factors related to intraspecific interactions or size differences. The eurybiontic lifestyle of lizards in this population contrasts with the reports from the range's edges, where the species becomes stenobiontic. This confirms, that in the study, conservation, and management of central populations of *L. agilis*, data from the range edges might not apply and local data is needed.

We now know, that this central population of *Lacerta agilis* has different weather and habitat dependent spatio-temporal patterns in weather and microhabitat choice from populations at the range's edge, but we do not yet know the weather and habitat preferences of the population in detail. While principal component analysis as applied in chapter 2 is a great tool for reducing a large number of variables to a manageable number without taking explanatory value out of the variables, it does so at the cost of the ability to explore concrete variables in detail. Conservation and management especially however favour concretely defined parameters and statements over difficult to unravel principal components (See examples of monitoring guides: SCHNITTER et al. 2006, ALBRECHT et al. 2013, LÜTTMANN et al. 2017, HESSEN MOBIL 2020). Here, I focus on three further questions to define the ecology of *L. agilis* in this population: What are the detection rates and by extension activity rates of *L. agilis* depending on weather conditions? What is the home range of individuals of *L. agilis*? And which microhabitat structures do they prefer or avoid in their home range compared to their availability? I focus on these variables, because despite the broad range of weather and habitat tolerance of *L. agilis* in this population, there are bound to be favoured conditions. Favoured weather conditions are important to know for example for time effective monitoring, relocation efforts, or environmental impact assessments. Meanwhile, home range and habitat selection have been shown to be a widely applied technique to characterize habitat selection and is important in species conservation and associated habitat management.

In chapter 3 of my study, I found out, that the majority of *L. agilis*' detection probability can be explained by five weather variables: average maximum temperature six hours prior to the sampling interval, mean wind speed and relative humidity during the sampling interval, mean precipitation duration in the 24 hours before the sampling interval and sunshine duration in the three hours prior to the sampling interval. Temperature has a squared relationship with detection probability, peaking around 20°C, while wind speed and relative humidity have a negative linear relationship and precipitation duration and sunshine duration have a positive linear relationship with detection probability. In other words, *L. agilis* prefers dry and sunny weather conditions with temperatures around 20°C prior to their activity phase and low wind speeds during their activity. Additionally, lizards are more likely to be active, if it rained a lot in the 24 hours prior, but not immediately before. These results are in line with other studies, especially in northern and central Europe (e.g., HOUSE et al. 1979, HOUSE & SPELLERBERG 1983b, DENT & SPELLERBERG 1987, BLANKE 1999, EDGAR & BIRD 2006, FEARNLEY 2009, HELTAI et al. 2015) suggesting weather dependent activity of *L. agilis* is similar. However, it is important to note that these exclamations are only true within the observed weather variables, for which data is present. Despite this similarity, this is not to be viewed as a contradicting our previous statement on the distinctness of central populations versus the populations at the range’s edge. Differences between northern and this central population lie in the availability of favourable weather conditions and northern populations often show very distinct habitat and microhabitat choice in order to compensate for worse weather conditions (EDGAR & BIRD 2006, BLANKE & FEARNLEY 2015). The unpruned regression tree with the variables deemed relevant by the Bayesian model shows concrete threshold values for the different variables and explains, which combination of values leads to which encounter rates. The tree shows for example multiple options for high encounter rates: Humidity has to remain below 63.7%. If it is, the highest encounter rates are expected in sunny conditions with low, but not absent wind speed. Alternatively, high encounter rates are also possible at higher wind speeds if average max temp 6 hours prior remained below 21.1°C and humidity either remained below 35.5% or, if it was higher, sunshine duration 3 hours prior should have been above 0.038 hours per 10 minutes (meaning on average, in 10 minutes, the sun would need to shine for at least little over 2 minutes) or be above 0.011 hours per 10 minutes and average temperature 6 hours prior should be above 20.6°C. While the Bayesian model identifies the important variables, the regression tree puts them into a context, that is easy to understand and convenient to predict with common weather forecasts as it provides concrete thresholds. This and the fact, that weather data can be readily available makes this two-step method useful in conservation. However, due to the large number of encounters needed, the method would only be useful in previously studied populations or in long-term monitoring.

The home range and habitat preferences of *L. agilis* in this population have been studied in chapter 4 of the thesis. One key result is that in this population, lizards tend to prefer blackberry bushes, while sand and high vegetation are mostly used less compared to their availability. Lizards show on average neither strong preference nor avoidance for grass and low vegetation but do show individual differences. The importance of blackberry bushes is hypothesised to be due to blackberry providing good protection while also not growing too tall in the area and thus letting through some sunlight as vegetation openness is recorded to be beneficial for *L. agilis* (MIZSEI et al. 2020). Tall vegetation structures like trees and tall bushes casts a lot of shade without really providing much protected ground space for lizards to hunt. As sand lizards are not particularly arboreal, it makes sense that they would avoid tall vegetation. While sand is certainly beneficial to thermoregulation, wide open areas of sand are unsuitable for lizards due to the exposition to predators which leads to lizards not using the available sand areas to their full extend. Additionally, in core areas, variability in electivity is overall higher between individuals than in K95 and MCP home ranges leading to the conclusion, that core areas are not defined by certain habitat compositions but other, unstudied factors. This also supports our findings in chapter 2, that microhabitat conditions for lizards are overall favourable enough to not be a crucial concern for lizards and overlap broadly with lizards' range of tolerance. In this population, home ranges of sand lizards are quite large, which could be a sign of sub-optimal resource distribution or habitat quality (ROSE 1982), forcing the animals to move further to satisfy their needs. It could also be an artifact created by human disturbance from researchers and other people creating avoidance behaviour in the animals. Depending on the calculation method of home ranges, home range size also correlates with observed preferences or avoidances. Size of home ranges calculated with 95% kernel density estimation correlate negatively with the electivity index of grass and positively with the electivity index of sand. These relationships are lost when an ecological niche model is added to the home range calculation to cut out unused areas, suggesting that the assumption, that home ranges might include areas only used as travel routes between resources might be correct. It further suggests, that in that case, sand is preferable to grass possibly due to ease of traversing it quickly or the aforementioned benefits for thermoregulation. No significant difference between males and females have been observed, which is mainly allocated to the small sample size, but could also be further proof of the previous findings made in chapter 2, that males and females are just not very different in their ecology in this population, especially since previous differences in microhabitat selection have been allocated to male behaviour during the breeding season which was long over at the point of this study (BLANKE & FEARNLEY 2015). I see this study as a notable step in improving population specific conservation efforts. Not only do I highlight lizard habitat preferences in the area but I also show the usefulness of UAVs in crafting habitat maps of high spatial and temporal resolution to analyse habitat use of species, whose selection process happens mainly on small scales. Additionally, my collaborators and I developed a method to successfully tag *L. agilis* with radio-transmitters.

To summarize the ecological profile of *Lacerta agilis* in the Dellbrücker Heide:

Spatio-temporal patterns in space use of *Lacerta agilis* in this populations are unrelated to weather, seasonality and microhabitat choice. While small differences between subadults, males and females can be found, and space use is somewhat different depending on time of day, *Lacerta agilis* overall occupies a broad niche in this central population and can tolerate a wide range of weather conditions and habitats. Favoured conditions are however distinguishable and *Lacerta agilis* in the Dellbrücker Heide prefer incorporating blackberry bushes in their home ranges while avoiding the majority of present tall vegetation and sandy areas. Lizards are most active during dry and sunny weather after temperatures reached 20°C and while wind speeds are low. Lizards are not very active at humidity above 63.7% and can be encountered with reliable frequency in different conditions when below that threshold.

These results paint a familiar, yet more precise picture of the ecology of *Lacerta agilis* when compared to previous knowledge. At the edges of their distribution like in northern Europe or the Pyrenees, *Lacerta agilis* has been proven to be a stenobiontic species and restricted to specific habitats with high sun exposure (BÖHME 1978, EDGAR & BIRD 2006, AGHASYAN et al. 2021). Differences between sexes and/or age in habitat use and thermal ecology have been shown for populations in the Pyrenees (AMAT et al. 2003), Romania (NEMES et al. 2006), Latvia (ČEIRÂNS 2007), Bulgiaria (GROZDANOV et al. 2014) or the United Kingdom (WOODFINE et al. 2017). These results show a very different picture where lizards in this population from the core distribution are much more generalist and thrive in a large number of microhabitats. We do not observe large differences in lizard habitat choice or thermal ecology based on weather, time of day, time of year, or habitat composition and observe only small differences based on ontogeny and sex. This proves the principal of KÜHNELT (1943) true for *Lacerta agilis*, that a widespread animal can occupy a greater variety of ecological conditions in the center of its distribution than at the edges. To my knowledge, this is the first time this principle has been tested for *Lacerta agilis* and in my opinion, it is of special importance for the species due to its frequent need of management. The logical conclusion of KÜHNELT's principle being true for *L. agilis* is that we cannot rely on literature from elsewhere to manage local populations no matter where we are. Local knowledge is of utmost importance. At the edges of its distribution, management according to knowledge from the centre could be devastating to a population, while in the centre, many opportunities for suitable conditions might be overlooked or misinterpreted leading to incorrect assessments and wrong decisions. Despite broad tolerance, the results reveal clear preferences for dry and windstill weather with moderate air temperatures as well as a preference for blackberry bushes and avoidance of high vegetation and sand. Favourable weather conditions are in accord with other observations from around the world (e.g., AMAT et al. 2003, BLANKE 1999, FEARNLEY 2009, HOUSE et al. 1979) but fail to be incorporated into monitoring guides

(ALBRECHT et al. 2013, LÜTTMANN et al. 2017, HESSEN MOBIL 2020) which highlight the importance of correct weather conditions to maximise encounter chances but only give a brief and unprecise description of weather for all reptiles. The method used in this thesis works twofold and first filters best explaining variables out of a broad collection of possible candidate variables and then uses those best explaining ones to describe real weather conditions that can be checked at the daily forecast with the help of a CART model. While this method requires pre-collected data, I expect it to be a great help in maximising encounter rates when consistently applied to studied populations. Similar to weather preferences, my findings on habitat choice of *L. agilis* agree with the general characterization found in literature. While *L. agilis* occupies a wide variety of habitats across its distributional range, common characteristics of sand lizard habitat are that they are sun exposed and structure rich with bare ground for egg incubation, opportunities for basking and cooling off (HOUSE & SPELLERBERG 1983b, BLANKE & FEARNLEY 2015). It is further stated, that for *Lacerta agilis*, the general description of suitable habitat is open, bushy habitat which is also true for this population (HOUSE & SPELLERBERG 1983a, CORBETT 1988, SPELLERBERG 1988, BLANKE & FEARNLEY 2015). The main new finding in terms of habitat choice is the preference of blackberry bushes over other vegetation similar in height. *L. agilis* has been cited to show no close relationship with any plant species and instead, vegetation structure is more important to sand lizards (GLANDT 1979, HOUSE & SPELLERBERG 1983a, DENT & SPELLERBERG 1987, BLANKE & FEARNLEY 2015). My findings do not necessarily contradict these assessments but could also display a clear preference for one species due to structural properties over others. While overall vegetation structure is often characterized as open, sparsely covered (GLANDT 1979), or structurally diverse (BLANKE & FEARNLEY 2015), I could not find any information of what properties sand lizards look for in singular vegetation structures. In future studies, a clear investigation of what makes vegetation structures attractive to *L. agilis* could bring many advancements in habitat management for the sand lizard. Last but not least, in these studies, I provided an effective way of attaching radio transmitters to sand lizards, which is useful in management as well and I was among the first to use UAVs for high resolution habitat monitoring for such small organisms with similar pioneer studies focusing on other animals (e.g., HABEL et al. 2016, FRITZ et al. 2018, OOSTHUIZEN et al. 2020). My aim was to keep this study focused on and suitable to conservation efforts. However, the integration of my work is not just dependent on scientific methods and approaches, but by a multitude of things as conservation is a complicated topic that does not only include science and therefore warrants separate discussion.

Integrating this work into conservation

Problems and challenges

Conservation is a wide field that brings people from lots of backgrounds together. With this diverse cast of stakeholders comes a large diversity of interests, opinions and widely varying areas of expertise. As such, conservation is not without its problems and challenges, some of which have found discussion in literature (e.g., GLASBERGEN 1996, BOTTRILL et al. 2011, CANESSA et al. 2015, EHRENFELD 2000). Much of the work presented in this thesis is meant to be actively used in conservation. I see especially the method for determining habitat use based on high resolution habitat maps (chapter 4), the use of radio transmitters on *L. agilis* (chapter 4), and the work on weather dependent detection probability (chapter 3) as helpful and applicable in day-to-day conservation. It is therefore important that we understand how new approaches find their way into conservation practices and what known problems I should be aware of and avoid if I want my methods to reach the intended audience. Here I focus on examining problems, mainly between my branch (the scientists) and the branch I want to be able to use these methods (the practitioners). I want to highlight what we see as the main challenges of conservation concerning those two groups. This is not to say, that these are constant, ever-present barriers but rather potential challenges to be aware of. I aspire to examine these barriers from a neutral perspective and with the ultimate goal to understand how to make my current and future work better available to conservation practitioners.

The problem of communication and access

Conservation as a discipline does not just include scientists from biological or environmental sciences but people from all possible backgrounds (SUTHERLAND et al. 2018). However, researchers, policy makers, practitioners and other stakeholders do not always see eye to eye leading into research not always being implemented (LAUBER et al. 2011). For one, methods developed, or observations published by researchers can be ignored or overlooked by practitioners (TEAR et al. 1995, KNIGHT et al. 2008). One reason can be a missing understanding or dismissing of the methods and results presented by science (PRENDERGAST et al. 1999). According to GERMANO & BISHOP (2009) and GERMANO et al. (2015), translocations of reptiles often fail with one of the prime reasons for failure being the release into poor habitat which can be viewed as a failure to consult the scientific basis. They further state that economically driven translocations, such as those employed as compensation measures for a developmental project tend to fail more often than those with conservation background. GERMANO et al. attribute this to lack of transparency and failure to document outcomes (GERMANO et al. 2015). On the other hand, researchers can fail to deliver valuable information when it is most needed, as was a case described by LINKLATER in 2003 where research on rapidly declining rhinoceros species was focusing on laboratory studies rather than ecological studies that could have informed conservation efforts. There is also a deficit in reptile extinction risk research which leads to most reptiles being assessed primarily on the size of their geographical range rather than population trends (TINGLEY et al. 2016). Similarly, gaps in research on the effectiveness on restauration efforts have been observed by HIGGS in 2005. Scientists might think their research adds towards conservation efforts while failing to address the questions most relevant to conservation practitioners or neglect to observe the problems at hand from other viewpoints like the political, social or economic standpoint (EHRENFELD 2000, STINCHCOMBE et al. 2002, MCNIE 2007). As a more concrete example, when asked how I could make my study visible to practitioners, Graduate Biologists and staff members of the “Biologische Station Bonn/Rhein-Erft e.V” MONIKA HACHTEL and PETER SCHMIDT stated that, in general, German conservationists do not subscribe to English speaking scientific literature but rely mostly on German sources published by and directed at conservationists (M. HACHTEL & P. SCHMIDT pers. comm). According to HACHTEL and SCHMIDT, new methods are rarely acquired from purely scientific literature, as it is often too broad or lacking applicability. Consequently, new methods mostly establish themselves through a combination of conservationist publications, mouth-to-mouth propaganda, and conferences. This is hardly surprising as scouring the broad, scientifically focused scopes of journals costs a lot of time for the occasional article, that might find application in practices while there are entire professional journals dedicated wholly to their work. This however also creates a problem as scientists (especially young ones) are encouraged to publish in high-impact, scientific journals in order to increase visibility and further their career (e.g., SWAN & BROWN 2004, PASQUINI et al. 2014, BERENBAUM 2019) which prevents them from publishing the same work in regional journals and the methods would have to be published again separately. These personal accounts of the state of affairs in German conservation might not apply everywhere but illustrate a problematic situation, where conservationists realistically cannot afford to spend the time and money to search through the vast number of publications for potentially interesting new applications while scientists usually have to aim for publishing in high impact scientific journals. The problem of communication between science and conservation already exists in a very fundamental part of how both disciplines are structured and it takes a conscious effort (or considerable luck) from either side to exchange ideas through the avenue of mouth-to-mouth propaganda, a separate publishing of the relevant methods in conservationist literature or keeping up to date with literature of which most articles might not be of interest.

Evidently, problems emerge from both sides and in many cases come down to failed communication and both sides clinging to established habits (PLATT 1964, CLARK 1993, NICHOLS & WILLIAMS 2006, LAUBER et al. 2011). In conservation, different types of learning must be applied according to GLASBERGEN 1996. Those types are technical learning or the learning of new methods to achieve goals, conceptual learning or the learning of which goals are necessary and social learning or the learning how to communicate knowledge and information between stakeholders. GLASBERGEN further stated that while science is always eager to contribute to technical and conceptual learning, social learning is often neglected despite being the prerequisite to advance both other types. In other words, for research to be applied in conservation, scientists and practitioners must first learn to communicate with each other. This claim, while seeming self-evident in theory, is not always applied as evidenced by the examples already discussed. On the other side, interviews conducted by LAUBER et al. (2011) have shown, that good communication between all parties during conservation projects led to successful studies and a positive response from stakeholders. Communication facilitates the availability for sufficient labour and funding to make scientific information on a required topic available to practitioners either in the form of published research or expert opinions. The establishment of common goals, all stakeholders be they scientist, economist, politician, etc., can agree upon leads to everyone knowing what to expect and staying the course together (LAUBER et al. 2011). All parties need to learn how to apply the mix of knowledge, how to create new knowledge as needed, and strive to eliminate the biases towards each other together (CLARK 1993). While conservation is important in its own, social and economic reasons for conservation are also beneficial as they improve public willingness to engage in conservation (BOTTRILL et al. 2011). LAUBER et al. summarize their findings from the perspective of a scientist in a simple sentence: “Increasing the probability that conservation is guided by science depends on the recognition that science is only one of many elements that determines whether conservation will be successful.”

The problem of limited resources

Another problem in conservation is the availability of time and resources (BOTTRILL et al. 2011, HACHTEL & SCHMIDT pers. comm.). For tools and methods to be applicable in conservation, they need to be cheap enough and easy enough to see widespread use (STEPHENSON 2020). STEPHENSON identifies data availability, data quality and usability, willingness to collect and use data, and financial and technical capacity as main prerequisites for enabling monitoring in the first place (STEPHENSON 2020). The question how much monitoring is needed is a difficult one as more monitoring means more delays and more costs. Furthermore, some are of the opinion, that using monitoring to collect information for information's sake is wasting these already thinly spread resources (e.g., NICHOLS & WILLIAMS 2006, CANESSA et al. 2015). On the other hand, many people would like to see more monitoring over the course of conservation projects. As discussed above, GERMANO & BISHOP (2009) and GERMANO et al. (2015) state, that economically driven translocations, such as those employed as compensation measures for a developmental project tend to fail more often than those with conservation background in part due to a failure to document outcomes adequately (GERMANO et al. 2015). This observation has also been shared by (TINGLEY et al. 2016). Another proposition, that includes more monitoring is the increase in use of adaptive management, where monitoring is not only used before the management actions to assess system state, but also during the implementation of measures to assess progress and efficacity and to inform possible changes in management course going forward (NICHOLS & WILLIAMS 2006, TINGLEY et al. 2016, YOUNG et al. 2016). Another approach is to avoid simple broad scale monitoring conducted in hopes to detect declines where possible and include investigations of potential causes and remedies for possible declines directly into monitoring from the beginning (NICHOLS & WILLIAMS 2006). Furthermore, POLLOCK et al. (2020) criticised that in praxis, conservation evaluation often focuses on habitat quality and quantity as indicators of biodiversity and neglects to consider biodiversity itself which can lead to parts of an ecological community to be overlooked by broadly applied, habitat focused conservation measures. In conclusion, when it comes to the question of limited resources, the push seems to be to work smarter and not harder and a call is made to use resources wisely but there are many opinions on what is important and how to achieve it.

Integrating the work

In my opinion, for this work to be applied in conservation, it needs to fit into the existing framework of methods and circumvent the usual problems of communication and resources.

Here, I argue, that this work can fulfil those requirements. As established, the need for pre-existing knowledge on habitat and weather preferences is of utmost importance in the monitoring of reptiles and listed as a prerequisite for successful visual encounter studies. This information is however not always given and, as proven in chapter 2 in Part B, can change even within a species if the species is widespread enough. Making inferences about population based on studied populations far away can overall lower success rate. Our methods to assess weather-based detection probability described in chapter 3 give conservationists the means to assess populations themselves. I admit that the methods take a while of observation, but especially in the context of adaptive management, where populations are monitored for extended periods of time, local populations can be examined to the benefit of future studies in the area. Meanwhile my work on using unmanned aerial vehicles to assess habitat of a small to medium sized area can be done within a few days, preparation included, once the method is established and if data on the animals is already present. Even when not, the method can be a great help in translocation projects to find areas that are structurally similar to the original location. If visual encounter surveys are ever conducted via UAV as is already studied for certain groups including reptiles (e.g., HODGSON et al. 2017, ANICETO et al. 2018, ROGERS 2018, HUERTA et al. 2020), collection of necessary field data could even be included within the process. One problem I see is the reported conundrum that conservationists do not have the time to look for potentially interesting studies among scientific literature while I did not publish it in media, conservationists do track regularly. For now, I see only one solution, which is to further mouth-to-mouth propaganda as much as possible through conferences and dialogue. This approach has already been started by the participation and presentation of some of the methods by myself and RIEKE SCHLUCKEBIER at the “Internationale Fachtagung zur Zauneidechse in Offenburg” of the DGHT and then again by myself at the “30. Internationale Naturschutztagung Zoologischer und botanischer Artenschutz in Mitteleuropa“ in Jena which was met with interest at both occasions. Lastly, this chapter is my attempt at including and hence understanding the view of conservationists and thereby avoid approaching the problem from only my background as a scientist.

Personal outlook

During my thesis, I was fortunate enough to not only learn a lot of theoretical approaches to ecological topics, but also about practical conservation. I am grateful, that my studies brought me into contact with theoretical researchers, conservation practitioners and everything in between in equal measure. I learned the value of the home range concept and how to quantify habitat choice, weather preferences and other ecological values from working with excellent researchers while also being able to see, how practical conservation works and implements their knowledge. Be it learning radio-telemetry with the help of the BAFF, getting taught how to operate a drone during a weekend, visiting a DGHT conference on the conservation of the sand lizard, or just discussing topics with researchers at the LIB, it became apparent, that bridging research and practices was what interested me the most about my work. In this thesis, I started to look for gaps in research on home ranges and habitat selection in vertebrates, I furthermore aimed to provide data relevant to the conservation of local populations of *Lacerta agilis* as I learned of their continuous relevance to conservation projects and compensation measures. During the whole time, I tried as best as I could, to keep the methods easily applicable and effective for practical use for the same reason. My goal going forward is to continue to work on topics that connect research with conservation and allow me to deepen my understanding of both and to contribute to the communication between science and conservation. My concrete goals would be to further investigate and fill the gaps in knowledge on home range and habitat studies and expand the methods I learned over the years to new applications, modifying and refining them. There are many small animals, the study of which would benefit from high resolution habitat maps via UAV. Similarly, there are many opportunities to improve current guidelines on monitoring animals by more closely assessing weather dependent detection probability. Whatever I will end up doing, I hope for my past and future work to remain relevant to conservation and science alike.

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This illustration was made by MANUEL SCHUMACHER and commissioned by the author of this thesis. The artist consented to the inclusion and publication of the illustration.

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This illustration was made by MANUEL SCHUMACHER and commissioned by the author of this thesis. The artist consented to the inclusion and publication of the illustration.

Publication List

- RYSTROM, T.L., V.F. CLEMENT, I.P. RICK, T.C. BAKKER, & M. MEHLIS (2018): Shoal sex composition and predation risk influence sub-adult threespine stickleback shoaling decisions. – Behavioural Processes, **157**: 495–501. doi: https://doi.org/10.1016/j.beproc.2018.06.009.

The following articles have been published based on my doctoral studies done in this thesis. One chapter of this thesis corresponds to one article. The publications corresponding to the chapters are noted at the beginning of each chapter.

- CLEMENT, V.F., & D. RÖDDER (2021): Playing favourites – a review and discussion on the allocation of vertebrate orders and foci in home range and habitat selection studies. – North-Western Journal of Zoology, **17(1)**: 134–148. Article No. e203801.
- CLEMENT, V.F., R. SCHLUCKEBIER, & D. RÖDDER (2022): About lizards and unmanned aerial vehicles: assessing home range and habitat selection in *Lacerta agilis*. Salamandra **58(1)**: 24–42.
- SCHMITZ M.L., V.F. CLEMENT, P. GINAL, & D. RÖDDER (2022): Spatiotemporal patterns of habitat use by the sand lizard (*Lacerta agilis* LINNAEUS, 1758): Effects of climatic seasonality? – Salamandra, **58(4)**: 302-316.
- CLEMENT, V.F., J. EDANACKAPARAMPIL, L.M. SCHMITZ, R. SCHLUCKEBIER, & D. RÖDDER (2022): Weather-related detection probability of *Lacerta agilis* LINNAEUS, 1758 within the core range in western Germany. – Basic and Applied Herpetology, **38**: 1-21. doi: https://doi.org/10.11160/bah.242.