WSL

Master Thesis

Forests suitable for Greater Mouse-eared Bat's (*Myotis myotis*) foraging

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Abstract

Habitat shift caused by human impact on vegetation structure and composition poses a great threat to species like bats, since many of them are highly dependent on certain habitat types. Due to considerable population losses until the 1970s, Greater Mouse-eared Bats (*Myotis myotis*) are listed as vulnerable on the Swiss Red List and are protected under federal law. However, their habitat consisting of maternity roost, commuting corridors and foraging areas are still threatened by various impacts like renovations of old buildings, fragmentation of the habitat, light pollution or intensification of agriculture. Silvicultural practices altered Swiss forests over centuries, whereby today spruce monocultures and mixed forests are widespread. Since Greater Mouse-eared Bats are able to glean their prey from the ground, special requirements for their foraging habitat were assumed. To identify the important forest structures defining suitable foraging habitat, the activity of Greater Mouse-eared Bats was recorded in different types of forests (assumed suitable, less suitable and not suitable) and various forest variables based on LFI4 (Swiss National Forest Inventory) were listed. During three nights of recording at totally 216 sampling sites around 18 maternity roosts of *M. myotis* in Switzerland, a higher activity in foraging areas classified as suitable could be found. Characteristics indicating a higher bat activity were identified as single-layered pure deciduous or mixed forests, with a closed canopy, a free flight space, hardly any shrub layer and trees older than "young timber". Surprisingly, the herbaceous layer did not predict Greater Mouse-eared Bat activity, though its influence should be further investigated; especially since the guidelines to substantiate the Forest Policy 2020 intend to promote light forests with a diverse herbaceous layer. With the insights of this study defining the preferred forest variables of Greater Mouse-eared Bats, the classification model based on LiDAR data (Airborne Light Detection and Ranging) to predict suitable foraging habitat can be refined. This enables a preservation of preferred forests throughout Switzerland and therefore the protection of an important part of Greater Mouse-eared Bat habitat.

Keywords: Chiroptera, habitat modelling, foraging habitat, vegetation structure, gleaning, echolocation, generalized linear mixed modelling

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List of abbreviations

UNECE	United Nations Economic Comission for Europe
UNEP	United Nations Environment Programme
Eurobats	Agreement on the Conservation of Populations of European Bats
BAFU	Bundesamt für Umwelt (= FOEN)
FOEN	Federal Office for the Environment (= BAFU)
NHG	Natur- und Heimatschutzgesetz
WSL	Swiss Federal Institute for Forest, Snow and Landscape Research (Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft)
SSF	Bat Conservation Switzerland (Stiftung zum Schutze unserer Fledermäuse in der Schweiz)
SWILD	Urban Ecology & Wildlife Research
SZKF	Schweizerisches Zentrum für die Kartografie der Fauna
DDT	Dichlorodiphenyltrichloroethane
LiDAR	Light detection and ranging
LFI	Swiss National Forest Inventory (Schweizerisches Landesforstinventar)
DBH	Dominating diameter at breast height
DDOM	Mean DBH of the strongest trees
M. myotis	*Myotis myotis*, Greater Mouse-eared Bat
M. blythii	*Myotis blythii*, Lesser Mouse-eared Bat
GLM	Generalized linear model
GLMM	Generalized linear mixed model
AIC	Akaike's Information Criteria
WGM	Layer of degree of mixture of Swiss forests
DTM25_L2	Digital Elevation Model
SwissTLM^{3D}	3D Vector Dataset
CLIMAP	Weather data of MeteoSchweiz

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Introduction

The structure and composition of vegetation are important factors affecting the species composition in different types of communities (Begehold et al., 2015; Finegan, 1984; Odum and Barrett, 1971). Human impact on vegetation structure can alter the habitat, the species composition and abundance strongly (Becker et al., 2017; Brockerhoff et al., 2008; Du Bus De Warnaffe and Deconchat, 2008). Especially species like bats (order Chiroptera) with a low reproductive rate (Barclay et al., 2004), longevity (Wilkinson and South, 2002) and a high metabolic rate (Speakman et al., 2003) are at risk of population decline or extinction due to habitat change (Voigt and Kingston, 2015). Therefore, detailed knowledge about the habitat requirements of bats is crucial to be able to take effective conservation measures.

Most of the 30 bat species in Switzerland spend at least part of their lives in forests, either for hiding, rearing the young or hunting (Gebhard, 1997). Since forests in Switzerland have been exploited and shaped by humans for many centuries, the changing managements entailed both positive and negative effects on species (Brockerhoff et al., 2008; Imesch et al., 2015). Until the 18th century, the agricultural and silvicultural land use of Swiss forests including wood pasture, litter raking, hay-making, coppicing and intense logging, had created a light forest with a high biodiversity which, however, was not sustainable (Gimmi et al., 2008; Rackham, 2008; Sebek et al., 2015). In the 19th, century coppice forests with originally broad-leaved species were intensively reforested with spruce (*Picea* sp.), since they were easy to establish and manage (Geburek and Myking, 2018; Spiecker, 2003). The woodland management shifted from coppice stands to high forests, what led to dark, homogeneous and coniferous forests (Imesch et al., 2015; Schuler et al., 2000).

Despite low incidence of light in high forests with closed canopies, the ground vegetation is often able to grow densely in many areas of Switzerland, since high nitrogen inputs from agriculture and transport has been reaching the forest via water or air (Baeten et al., 2009). 95% of Swiss woodland exceed the critical load of 30kg nitrogen/(ha x year) set by the United Nations Economic Comission for Europe (UNECE) (Bobbink et al., 2011; Schweizerischer Bundesrat, 2017). The consequences are, amongst others, a decline of biodiversity and a higher amount of nitrophilous plants like blackberries (*Rubus fruticosus agg.*), raspberries (*Rubus idaeus*), stinging nettle (*Urtica dioica*), broad buckler fern (*Dryopteris dilatata*) and elder (*Sambucus sp.*) (Braun et al., 2012; Schweizerischer

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Bundesrat, 2017). To reduce these deficits, the Federal Council defined enforcement guidelines to substantiate the Forest Policy 2020 (Bundesamt für Umwelt, 2013) and the Biodiversity Strategy (Schweizerischer Bundesrat, 2012). The aim is to restore and maintain light forests with a diverse herbaceous layer, whereby measures like logging and mowing are adapted (Imesch et al., 2015).

Although biodiversity is likely to benefit from these interventions, endangered species like the Greater Mouse-eared Bat (*Myotis myotis*) or the Wood Warbler (*Phylloscopus sibilatrix*) seem to need open ground beech forests (*Fagus sylvatica*) with a dense canopy (Awa et al., 2018; Güttinger, 1997; Marti, 2007; Pasinelli et al., 2016; Rudolph et al., 2009). However, beech forests are scarce and fragmented across vast parts of Switzerland and their global range (Begehold et al., 2015; Delarze et al., 2016). Nowadays, Swiss forest consists of 18% beech trees, whereby most of them occur in mixed forests (Abegg et al., 2014). In addition to the already small proportion of suitable hunting areas for the Greater Mouse-eared Bats or nesting areas for the Wood Warbler respectively, the targeted forest management to maintain light forests with a dense herbaceous layer might be unfavourable for these threatened species by narrowing their habitat even more.

Even though bats are the second largest mammalian order and provide essential ecosystem functions and services like pest insect suppression (Bader et al., 2015; Kunz et al., 2011; SPSC, 2010), 15 of the 30 bat species in Switzerland are listed as critically endangered, endangered, or vulnerable on the Swiss Red List (Bohnenstengel et al., 2014). Due to the alarming state of bat populations in the last decades, all bat species in Switzerland became protected under federal law in 1966 (NHG, Natur- und Heimatschutzgesetz) (BAFU, 2012; Bohnenstengel et al., 2014) and an international agreement on the conservation of European bat populations was established in 1991 (UNEP/Eurobats) (Hutson et al., 2015). Bat species which live and bear young in attics and hunt in strongly structured landscapes like farmland and forests are the most threatened species since these habitats are strongly influenced by human (Bohnenstengel et al., 2014). These characteristics also pertain to the Greater Mouse-eared Bat, which is listed as vulnerable on the Swiss Red List. Until the second half of the 20th century, *M. myotis* was widespread in Switzerland and could be found in almost every church attic (Dietz et al., 2007). Due to pesticide usage in agriculture and forestry (DDT) and highly toxic wood preservative (lindane), whereby the bats absorbed the

toxins through eating insects and living in attics, considerable population losses were caused up to the 1970s (Dietz et al., 2007; Meschede and Rudolph, 2004). But even after a ban on these highly toxic substances, today's pesticides also pose a risk to bats and some of the roosts are still contaminated (Stahlschmidt and Brühl, 2012). Further threats are renovations of old buildings and habitat fragmentation due to the intensification of agriculture and silvicultural practices as well as the expansion of infrastructure (roads) and light pollution (Frey-Ehrenbold et al., 2013; Spiecker, 2003; Stone et al., 2009; Voigt and Kingston, 2015; Wade et al., 2003).

Today only about 100 maternity roosts of Greater Mouse-eared Bats are known in Switzerland which are mainly located in human settlements like attics or church roofs (Bohnenstengel et al., 2014; Güttinger, 1997; Krättli et al., 2012; Rudolph et al., 2009). The protection of the maternity roosts is of particular importance since from spring to autumn the females live there in large colonies to bear their offspring, whereby they raise their young at the same maternity roost lifelong and over generations (Dietz et al., 2007; Meschede and Rudolph, 2004). Nevertheless, it covers only a part of the habitat of Greater Mouse-eared Bats. At dusk the bats fly on average between 2 and 9 km (but up to 25 km) to their hunting areas and normally hunt in several different foraging areas per night with a distances of around 500 m from each other (Arlettaz, 1996; Drescher, 2004; Rudolph et al., 2009). A broader knowledge of the commuting corridors (dark and linear connective structure between roost and foraging area) and foraging areas of *M. myotis* is important to perceive a clearer picture of all habitat components, what constitutes the basis for conservation measures (Bohnenstengel et al., 2014; Stiftung Fledermausschutz, 2005).

The Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) created a model to predict the commuting activity of Greater Mouse-eared Bats and Lesser Horseshoe Bats (*Rhinolophus hipposideros*) in agricultural land by comparing potential commuting corridors and numerous landscape variables with bat activity, whereby roost position and forests in general were connected in the model (Ravessoud, 2017). Three-dimensional arrangements of connected landscape features were positively related with bat activity, whereby routes with light pollution and open habitats seemed to be avoided (Ravessoud, 2017). A graphical presentation of the predictions of important commuting corridors and species-specific patterns of landscape use are significant for spatial planning and of valuable interest for bat

conservation. Until this day, only few models have been developed to predict suitable habitat for bat distribution (Bellamy et al., 2013; Scherrer et al., 2019) and roosts (Bellamy and Altringham, 2015) but neither predicts foraging areas in general nor the specific habitat for the species *M. myotis*. Therefore, a broader knowledge of the potential foraging areas is essential to obtain an appreciation of the habitat requirements of this species, including corridor models.

The Greater Mouse-eared Bat with a wingspread of 35 to 43 cm is one of the largest bat species in Switzerland (Dietz and Kiefer, 2014). Based on its size it prefers open flight space, whereby, due to its wide wings, it is still able to fly very agile and to hunt near the ground (Meschede and Rudolph, 2004). Different studies suggest forests as the most important foraging habitat of *M. myotis* (Audet, 1990; Güttinger, 1997; Rudolph et al., 2009; Steck and Güttinger, 2006; Zahn et al., 2005) though they also hunt in open landscapes like recently mown meadows or orchards (Arlettaz, 1996; Pereira et al., 2002; Rey, 2004; Zahn et al., 2006). Especially in spring, when bats show the lowest weights after hibernation, and during cold weather, it seems that forests offer better conditions for hunting in a more temperate climate than ruling in open landscapes (Zahn et al., 2006). Furthermore, the species composition of prey varies through the year and prey abundance seems to influence the choice of the bats' hunting habitat (Arlettaz, 1996). During most time of the year their main prey species are large ground-dwelling arthropods like ground beetles (Carabidae), whereby in May and June also mole crickets (*Gryllotalpa gryllotalpa*) and cockchafers (*Melolontha melolontha*) and in August European crane flies (*Tipula paludosa*) are part of their diet (Arlettaz, 1996; Güttinger, 1997; Steck and Güttinger, 2006).

Forest carabid beetles represent a constantly occurring food source, while mole crickets, cockchafers and European crane flies show strong fluctuations (Arlettaz, 1996). The temporal abundance of these species in combination with freshly cut meadows can be the reason why bats momentarily shift their hunting habitat from forests to meadows or orchards (Arlettaz, 1996). To catch the flightless ground beetles and crickets, the Greater Mouse-eared Bats show a typical gleaning behaviour: *M. myotis* are able to passively locate prey by the rustling noise the beetles make when crawling on the ground, and they can catch them by gleaning the prey from the ground (Audet, 1990; Rudolph et al., 2009). Therefore, suitable hunting habitats seem to be characterized by bare ground or only low-growing

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vegetation and a free flight space, since lower tree layers or shrubs would hinder a search flight by reduced accessibility, and make it nearly impossible to detect and especially access the prey (Güttinger, 1997; Rudolph et al., 2009; Zahn et al., 2006).

Forests which fulfil the premise are often single-layered, old beech and mixed forests with a high amount of broad-leaved trees what impedes ground vegetation and enables a free flight space (Meschede and Rudolph, 2004; Rudolph et al., 2009). Different studies indicate that Greater Mouse-eared Bats prefer deciduous forests over coniferous forests (Audet, 1990; Rudolph et al., 2009; Steck and Güttinger, 2006; Zahn et al., 2006). Not the least because deciduous forests seem to provide a higher density of carabids than coniferous forests, probably due to lower pH values and soil humidity in the latter (Finch, 2005; Rudolph et al., 2009). Other studies suggest that the foraging habitat is not selected on the basis of forest composition but is rather influenced by the spatial structure of the forest (Güttinger, 1997; Zahn et al., 2005).

Even if previous studies have investigated the foraging behaviour and habitat of Greater Mouse-eared Bats, the fewest examined the spatial structure in detail: In many studies, the foraging habitat was inferred from habitat requirements of prey found in faecal samples (Steck and Güttinger, 2006; Zahn et al., 2006) but the investigations rather allowed a rough classification into forest and grassland. Other studies classified the hunting habitats into the same groups but received the data by radio-telemetry or visual observations (Arlettaz, 1996; Audet, 1990) or additionally distinguished between deciduous and coniferous forests (Drescher, 2004; Rudolph et al., 2009). An investigation of the foraging area in relation to spatial structure and forest composition did Zahn et al. (2005) who radio-tracked individuals of two maternity roosts in Bavaria and also Güttinger (1997) who explored in more detail the foraging behaviour of several individuals of a maternity roost in Switzerland. Both indicated a preference of open ground forests as foraging habitat.

Even though these findings help to understand the behaviour and requirements of Greater Mouse-eared Bats in relation to foraging, the data basis refers to only few maternity roosts each surrounded by a specific environmental situation. The aim of this research project was to compare the spatial structure of forests at several maternity roosts in Switzerland with the activity of *M. myotis* to get a broader picture of the demands on the structure of the foraging habitat. The question was, if the findings of Güttinger (1997) and Zahn et al. (2005)

apply generally at various locations across Switzerland, namely if Greater Mouse-eared Bats show a higher activity at assumed suitable sampling sites, which correspond to forests with open ground, free flight space and dense canopy? Furthermore, which variables of the forest structure correlate with the activity of Greater Mouse-eared Bats and indicate suitable hunting area?

This study investigated the relevance of different variables displaying forest structure in relation to Greater Mouse-eared Bat activity with the aim to receive insights into the requirements of *M. myotis* for their hunting habitat. By using remote sensing the forest structure can be modelled with LiDAR data (Airborne Light Detection and Ranging) and important foraging areas exhibiting the required vegetation structure can be displayed. Furthermore, with data of *M. myotis'* favoured foraging habitat the model predicting the commuting corridors of Greater Mouse-eared Bats can be refined by including the quality of the target forests. Such a map of suitable foraging areas of Switzerland and improved predictions of commuting corridors facilitates the protection of the Greater Mouse-eared Bat's habitat.

Material and method

Selection of study sites

The study was conducted in forests around 18 different maternity roosts of *M. myotis,* which were mainly located in the Swiss Central Plateau (Fig. 1). Of the 106 known locations, 18 bat colonies consisting of more than 100 individuals (last counting 2018) were selected that have been monitored over the last few years by caretakers to ensure their occupation (Table 1).
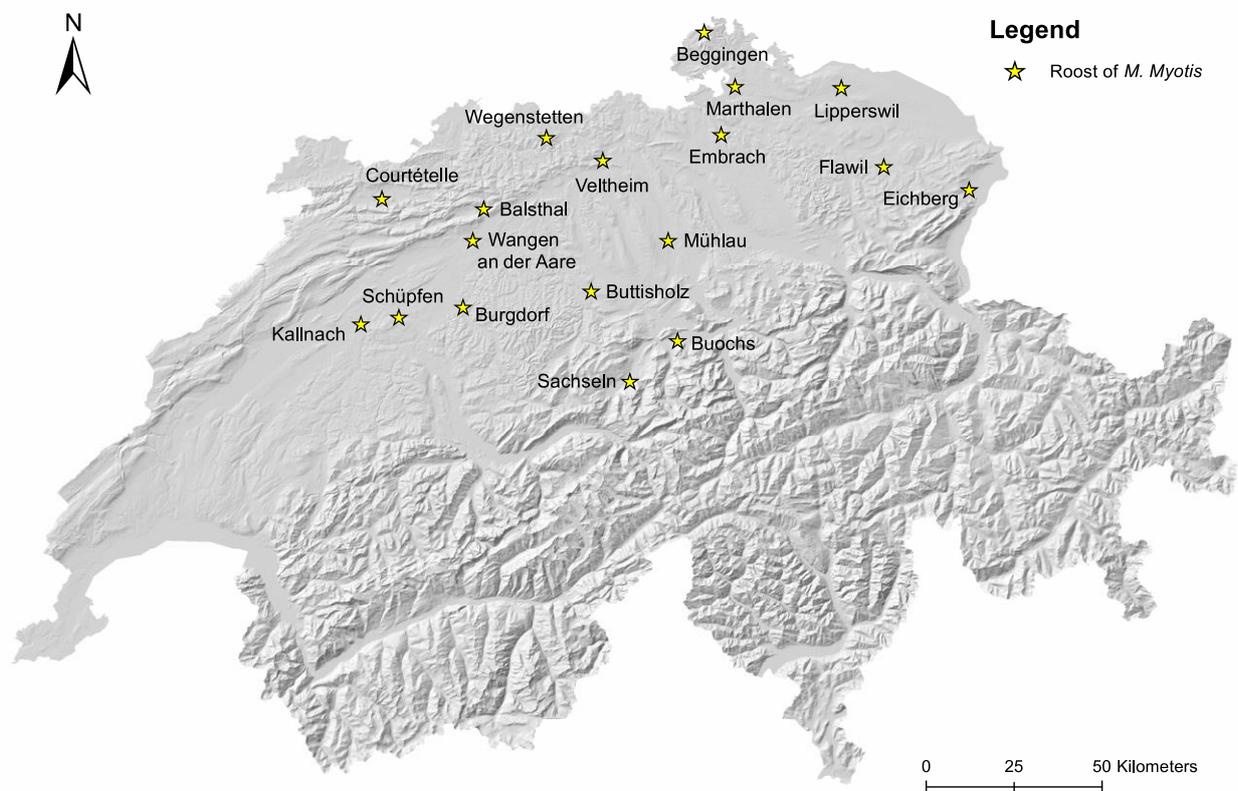
Fig. 1: The distribution of the 18 selected study locations (maternity roosts of *M. myotis*).

Table 1: The selected study locations (maternity roosts of *M. myotis*) listed with coordinates, the colony size, the closest weather station and the timespan of data collection.

Roost	Canton	x-coordinate	y-coordinate	Colony size	Data collection	Closest weather station
Courtételle	JU	590550	243400	804[1]	19.05.2019 – 23.05.2019	Delémont
Balsthal	SO	619500	240575	194	20.05.2019 – 23.05.2019 & 23.07.2019 – 26.07.2019	Wynau
Sachseln	OW	661100	191000	190	27.05.2019 – 01.06.2019	Giswil
Buochs	NW	674700	202725	265	28.05.2019 – 01.06.2019	Gersau
Schüpfen	BE	595334	209446	220	03.06.2019 – 07.06.2019	Bern
Kallnach	BE	584592	207473	423[2]	04.06.2019 – 07.06.2019	Mühleberg
Eichberg	SG	757675	246050	543	10.06.2019 – 15.06.2019	Oberriet
Flawil	SG	733475	252675	229	11.06.2019 – 15.06.2019	Bischofszell
Beggingen	SH	682350	291275	619	17.06.2019 – 21.06.2019	Hallau
Lipperswil	TG	721375	275275	273	18.06.2019 – 21.06.2019	Salen-Reutenen
Mühlau	AG	672050	231450	516	25.06.2019 – 29.06.2019	Cham
Buttisholz	LU	650150	216950	540	26.06.2019 – 29.06.2019	Egolzwil
Marthalen	ZH	691050	275625	247	01.07.2019 – 05.07.2019	Schaffhausen
Embrach	ZH	687150	261800	334	02.07.2019 – 05.07.2019	Kloten
Burgdorf	BE	613655	212316	250	08.07.2019 – 12.07.2019	Koppingen
Wangen an der Aare	BE	616393	231408	150	09.07.2019 – 12.07.2019	Wynau
Veltheim	AG	653450	254400	973	15.07.2019 – 19.07.2019	Buchs
Wegen-stetten	AG	637427	260993	144	16.07.2019 – 19.07.2019	Rünenberg

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[1] Last counting 2009
[2] Last counting 2015

Field design

To investigate the activity of *M. myotis* in different forests around the maternity roosts, the targeted forest type in the surrounding area had first to be located. To simplify the search for assumed suitable stands in Swiss forests, a supervised classification of LiDAR data[3] was employed to locate promising locations. The classification was trained on 1360 field surveys from the fourth Swiss National Forest Inventory[4] (LFI4), using appropriate variables on species mixture, stand layering and layer cover to discriminate stands of high potential for foraging as described by Güttinger (1997). In this study *M. myotis* showed a high preference for foraging in forests with closed canopy and open ground. The classification models reproducing this type of forest best contained the following five conditions (Table 2). These calculations were performed by Dr. Klaus Ecker of the Research Group Ecosystems Dynamics at WSL.

Table 2: Conditions of the classification models predicting suitable foraging areas.

	Decision rule	Data origin	Model 1	Model 2	Model 3
1.	The percentage of the number of first returns above 7 m to the number of all first returns must be greater than 80%*	LiDAR			
2.	The ratio of the percentage of points in the range of 1 m to 7 m to the percentage of points in the range of -3 m to 1 m must be less than 0.06 *	LiDAR			
3.	The skewness of points in the height range from -3 m to 7 m must be greater than 5 *	LiDAR			
4.	The proportion of coniferous wood must be less than 50%	WGM[5] (raster resolution 25 x 25 m)			
5.	The slope must be less than 20 degree angles	DTM25_L2[6]			

* gridded on a raster of 12.5 x 12.5 m

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[3] Projekt landwirtschaftliche Nutzflächen LWN (Swisstopo)

[4] WSL, 2019: Schweizerisches Landesforstinventar LFI, Daten der Erhebung 2009/17 (LFI4). Christoph Düggelin. 18.01.2019

[5] WSL, 2017: Schweizerisches Landesforstinventar LFI. Datenbankauszug vom 28.04.2017. Christian Ginzler. Eidg. Forschungsanstalt WSL, Birmensdorf.

[6] Bundesamt für Landestopografie swisstopo (Art. 30 GeoIV): 5704 000 000

Complementary information in the Appendix III (Table 14)

The first condition defined that most of the LiDAR laser pulses have to return above 7 m, what is fulfilled at forests with a closed canopy. The second condition is accomplished if only few LiDAR laser pulses return in the flight space (1 m – 7 m) compared with the returns from the ground. This leads to forests with an open flight space and hardly any shrub layer. The third condition specifies forests with a low proportion of shrub and herbaceous layer, since the high skewness defines a lot of returns from the ground and only few from above. Therefore, the application of the five conditions identified forests with a closed canopy (condition 1), a free flight space (condition 2), hardly any shrub and herbaceous layer (condition 3), which are mainly constituted of deciduous trees (condition 4) and do not have a steep slope (condition 5). The first three conditions modelled the targeted one-layered beech forests with a dense canopy and a bare ground as realistically as possible. In addition, the fourth condition targeted forests which consisted to a greater extent of deciduous trees, since these seem to be preferred by Greater Mouse-eared Bats according to literature (Audet, 1990; Rudolph et al., 2009; Steck and Güttinger, 2006; Zahn et al., 2006). The last condition was included since firstly, in a study by Güttinger (1997), the activity tended to be lower on slopes than on hilltops or lowland and secondly to simplify the fieldwork by excluding very steep slopes. The five conditions together resulted in model 1.

To prepare for field verification of predicted forests, two less constrained versions of the model were calculated by Dr. Klaus Ecker, which provided more suggestions in case of only few available predictions: Model 2 contained condition 1 to 4 without limitation of the slope, model 3 fulfilled condition 1 to 3 and did neither limit the slope nor the proportion of the coniferous wood. The models had a resolution of 12.5 m x 12.5 m pixels. A colour coded map of Switzerland was prepared for field site evaluation, indicating areas for model 1 (red), model 2 (yellow) and model 3 (blue) (Fig. 3).

The classification models enabled a targeted search of the suitable survey areas in the field. Since *M. myotis* normally commute in average between 2 and 9 km to different hunting areas (Arlettaz, 1996; Rudolph et al., 2009) firstly, the forests within a radius of 5 km around the roost were examined in the field guided by predictions of model 1. If no suitable location could be found, the predictions of model 2 respectively model 3 were inspected, including areas with a higher proportion of coniferous trees or a steeper slope. If this still did not lead to success of finding a suitable foraging area, the radius around the roost was extended to

10 km or even 15 km, targeting the predictions of model 1, then 2 and lastly model 3, since Greater Mouse-eared Bats have already commuted up to 25 km per night (Arlettaz, 1996).

If a suitable sampling site was found, less suitable and not suitable sampling sites were selected within distance of 50 m to 200 m to ensure similar reachability and to minimize other possible local differences. Whereas one-layered forests with a dense canopy and a bare ground were targeted for suitable sampling sites as expected preferred foraging areas of *M.myotis*, the assumed less suitable areas were composed either of vegetated ground, light shrub layer or sparse canopy. The third group comprised forests with open canopy, heavily vegetated ground and/or dense shrub layer which were expected to be unsuitable hunting places. Distances between sampling sites below 50 m were avoided, since the estimated maximum detection range of the recording devices, to detect Greater Mouse-eared Bat calls, is approximately 25 m (Ravessoud, 2017). A sampling site had to consist of the sought type of forest (suitable, less suitable or not suitable) and cover a circular area with a minimum radius of 12.5 m (≈500 m^2).

Fig. 2: Examples of sampling sites.

1: Suitable sampling site in Embrach
2: less suitable sampling site in Lipperswil
3: not suitable sampling site in Embrach

This process was repeated four times to obtain four triplicates of suitable, less suitable and not suitable sampling sites around a roost (Fig. 3). We aimed at locating each of the four groups in different forests and evenly distributing them across the circle.
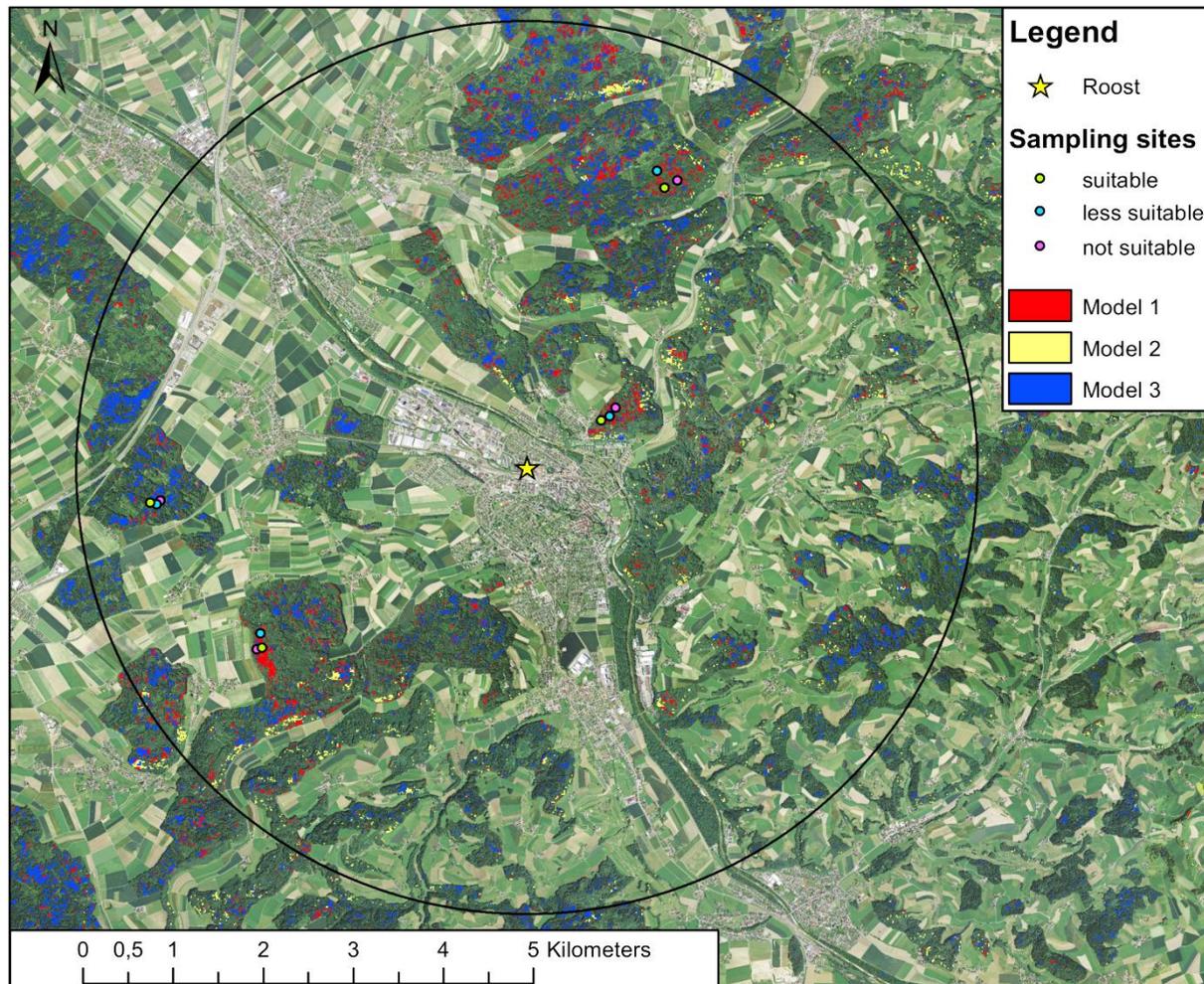
Fig. 3: Field design with four triplets of sampling sites (suitable, less suitable, not suitable) in the forests around the maternity roost of *M. myotis* in Burgdorf. The classification models 1, 2 and 3 predicted sampling sites of different suitability. The circle defines the sampling area of 5 km around the roost.

Data collection

Greater Mouse-eared Bats use echolocation to get a sound picture of their surroundings during darkness by comparing the ultrasound that they emit with the echo returned from the environmental structures (Middleton et al., 2016). The bats use this sophisticated system for spatial orientation and may also use it for localizing prey (Ratcliffe and Dawson, 2003; Russo et al., 2007; Schnitzler et al., 2003).

The activity of *M. myotis* was measured by recording its echolocation calls with ultrasound bat recorders (BATLOGGER, Elekon AG, Lucerne, Switzerland). Since most bat species can be recognized by their species-specific echolocation calls and automated recording can take place at the same time at different locations without disturbing the bats, the method has proven to be particularly effective for species inventories and comparisons of habitat use (Dietz and Kiefer, 2014).

From a pool of 28 devices of Batlogger Type M, A+ and C, we used 24 devices alternatively, distributing them randomly between suitability classes. The ultrasound microphones were sensitive +/- 5 dB between 10 and 150 kHz and recorded the echolocation calls omnidirectionally. The microphones were mounted on poles about 1.5 m above ground in the middle of the selected 12.5 m radius sampling site (Fig. 4). The recording started automatically 15 min before sunset and stopped 15 min after sunrise and was triggered by ultrasound signals. The record trigger mode was set to "period" with a pre-trigger of 0.5 s, a post-trigger of 1 s and a maximal recording duration of 10 s. The recordings of passing bats were then stored as wav-files, which we termed a "sequence". An accompanying meta-data file contained information on trigger values, data, time, temperature and recording location.

Fig. 4: Batlogger A with information sign and microphone mounted on a pole in Eichberg.

Since the data collection took place from mid-May to the end of July 2019 during ten consecutive weeks, the recording time per night varied from 8 to 10 hours. Forests around two roost locations were examined in the same week for preferably three days with good weather conditions. At day one twelve batloggers were installed and activated at the first location, and the following day the remaining twelve batloggers were placed at the simultaneously sampled second location. After the three respectively four nights of recording all batloggers of both sites were dismantled at the same day. Whereby, in case of rain, strong wind or cold temperatures below 7° Celsius the devices were left to record longer to achieve at least two nights of recordings under favourable conditions. Since at cold temperatures high costs of thermoregulation in flight are needed to maintain body condition, while simultaneously foraging success is usually low due to decreased insect availability, bats normally avoid flying at temperatures below 10° Celsius (Catto et al., 1996; Wolbert et al., 2014). Also strong wind, mist and heavy rain inhibits emergence, since echolocation calls are heavily attenuated at high humidity and wind also makes flying more difficult (O'Donnell, 2010).

The fieldwork was consecutive during ten weeks with cold weather for the first two weeks (but over 10° Celsius at night) and warm to very warm summer weather for the remaining eight weeks. Due to the cold weather at the beginning, one of the sampling locations of the first weeks (Balsthal) was sampled in week 10 again to compare the bat activity with the recordings of Balsthal at the beginning. In the first week 53 sequences of M. myotis (2'649 sequences in total) and during the second sampling 33 sequences of M. myotis (3'809 sequences in total) were recorded. Since the bad weather in the first two weeks seemed not to influence bat activity strongly, the other sampling locations of the first two weeks (Courtételle, Sachseln and Buochs) were not repeated. However, the data of the second sampling at Balsthal were used for calculations since the general situation was more comparable with the other 14 sampling locations.

Habitat survey

A habitat survey was performed at each of the sampling sites in a 12.5 m radius circle in the field, whereby different habitat variables were measured and estimated. All variables used in the habitat survey, enumerated in the following brackets, are listed and described more precisely in the Appendix I.

Precisely measurable data of the sampling site like *coordinates* of the batlogger (1), *aspect* (north, northeast, east, southeast, south, southwest, west and northwest) (2) and *elevation* (in meter above sea level) (3) were recorded with a Garmin GPSMAP 62st in the field and verified with swisstopo[7]. The *slope gradient*, *target forest size* and *free flight space* were measured with a Bosch GLM 80 Professional laser rangefinder, whereby the average *slope* (4) within the 12.5 m sampling site was only taken if the gradient was higher than 10%. The *target forest size* (5) meant to be the total area of connected forest patches categorised as "suitable" which went beyond the 12.5 m radius sampling site. This variable gave an impression about the total area of possible good hunting space in the surrounding area of the sampling site. The *free flight space* (6) was defined as the height of the free airspace as flight zone for bats, measured from 0.5 m to the first tree or shrub layer which inhibited a free flight.

Other variables like *forest form*, *stand structure*, *degree of mixture*, *stage of stand development* and *relief* were categorized according to the LFI4 classification (Düggelin, 2019) for the range of 12.5 m around the batlogger (Table 3).

The *forest form* (7) described the basic type of forest and reflected the exerted forest management. The *stand structure* (8) was defined by the different vertical layers using the categories "single-layered", "multi-layered", "all-sized" and "clustered". The proportion of coniferous wood to deciduous forest was indicated by the variable *degree of mixture* (9) and categorized into four groups whereby the percentage of the tree species within the study site has been estimated. The *stage of stand development* (10) was determined by the dominating diameter at breast height (dbh) of the strongest trees of the sampling site (ddom= mean dbh of the strongest trees). If no diameter class dominated or the trees varied over at least three diameter classes, the sampling site was categorised as "mixed". For the *relief* (11) not only the 12.5 m circle of the sampling site was taken into account but also the area around to get a basic impression of the relief. Categories were "flat area", "upper slope", "middle slope", "foot slope" and "undeterminable" whereby only at upper-, middle- and foot slope the aspect and the slope was recorded.

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[7] www.map.geo.admin.ch – complementary information in the Appendix III (Table 14)

Table 3: LFI4 classifications for forest structure (selection from the list in the Appendix I).

	Parameters	Levels	
(7)	Forest form	· High forest · High forest with area-wise cut · Plenter forest · Coppice forest · Coppice with standards · Special forms (Selvas and plantations)	
(8)	Stand structure	· Single-layered · Multi-layered · All-aged/all-sized · clustered	
(9)	Degree of mixture	· 91–100% conifers · 51– 90% conifers · 11– 50% conifers · 0– 10% conifers	Pure coniferous forest Mixed coniferous forest Mixed deciduous forest Pure deciduous forest
(10)	Stage of stand development	· Young growth · Pole wood · Young timber · Medium timber · Old timber · Mixed Trees	ddom < 12 cm ddom = 12–30 cm ddom = 31–40 cm ddom = 41–50 cm ddom > 50 cm
(11)	Relief	· Plain, flat area · Top, upper slope · Middle slope · Foot slope, depression · Undeterminable	

Furthermore, estimations of the *degree of herbaceous layer*, *shrub layer*, *canopy* and *abiotic factors* gave a broader picture of the sampling site. These variables were based on the LFI4 classifications but slightly adapted to this research project. All variables were estimated continuously. *Abiotic factors* (12) included all abiotic structures like stones and rocks from the size of about 10 cm. The *degree of herbaceous layer* (13) described the percentage of the circular area covered by biotic factors excluding moss and foliage. Additionally, the main *type of herbaceous layer* (14) was recorded and roughly categorized into six groups of assumed severity of the obstacles for bats to reach the ground (clover/ivy, grass, ramson/woodruff, fern/little trees, small bramble bush, large bramble bush/small firs). The *degree of shrub layer* (15) was the percentage cover of biotic factors between 0.5 m and 3 m

including all branches, trees and shrubs within this range. *The degree of crown cover* (16) described the area covered by the canopy. Each sampling site was classified as *homogeneous or heterogeneous* (17) depending on the general aspect gained by considering forest type, stand structure, ground-, shrub-, crown cover, size of airspace etc.

Weather data (18) could be used from CLIMAP-net[8] for the average of air temperature, humidity, precipitation and wind velocity per night measured from 21.00 to 06.00 o'clock. Air temperature and the relative humidity were measured 2 m above ground, precipitation and wind velocity as a sum of ten minutes. The closest weather station of each roost used for weather data is listed in Table 1.

The *total forest size*, the *relative forest size* and the *distance* from the roost to the sampling site were all calculated in ArcGIS[9]. The *total forest size* (19) meant the area of the total connected woodland in km[2] where a batlogger was placed and is independent of the categorisation into suitable foraging areas (not to be confused with the *target forest size* which is the size of connected suitable foraging areas). The *relative forest size* (20) was calculated as the ratio of forest to non-forest of an area of 300 m radius around a batlogger. This variable is to differentiate from the *total forest size* since the percentage of forest nearby the sampling site (on an area of around 0.28 km[2]) might have a higher influence on bats than the total size of forest. The *distance* (21) from the roost to the sampling site stated the straight-line distance in km. For calculation, the exact GPS of maternity roost and batlogger locations were used.

Analysis of the recordings

Calls of *M. myotis* are frequency modulated, starting at 120 – 70 kHz and decreasing to 25 – 29 kHz with a call duration of normally 2 – 3 ms but up to 10 ms (Dietz and Kiefer, 2014). The differentiation from other bat species is possible even if confusion with other *Myotis* species can occur. Only the closely related Lesser Mouse-eared Bat (*Myotis blythii*) is hardly to distinguish by echolocation calls (Dietz et al., 2007). However, *M. blythii* lives mainly in open country on extensively used hay meadows and avoids closed woodland areas where the Greater Mouse-eared Bat dominates (Arlettaz, 1996). Moreover, the nationwide distribution

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[8] Bundesamt für Meteorologie und Klimatologie MeteoSchweiz – complementary information in the Appendix III (Table 14)
[9] ArcGIS Desktop 10.7, Version 10.7.0.10450

of *M. blythii*[10] does not match the selected sampling locations of this study. Therefore, it can be assumed that no Lesser Mouse-eared Bat was recorded at the sampling sites.

The echolocation call sequences were analysed with the software BatScope4[11] (Obrist and Boesch, 2018). First, an automated identification of the software using six different classifiers (KNN, QDA, RF, SVM, KKNN, NN) assigned the most likely bat species to each call, and then calculated the most probable bat species for each sequence. Calls of *M. myotis* are often erroneously allocated by BatScope4 to the species *Nyctalus leisleri*, *Eptesicus serotinus*, *Eptesicus nilssonii*, *Vesptertilio murinus* and different species of the genus *Myotis* since their calls can look quite similar in certain situations (Dietz and Kiefer, 2014). Therefore many of the sequences assigned to one of these species were checked manually for *M. myotis.* Additionally, different filters were used to verify the calls of the Greater Mouse-eared Bats (Table 13 in the Appendix II). The output consisted of the number of echolocation sequences comprising calls of *M. myotis* per night per sampling site (batlogger).

Statistical analysis

The dataset contained 32 different variables whereof 20 described the forest habitat, nine adjusted for influences independent of the habitat like weather or equipment failures and two for random factors (*sampling location* and *batlogger*). Activity as the response variable comprised poisson distributed count data. The variable *aspect*, containing eight categories (north, northeast, east, southeast, south, southwest, west and northwest), was transformed into radian measure whereby two new variables *easterness* and *northerness* originated. Also the date was transformed into *day of the year* to simplify calculations in RStudio[12]. The variables *abiotic* and *precipitation* were excluded from the statistics due to rare occurrences: abiotic factors hardly occurred at the sampling sites and since the fieldwork was preferably carried out during dry weather conditions, it barely rained while recording.

From the total sample, two distinct sub-datasets were created: a) only suitable sampling sites where the target forest size was measured (subsample A), and b) sampling sites with ground vegetation where the type of herbaceous layer was recorded (subsample B).

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[10] © info fauna (Schweizerisches Zentrum für die Kartografie der Fauna (SZKF))
[11] http://www.batscope.ch
[12] © 2009-2019 RStudio, Version 1.2.5001

In a first step, the variables were normalised using the scale function in RStudio (Becker et al., 1988). To check for correlated explanatory variables, a non-parametric rank correlation with Spearman's (rho) rank correlation coefficient was calculated (Becker et al., 1988) whereby variables with a correlation coefficient equal or bigger than 0.7 were examined more closely (Field et al., 2012). In direct comparison, the one of the variables in question which explained more of the variation was kept.

Kruskal-Wallis tests were conducted to examine the differences of categorical variables on bat activity (number of sequences per night per sampling site) (Hollander et al., 2013). To test pairwise comparisons between the groups, a post hoc test (Dunn's test) was used (Dunn, 1964). The continuous explanatory variables were analysed with a basic logistic poisson regression (GLM) with activity as the response variable (McCullagh and Nelder, 1989). These tests were used for first insights into the data and allowed principal hypothesis testing.

The data was then analysed by a poisson generalized linear mixed model (GLMM) with bat activity as response variable, the environmental predictors as explanatory variables and *sampling location* and *batlogger* as random variables, to determine how the Greater Mouse-eared Bat activity was related to the forest variables. Since a stepwise method implies several risks like the inclusion of variables with random sampling variation due to slight differences in semi-partial correlation or the selection of variables based on mathematical criteria instead of biological knowledge, the model was built based on theoretical literature to test the hypotheses and was then stepwise improved by switching explanatory variables in and out (Field et al., 2012). To determine whether the model was significantly improved by the fitting, the Akaike Information Criterion (AIC) was compared (Burnham and Anderson, 2004). Further the collinearity of the explanatory variables in the final model was checked by using variation inflation factors (VIFs) whereby a VIF > 4 indicates collinearity (O'Brien, 2007).

Verification of the classification model

To verify the classification model, the predictions of the suitable sampling sites of model 1, model 2 and model 3 were combined and compared with the findings in the field by using ArcGIS. For a better reflection of the overall situation at the sampling site, not only the pixel

containing the batlogger was analysed but a square of nine pixels (each pixel 12.5 m x 12.5 m) comprising the batlogger in the middle. Red pixels predicted as suitable by the classification model were counted as 1, the other pixels as 0 (Fig. 5). The sum of the nine contiguous pixels resulted in a number from 0 to 9 for each pixel whereby high numbers represented high suitability according to the classification model (Fig. 6). The suitable sampling site in Fig. 6 (green dot) exhibits the maximum number "9" since all nine pixels within the square predicted suitable sampling sites. The less suitable sampling site (blue) exhibits the number "7" due to seven red pixels and the not suitable sampling site (pink) "5".
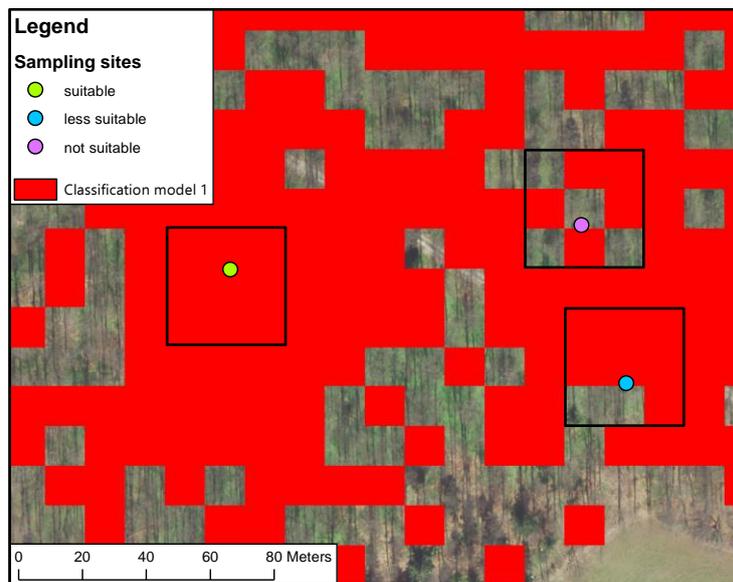

Fig. 5: Predictions of the classification model 1 for suitable forests.
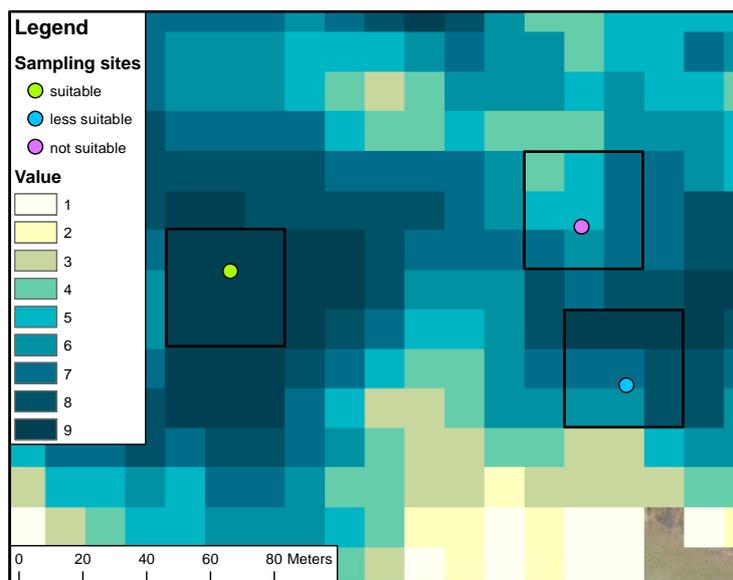

Fig. 6: Each pixel displays the sum of the nine contiguous pixels whereby as suitable predicted pixels counted 1, the others 0.

Results

At 18 different sampling locations (maternity roosts) recordings were made during 810 sampling nights (216 sampling sites, 3 – 5 recording nights per site). The batloggers registered a total of 244'501 sequences during a total of 6'639 microphone recording hours (Table 4). Thereof 2'057 sequences were attributed to *M. myotis* after automatic classification by BatScope4, filtering and manual verification (Appendix II, Table 13).

Table 4: Number of sequences of Greater Mouse-eared Bats in total, at suitable sampling sites, less suitable sampling sites and not suitable sampling sites.

Sampling location	Total sequences of *M.myotis*	Sequences at suitable sampling sites	Sequences at less suitable sampling sites	Sequences at not suitable sampling sites
Courtételle	19	19	0	0
Balsthal	33	24	9	0
Sachseln	73	69	4	0
Bouchs	78	78	0	0
Schüpfen	279	180	71	28
Kallnach	143	80	57	6
Eichberg	78	3	61	14
Flawil	127	81	12	28
Beggingen	222	180	27	15
Lipperswil	75	62	12	1
Mühlau	93	38	54	1
Buttisholz	32	20	4	8
Marthalen	87	79	8	0
Embrach	211	174	37	0
Burgdorf	154	95	57	2
Wangen an der Aare	40	6	30	4
Veltheim	214	97	117	0
Wegenstetten	99	81	17	1
Sum	**2057**	**1366**	**583**	**108**

Kruskal-Wallis test was conducted to examine the differences on bat activity according to the *suitability* of sampling sites. Significant differences were found between the three types of suitability and the activity (Chi-squared = 135.52, df = 2, *p* < .001) (Fig. 7). 67% of Greater Mouse-eared Bat activity (1366 sequences) was recorded at "suitable sampling sites", 28% (583 sequences) at "less suitable sampling sites" and 5% (108 sequences) at "not suitable sampling sites". The conducted post hoc test (Dunn's test) to test pairwise comparison resulted in a significant difference between all three groups (all three comparisons: *p* < .001).
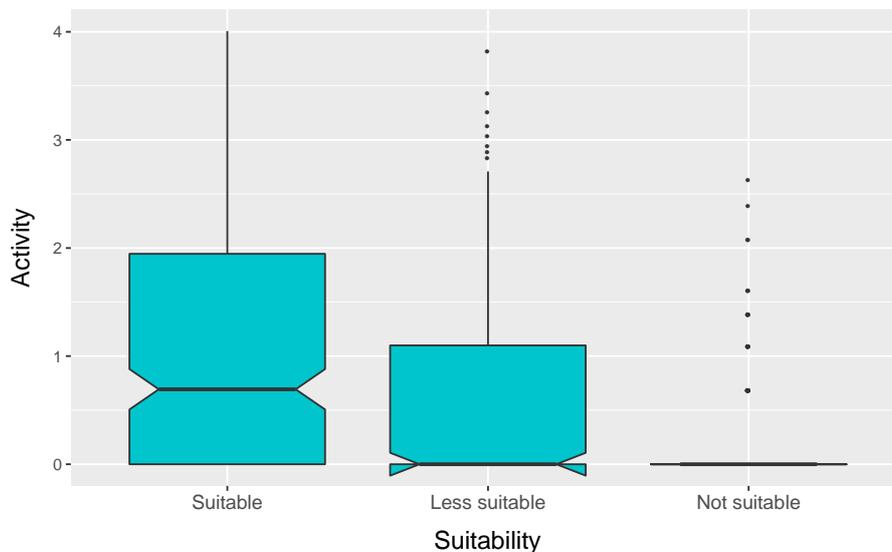

Fig. 7: Activity of *M. myotis* (log transformed) at suitable, less suitable and not suitable sampling sites.

Accuracy of the classification model

The classification model predicting suitable forest patches of 12.5 m x 12.5 m (red pixels, see Fig. 6) was compared to the selected sampling sites in the field. The sum of the surrounding red pixels around a batlogger within the square of nine pixels resulted in a number from 0 to 9, what is termed "number of pixels" in Fig. 8.

By using a Kruskal Wallis-test, a significant difference on the number of predicted pixels between "suitable", "less suitable" and "not suitable" could be found (Kruskal-Wallis chi-squared = 67.384, df = 2, *p* < .001) (Fig. 8). Further, both suitable and less suitable sampling sites differed significantly from not suitable sampling sites by using the post hoc Dunn's test (both comparisons: *p* < .001) but suitable and less suitable did not differ significantly (Dunn's test: *p* = 0.087).
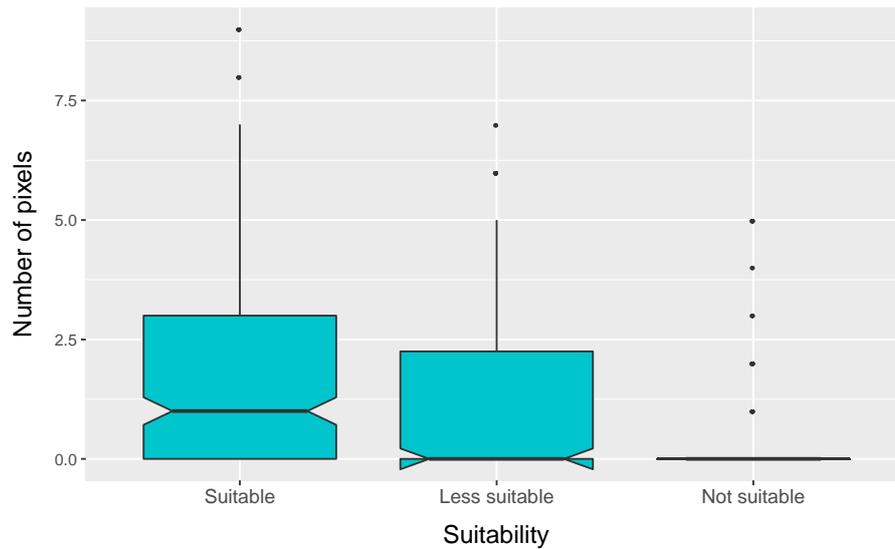
Fig. 8: Number of predicted pixels in relation to the suitability of sampling sites.

Effect of single variables

The Greater Mouse-eared Bat activity at different types of *forest form* varied between the groups (Kruskal-Wallis chi-squared = 10.131, df = 3, *p* = 0.017) (Fig. 9) whereby "plenter forest" was significantly different to "high forest with area-wise cut" (Dunn's test: *p* = 0.013). The further pairwise comparisons did not differ significantly between the groups.
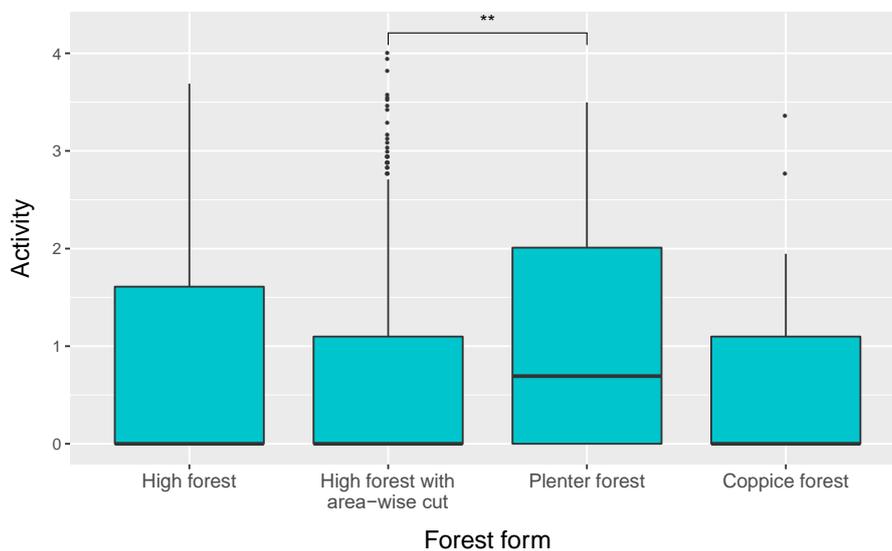

Fig. 9: Activity of *M. myotis* (log transformed) at different forest forms.

Stand structure showed a clear differentiation of bat activity (Kruskal-Wallis chi-squared = 169.73, df = 2, *p* < .001) (Fig. 10). The conducted post hoc test (Dunn's test) to test pairwise comparison resulted in a significant difference between "single-layered" and "multi-layered" (*p* = 0.008) as well as between both of them and "all-sized" (both: *p* < .001).
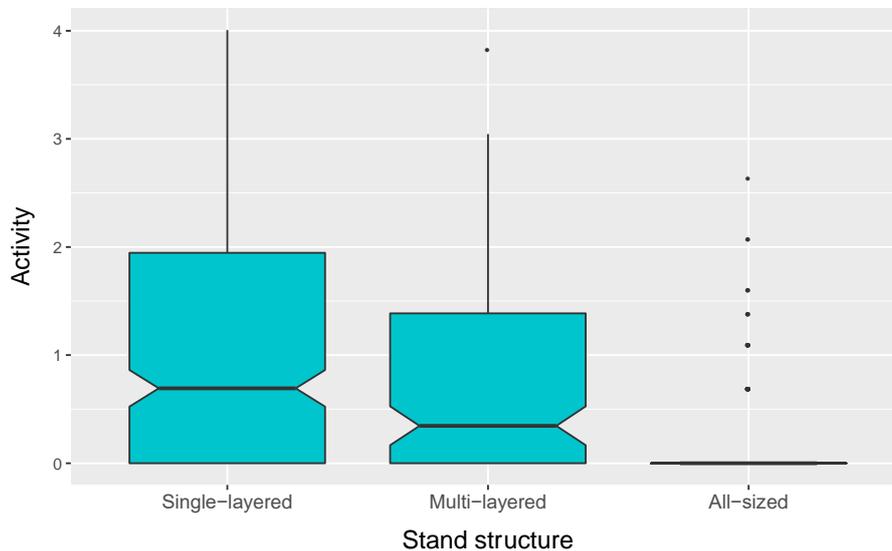
Fig. 10: Activity of *M. myotis* (log transformed) at different stand structures.

Kruskal-Wallis test showed significant differences on bat activity between the four *degrees of mixture* (Chi-squared = 11.70, df = 3, *p* = 0.008) (Fig. 11). Whereby a significant difference between "pure deciduous forests" and "pure coniferous forests" was detected (Dunn's test: *p* = 0.043) but no significant difference between "pure deciduous forest", "mixed deciduous forest" and "mixed coniferous forest".
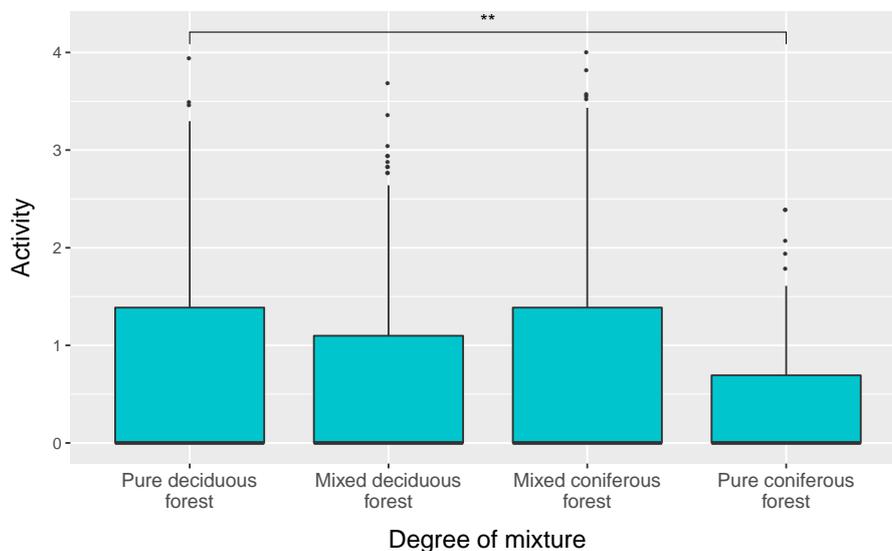

Fig. 11: Activity of *M. myotis* (log transformed) at different degrees of mixture.

A significant difference between the various *stage of stand developments* according to bat activity was indicated by the Kruskal-Wallis test (Chi-squared = 161.74, df = 5, *p* < .001) (Fig. 12). The performed post hoc Dunn's test showed no significant differences between "mixed trees", "young growth" and "pole wood" but these three differed significantly to "young timber", "medium timber" and "old timber". Furthermore, "young timber" and "old timber" were significantly different (Table 5).

Table 5: *P*-values of pairwise comparisons using Dunn's-test.

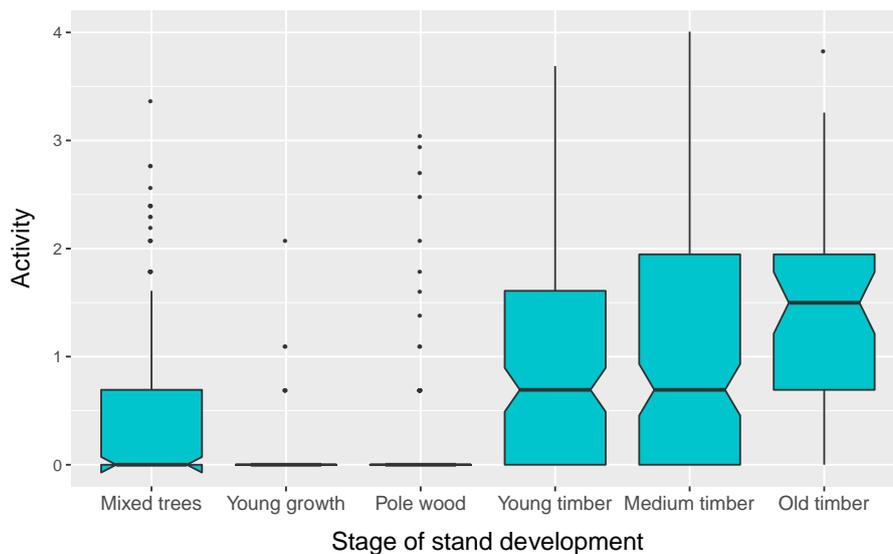|	Mixed trees	Young growth	Pole wood	Young timber	Medium timber
Young growth	0.257	-	-	-	-
Pole wood	0.226	1.000	-	-	-
Young timber	< .001	< .001	< .001	-	-
Medium timber	< .001	< .001	< .001	1.000	-
Old timber	< .001	< .001	< .001	0.002	0.071

Fig. 12: Activity of *M. myotis* (log transformed) at different stages of stand development.

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A poisson regression was performed to analyse the influence of the *degree of herbaceous layer* on bat activity (Table 6). There is evidence that ground vegetation is a significant predictor of Greater Mouse-eared Bat activity whereby a higher degree of herbaceous layer resulted in a lower bat activity (Fig. 13).

Table 6: Parameter estimates of the model with herbaceous layer as explanatory variable.

	B (SE)	Lower (2.5 %)	Odds ratio	Upper (97.5 %)	Model χ^2	z value	Pr(>|z|)
		95% CI for odds ratio					
Intercept	0.880 (0.023)						
Herbaceous layer	-0.330 (0.023)	0.687	0.720	0.753	210.17	-14.15	< .001
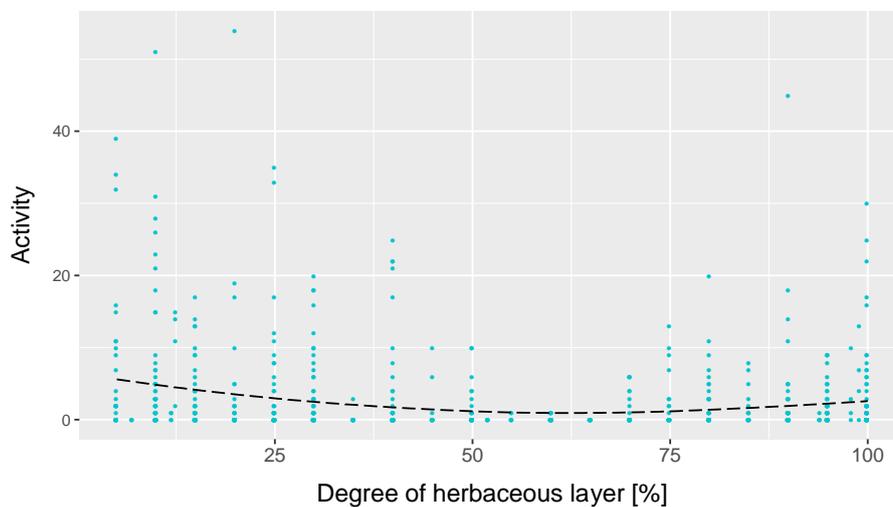
Fig. 13: Activity of *M. myotis* at different degrees of herbaceous layer.

To investigate if the *type of herbaceous layer* had a significant influence on bat activity, a Kruskal-Wallis test was conducted in subsample B with 325 observations and 830 sequences of Greater Mouse-eared Bat activity (Fig. 14). Significant differences between the six types of herbaceous layer and the bat activity were found (Chi-squared = 16.221, df = 5, *p* = 0.006). But the performed post hoc Dunn's test to test pairwise comparison resulted only in a significant difference between group 2 (Grass) and group 4 (Fern, little trees) (Dunn's test: *p* = 0.009).
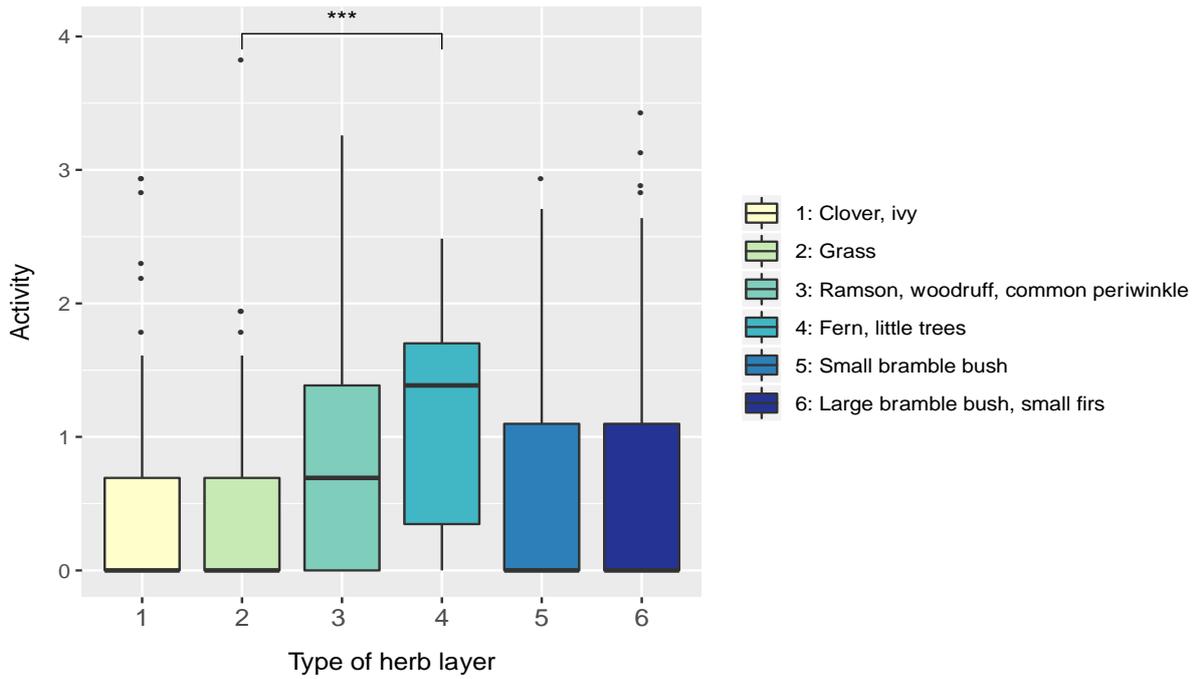
Fig. 14: Activity of *M. myotis* (log transformed) at different types of herbaceous layer.

A basic logistic regression was accomplished to study the influence of the *shrub layer* on Greater Mouse-eared Bat activity (Table 7). The data is inconsistent with the null hypothesis and it suggests that a lower shrub layer predicts a significantly higher bat activity (Fig. 15).

Table 7: Parameter estimates of the model with shrub layer as explanatory variable.

| | B (SE) | 95% CI for odds ratio | | | Model χ^2 | z value | Pr(>\|z\|) |
		Lower (2.5 %)	Odds ratio	Upper (97.5 %)			
Intercept	0.471 (0.035)						
Shrub layer	-1.094 (0.038)	0.310	0.335	0.361	1317.5	-28.58	< .001

Fig. 15: Activity of *M. myotis* at different degrees of shrub layer.

The performed GLM with bat activity as response variable and *crown cover* as explanatory variable (Table 8) implied that higher canopy coverage significantly predicted a higher bat activity (Fig. 16).

Table 8: Parameter estimates of the model with crown cover as explanatory variable.

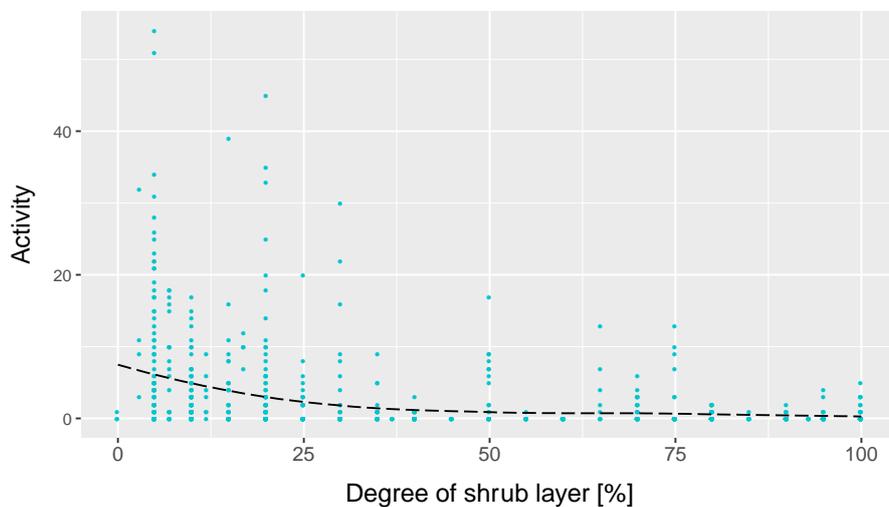| | B (SE) | 95% CI for odds ratio | | | Model χ^2 | z value | Pr(>\|z\|) |
		Lower (2.5 %)	Odds ratio	Upper (97.5 %)			
Intercept	0.867 (0.024)						
Crown cover	0.393 (0.028)	1.402	1.481	1.566	228.41	13.86	< .001
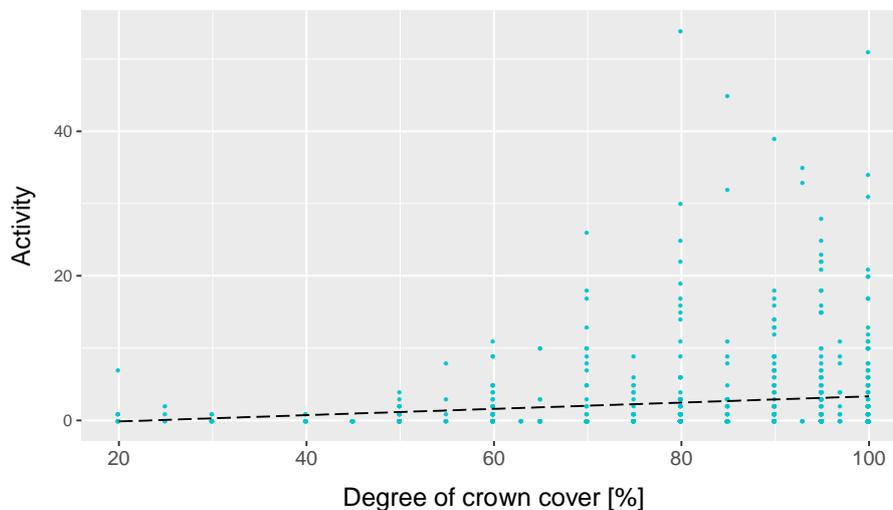
Fig. 16: Activity of *M. myotis* at different degrees of crown cover.

The execution of a logistic regression with bat activity as response variable and *free flight space* as explanatory variable (Table 9) showed that a larger flight space presumably resulted in a higher bat activity (Fig. 17) at least up to a certain height.

Table 9: Parameter estimates of the model with free flight space as explanatory variable.

| | B (SE) | 95% CI for odds ratio | | | Model χ^2 | z value | Pr(>\|z\|) |
		Lower (2.5 %)	Odds ratio	Upper (97.5 %)			
Intercept	0.768 (0.025)						
Free flight space	0.540 (0.019)	1.654	1.717	1.781	748.77	28.59	< .001

Fig. 17: Activity of *M. myotis* at different heights of free flight space.

Further variables were tested by a poisson regression with Greater Mouse-eared Bat activity as response variable. No significant influence of *elevation* (B (SE) = -0.002 (0.022), *p* = 0.899) and only a slight influence of *slope* on bat activity was found (B (SE) = -0.051 (0.022), *p* = 0.024) whereby a steeper slope had a negative impact on activity. Furthermore, a 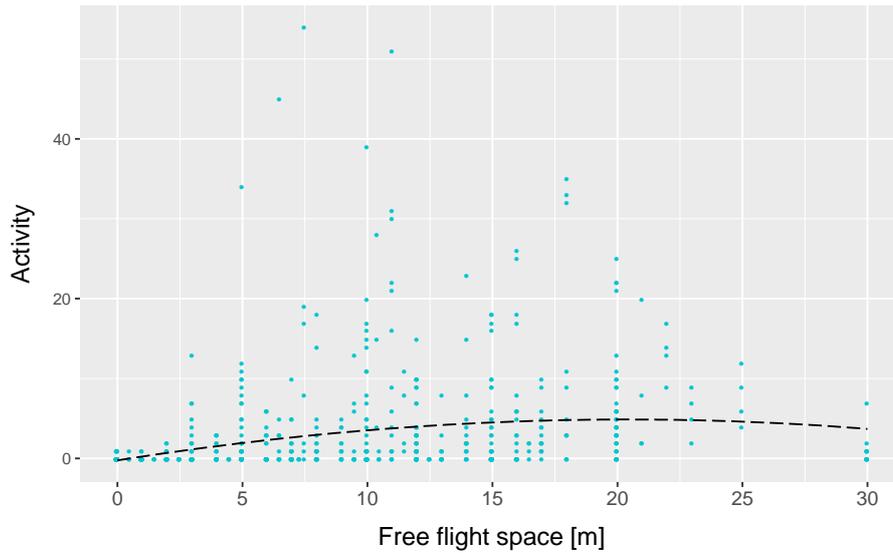significant influence of *easterness* (B (SE) = 0.086 (0.022), *p* < .001) and the combination of *easterness * northerness* (B (SE) = -0.168 (0.029), *p* < .001) but not of *northerness* (B (SE) = 0.036 (0.022), *p* = 0.105) on bat activity was found.

A Kruskal-Wallis test showed that *relief* did not significantly influence bat activity (Chi-squared = 4.066, df = 3, *p* = 0.255) but there is evidence that *homogeneous* sampling sites predicted a significantly higher bat activity than *heterogeneous* sampling sites (Chi-squared = 10.564, df = 1, *p* = 0.001).

The *total forest size* did not significantly influence bat activity (B (SE) = 0.012 (0.022), *p* = 0.588), however, the *relative forest size* (calculated as the ratio of forest to non-forest of an area of 300 m radius around a batlogger) seemed to predict a higher bat activity at larger proportions of forest (Table 10, Fig. 18).

Table 10: Parameter estimates of the model with relative forest size as explanatory variable.

| | B (SE) | 95% CI for odds ratio | | | Model χ^2 | z value | Pr(>\|z\|) |
		Lower (2.5 %)	Odds ratio	Upper (97.5 %)			
Intercept	0.926 (0.022)						
Crown cover	0.117 (0.025)	1.072	1.124	1.180	24.352	4.761	< .001
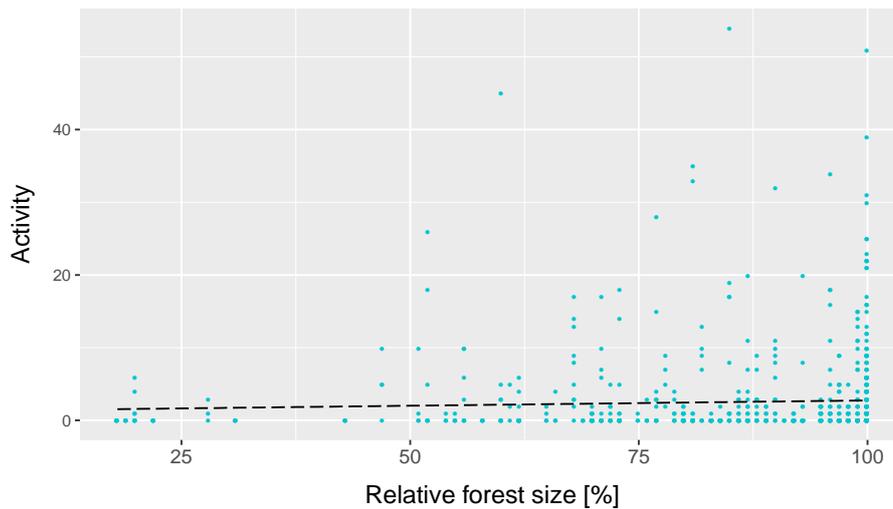
Fig. 18: Bat activity of *M. myotis* at different proportions of forest.

With a subsample (A) only from the suitable sampling sites (259 observations and 1'350 Sequences of *M. myotis*) a basic logistic regression was performed to analyse the influence of the *target forest size* (total area of assumed suitable sampling site) on Greater Mouse-eared Bat activity. A significant correlation was found, whereby a larger area of target forest predicted a higher bat activity (B (SE) = 0.092 (0.020), *p* < .001). Also the *distance* predicted bat activity significantly (B (SE) = 0.060 (0.021), *p* = 0.004) with a negative impact on bat activity the greater the distance to the roost. The longest flight distance was 12 km but most of the routes were about 3.6 km.

Weather also influenced bat activity significantly by *air temperature* (B (SE) = 0.093 (0.022), *p* < .001) and *humidity* (B (SE) = -0.146 (0.022), *p* < .001). Though *wind velocity* showed no significant influence on bat activity (B (SE) = 0.029 (0.022), *p* = 0.174). Instead the variable *recording hours per night* explained some part of the variation of bat activity (B (SE) = 0.065 (0.025), *p* = 0.009).

Variable selection process

To generate a complete overview of the variables influencing Greater Mouse-eared Bat activity the most, a generalized linear mixed model (glmm) was performed. In a first step eight selected variables describing forest structure were included into the model as explanatory variables. The random variables showed significant influence on bat activity when tested individually: *sampling location* (Kruskal-Wallis chi-squared = 124.36, df = 17, *p* < .001) and *batlogger* (Chi-squared = 79.372, df = 27, *p* < .001) and were involved in the model as well.

Two variables (*forest form* and *herbaceous layer*) showed no statistically significant effects and were therefore excluded from the model 2. The ΔAIC between model 1 and model 2 was < 7 which, according to the rules of thumb outlined e.g. in Burnham and Anderson (2004), shows only a slight difference between the models and therefore the simpler model 2 was kept (Table 11). Different explanatory variables were then switched in and out of model 2 to compare ΔAIC but a model improvement was only achieved with the variables *humidity*, *distance* and *recording hours per night*. The quadratic influence on the variables *free flight space* and *distance* and an interaction between *easterness* and *northerness* as well as *GPSx* and *GPSy* were included in the model but no advanced model was found. To make sure not to miss possible new interactions, the first two excluded variables (*forest form* and *herbaceous layer*) were included again in the final model but both did not result in an improvement.

Therefore the final model included six explanatory variables describing the forest habitat (*stand structure*, *degree of mixture*, *stage of stand development*, *degree of shrub layer*, *degree of crown cover* and *free flight space*), two random variables (*sampling location* and *batlogger*) and three variables which explained variances due to weather (*humidity*), equipment failures (*recording hours per night*) and different flight distances (*distance to the roost*) (Fig. 19).

Table 11: Model selection process.

Model	Response variable	Random variables	Explanatory variables		AIC
1	Activity	· Sampling location · Batlogger	· Forest form · Stand structure · Degree of mixture · Stage of stand development	· Herbaceous layer · Shrub layer · Crown cover · Free flight space	4071.4
2	Activity	· Sampling location · Batlogger	· Stand structure · Degree of mixture · Stage of stand development	· Shrub layer · Crown cover · Free flight space	4076.4
3	Activity	· Sampling location · Batlogger	· Stand structure · Degree of mixture · Stage of stand development	· Shrub layer · Crown cover · Free flight space + Humidity	4039.9
4 - 20	Activity	· Sampling location · Batlogger	Following variables switched in and out: · Relative forest size · Total forest size · Easterness · Northerness · Easter * Norther. · Air temperature · Elevation · Number of Greater Mouse-eared Bats · Homogeneous/heterogeneous · Target forest size (subsample A) · Type of herbaceous layer (subsample B)	· Slope · Wind velocity · Relief · Day of year · GSPx · GPSy · GPSx * GPSy	
21	Activity	· Sampling location · Batlogger	· Stand structure · Degree of mixture · Stage of stand development · Shrub layer	· Crown cover · Free flight space · Humidity + Distance to the roost	4019.9
Final	Activity	· Sampling location · Batlogger	· Stand structure · Degree of mixture · Stage of stand development · Shrub layer · Crown cover	· Free flight space · Humidity · Distance to the roost + Recording hours per night	3969.5

Final GLMM results

Several habitat depended variables predicted the Greater Mouse-eared Bat activity (Table 12). A dense *shrub layer* affected bat activity negatively whereas a high *degree of crown cover* and a *free flight space* had a positive effect on bat activity – at least up to a certain height, though tested as quadratic variable it did not explain more of the variation in the model. Also "single-layered forests" had a strong effect on bat activity, whereby Greater Mouse-eared Bats seemed to avoid forests with an "all-sized structure". There is evidence that also the different *stage of stand developments* influenced bat activity: forests with trees from the size of "young timber" upwards seemed to be preferred by *M. myotis* but "young growth" and "pole wood" were not often visited. However, the confidence intervals of the latter are wide and the effect might be weaker or stronger. A strong negative effect was revealed by "pure coniferous forests". "Pure deciduous" and "mixed coniferous forests" predicted a higher bat activity whereby the effect of "mixed coniferous forests" was even stronger. The model adjusted different bat activities due to equipment failures by the variable *recording hours per night*. Also *humidity* had a negative effect on bat activity as well as *distance*.
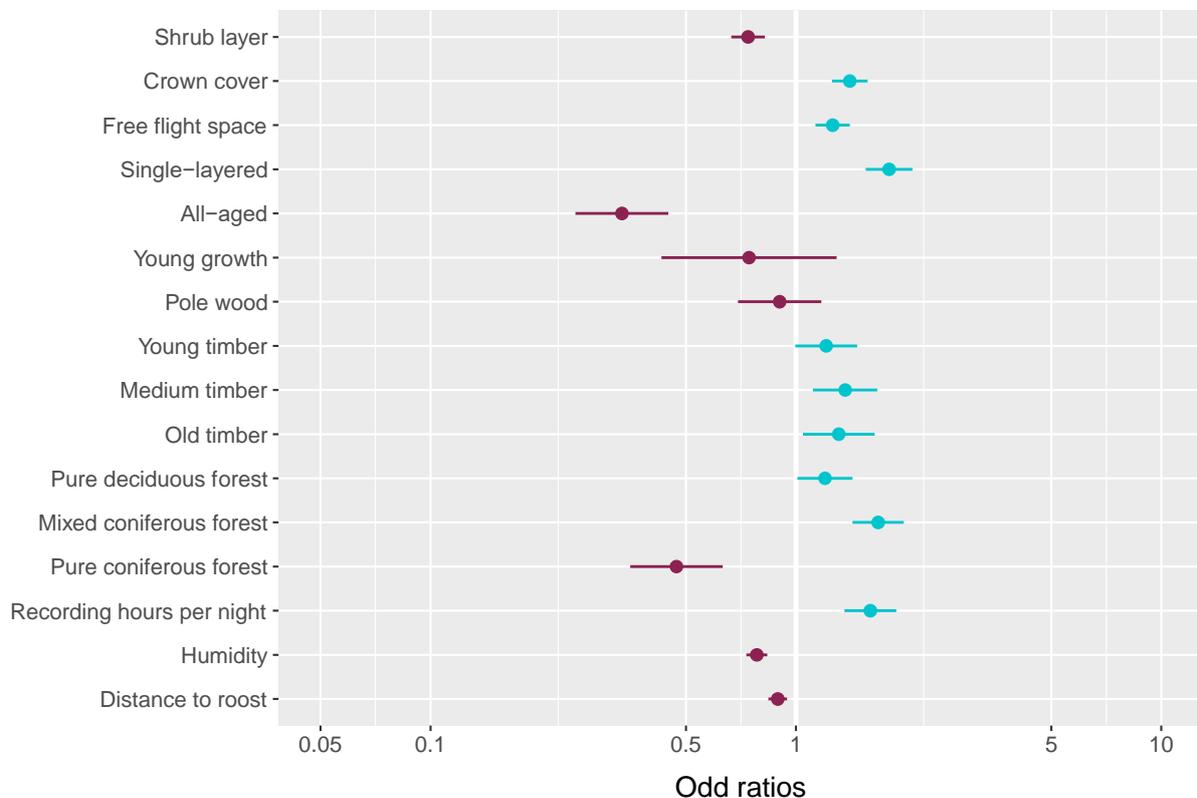

Fig. 19: Estimates of fixed effects of the generalized linear mixed model.

Table 12: Generalized linear mixed model with activity as response variable.

Fixed effects	B (SE)	95% CI for odds ratio			z value	Pr(>|z|)
		Lower (2.5 %)	Odds ratio	Upper (97.5 %)		
Intercept	-0.309 (0.249)					
Shrub layer	-0.301 (0.054)	0.666	0.740	0.822	-5.594	< .001
Crown cover	0.340 (0.057)	1.255	1.404	1.571	5.935	< .001
Free flight space	0.232 (0.055)	1.132	1.261	1.405	4.210	< .001
Single-layered	0.588 (0.075)	1.552	1.800	2.086	7.788	< .001
All-sized	-1.096 (0.149)	0.249	0.334	0.448	-7.340	< .001
Young growth	-0.295 (0.281)	0.429	0.745	1.293	-1.047	0.295
Pole wood	-0.102 (0.134)	0.694	0.903	1.174	-0.762	0.446
Young timber	0.191 (0.099)	0.997	1.211	1.471	1.925	0.054
Medium timber	0.311 (0.104)	1.114	1.365	1.672	3.000	0.003
Old timber	0.270 (0.115)	1.045	1.310	1.642	2.345	0.019
Pure deciduous forest	0.183 (0.088)	1.010	1.201	1.429	2.074	0.038
Mixed coniferous forest	0.519 (0.082)	1.430	1.680	1.973	6.310	< .001
Pure coniferous forest	-0.753 (0.149)	0.352	0.471	0.630	-5.066	< .001
Recording hours per night	0.469 (0.083)	1.358	1.599	1.883	5.631	< .001
Humidity	-0.246 (0.034)	0.732	0.782	0.835	-7.267	< .001
Distance to the roost	-0.114 (0.030)	0.841	0.892	0.946	-3.801	< .001
Random effects	σ^2	**SD**				
Batlogger	0.683	0.826				
Sampling location	0.493	0.702				

Discussion

In this study the activity of Greater Mouse-eared Bats in different forest types was compared to ascertain suitable hunting places. The results revealed that the assumed suitable hunting areas which were defined in previous studies (Güttinger, 1997; Zahn et al., 2005) as beech forests with open ground, free flight space and dense canopy indeed showed a higher activity of *M. myotis* than the less suitable and not suitable hunting places (Fig. 7). Therefore, the first hypothesis can be confirmed, since at forests around eighteen different maternity roosts spread over Switzerland a similar activity pattern was found, supporting the rough classification of forests into suitable, less suitable and not suitable foraging habitat.

By looking at the forest structure in more detail to detect which of the variables indicated preferred hunting areas the most, several variables seemed to be involved in distinguishing suitable from not suitable foraging habitat. Greater Mouse-eared Bats were found more often in single-layered forests with a free flight space and a dense canopy. Furthermore, forests with trees up the size of young timber which are at least partially deciduous were favoured. On contrary, forests with an all-sized stand structure, a dense shrub layer and young trees (young growth or pole wood) were avoided by Greater Mouse-eared Bats, as well as pure coniferous forests (Fig. 19).

Influence of herbaceous layer

Interestingly, the *herbaceous layer* did not seem to have a strong effect on Greater Mouse-eared Bat activity combined with other variables in the model (Fig. 19), although a significant effect was found when examined individually (Fig. 13). Also tested against the residuals of the final model, the herbaceous layer did not explain further variation. This suggested that at least one other variable predicting high activity of *M. myotis* is linked with the ground vegetation at high and low proportions but less at medium coverage. After inspecting various correlations of the herbaceous layer with other explanatory variables, the *degree of crown cover* was the only one which showed a pattern: Low proportions of ground vegetation appeared only at closed canopies but high degrees of herbaceous layer occurred both at low and high degrees of crown cover. The high bat activity allegedly due to low and high degrees of herbaceous layers is therefore more likely to be explained by a dense canopy. The fact that herbaceous layer is able to grow densely despite a high proportion of

crown cover might be because many plant species of the ground vegetation in beech forests complete their development cycle before foliation (Härdtle et al., 2003). Furthermore, based on high inputs of nitrogen from agriculture and transport, the ground vegetation can grow densely despite low incidence of light (Baeten et al., 2009).

Even if the proportions of the herbaceous layer did not predict their activity, possibly the *type of herbaceous layer* influenced the presence of Greater Mouse-eared Bats: It was assumed that within the subsample B of sampling sites exhibiting ground vegetation, a decreasing activity of *M. myotis* should be found with increasing assumed severity of the obstacles for bats (type of herbaceous layer, see list in the Appendix I). However, this hypothesis has to be rejected by comparing the results in Fig. 14. Hardly any variation was found between the six types of herbaceous layer, whereby only a significantly higher activity of *M. myotis* at type 4 (Fern, little trees) compared to type 2 (Grass) could be observed. Furthermore, it is unexpected that type 6 (Large bramble bush) shows a not significant but slightly higher bat activity than type 1 (Clover) or type 2 (Grass), since bramble bushes seemed to be a much larger obstacle to glean the prey from the ground than clover or grass.

One possible explanation might be that Greater Mouse-eared Bats are able to glean the prey not only of bare ground or foliage but also from ground vegetation like fern or ramson if the ground beetles are crawling on the leaves. Due to the lack of scientific studies exploring this question, it is unclear if Greater Mouse-eared Bats behave like this. Further, it is conceivable that Greater Mouse-eared Bats hunt their prey while flying in the free air space above bramble bushes or ferns. According to various studies different insects and especially Orthopteroids (including e.g. crickets) benefit from bramble bushes and might be more abundant close to these plants (Gardiner, 2010; Luppi et al., 2018). Thinkable is also that Greater Mouse-eared Bats hunting beyond the sampling site at possibly better forest patches were still recorded of the batlogger, since its maximum detection range of bat calls is approximately 25 m. But as the chosen sampling sites reflected the vegetation structures outside the 12.5 m circle, it is rather unlikely. Nevertheless, in future studies the area of the sampling site should be expanded to correct for this possibility. Another possibility is that the bats searched longer for insects over dense vegetation because it is more difficult to find the prey. Since we were only able to record Greater Mouse-eared Bat calls in general and

not the direct hunting behaviour, a high bat activity in forests strongly suggests foraging activity but hunting success cannot be deduced from it.

Another likely possibility for the higher activity of group 3 (Ramson, woodruff and common periwinkle) and group 4 (Fern, little trees) is that these plant species might be indicator species for suitable forests: Ramson occurs mainly in moist deciduous forests, woodruff in beech forests, broad buckler fern (*Dryopteris dilatata*) or common lady-fern (*Athyrium filix-femina*) in open, moist, shady forests and common periwinkle in deciduous or mixed beech forests (Dietiker and Kurt, 2009). Mixed beech respectively deciduous forest but also shady forests, what argues for a closed canopy, indicate suitable foraging habitats and coincide with the findings of this study as well as different other publications (Güttinger, 1997; Rudolph et al., 2009). Moist forests can be beneficial habitat for different species of ground beetles and therefore provide a higher food supply for Greater Mouse-eared Bats (Müller-Kroehling, 2008).

However, these findings are in contrast to the results of Güttinger (1997), where the Greater Mouse-eared Bats preferred foraging habitats with no or only sparse ground vegetation but never hunted at places with a degree of herbaceous layer higher than 75%. But since species are often able to adapt to new environmental situations, a shift in Greater Mouse-eared Bats' behaviour from 1997 to today is possible. To clarify these different patterns of Greater Moue-eared Bat activity in relation to the degree and the type of herbaceous layer, further investigations are needed. Especially, since the findings of this study regarding the type of ground vegetation based on a subsample with only few observations and a very rough categorisation of plants. A follow-up project focusing on the type of ground vegetation with a precise identification of the vegetation will potentially help to enlighten the situation.

Forest structure

The *degree of crown cover* explained a lot of Greater Mouse-eared Bat activity whereby a closed canopy predicted higher activity of *M. myotis* (Fig. 16). Since darker forests prevent strong incidence of light, a dense growing of the shrub layer might be impeded (Härdtle et al., 2003). A further explanation might be risk avoidance: since bats are exposed to various predators even at night, different strategies to minimize predation have been developed (Lima and O'Keefe, 2013). A possible protective behaviour is the avoidance of open habitats

where the risk of predation through owls is high (Henderson and Broders, 2008). Furthermore, several studies suggest that bats tend to shift their foraging habitat closer to vegetation under bright moonlight (Ciechanowski et al., 2007; Hecker and Brigham, 1999). Thus, hunting underneath a protective canopy might be preferred by Greater Mouse-eared Bats. Nevertheless, it is known that *M. myotis* also hunt in open landscapes like recently mown meadows or orchards without shielding crown cover though it is probably a weighing of interest between shelter through the forest and a faster food intake due to higher prey abundance on meadows at certain times of the year (Arlettaz, 1996; Pereira et al., 2002; Rey, 2004; Zahn et al., 2006).

A clear picture provided the *degree of shrub layer,* which had a distinct negative influence on Greater Mouse-eared Bat activity. A high proportion of shrub layer complicates flying and gleaning near the ground. Although *M. myotis* are able to fly very agile due to wide wings, as one of the largest bat species in Switzerland they prefer an open space to fly (Meschede and Rudolph, 2004). Therefore, a free space in the shrub layer (up to 3 m) with a vegetation density less than 25% seemed to be preferred by Greater Mouse-eared Bats (Fig. 15). Also the recorded variable *free flight space,* defined as the total free space from herbaceous layer to the first layer of vegetation which is inhibiting a free flight, showed a higher bat activity from around 5 m to 20 m. However, it is interesting to note that activity decreased again at free flight spaces higher than 20 m (Fig. 17). Dislike seems to exist for foraging habitats with too much open area and no or only very distant structure. Again, this might be explained by the avoidance of open habitats and the shift towards vegetation under bright moonlight to minimize the risk of predation (Ciechanowski et al., 2007; Hecker and Brigham, 1999; Henderson and Broders, 2008). Moreover, the frequency modulated calls of Greater Mouse-eared Bats are limited in distance and detection range (Schnitzler et al., 2003). Flying in forests with distant structure, which is further away than 20 m, might complicate orientation in space.

Forest categories

The variation of activity between different *forest forms* is not very pronounced, however, a significant difference between "high forest with area-wise cut" and "plenter forest" was recorded (Fig. 9). Since "plenter forests" as uneven-aged high forests are permanently sheltered by mature stand and the regeneration spreads over large areas, old trees are more

likely to be left and changes are not as extreme and sudden as at "high forests with area-wise cut". Since bats as creatures of habit are often hunting at the same places over generations, sudden forest changes might disturb them more than slow alterations (Lehnert et al., 2018). Additionally, old trees are represented more often in "plenter forests" than in "high forests with area-wise cut". Due to further findings of this study which revealed the importance of older trees with diameters of at least 30 cm ("young timber") or even better diameters bigger than 50 cm ("old timber") for Greater Mouse-eared Bats (Fig. 12), the presence of thicker trees in "plenter forests" might also explain the preference for this type of forest. With increasing forest age, biodiversity and insect biomass also rise, what leads to a better food supply for Greater Mouse-eared Bats (Lassauce et al., 2013; Moning and Müller, 2009). Moreover, older trees exhibit bigger crowns and a larger free flight space, whereby both variables correlate positively with activity of *M. myotis*. Greater Mouse-eared Bats need to rest from time to time during hunting at night and often seek for resting places like tree holes of old trees close to their foraging habitat; sometimes males even use tree holes as roosts during day time (Broggi et al., 2011). Therefore, older trees have several advantages for Greater Mouse-eared Bats and it is not surprising that the activity of *M. myotis* increases from "young timber" to "old timber". Young trees like within the categories "pole wood" or "young growth" do not have the benefits of older trees mentioned above but furthermore, they normally inhibit a free flight space and often exhibit a high proportion of shrub layer.

Greater Mouse-eared Bats provide a clear preference of the type of *stand structure*: they showed a significantly higher activity at single-layered than at multi-layered forests and hardly any activity could be found at forests with an all-sized structure (Fig. 10). Single-layered forests are uniform stands, whereby their crowns are horizontally closed in the upper layer. Further, the proportion of the medium and lower layer is less than 20%. A higher percentage of the lower layers occurs at multi-layered forests with two or more uniform layers. All-sized forests have several indistinct layers formed by trees and shrubs. Therefore, a free flight space is rather given at single-layered forests, since multi-layered forests would need to be very old to guarantee a lower layer that is grown high enough. All-sized forests with indistinct layers have often a shrub layer and no free flight space. Consequently, single-layered forests seem mostly to combine many factors which predict a

higher Greater Mouse-eared Bat activity: a free flight space, a dense canopy and no or only few shrub layer.

Yet not every single-layered forest seems to be suitable foraging habitat for Greater Mouse-eared Bats: pure coniferous forests are significantly rarer visited than pure deciduous forests. But no difference could be found between pure deciduous forests, mixed deciduous forests and mixed coniferous forests (Fig. 11). Forests with a certain proportion of deciduous trees seemed to be preferred, what excludes pure spruce plantations. Probably it is rather not explainable with an avoidance of coniferous trees due to their microclimatic changes (lower pH value, soil humidity, see Finch, 2005 and Rudolph et al., 2009), because then one would expect a higher bat activity the higher the proportion of deciduous trees in a forest. But since no significant graduation was detected between forests containing different amounts of coniferous trees, it is more likely due to the spatial structure of pure spruce plantations. As spruces are often cultivated in line and close together, free flight space and a low proportion of shrub layer are difficult to obtain, especially since the branches of spruce do often reach close to the ground.

Landscape variables and environmental influences

Other variables like *GPSx, GPSy* (either single or combined), *elevation, slope* or *relief* did not seem to influence Greater Mouse-eared Bat activity strongly what coincides with the results of Güttinger (1997). Interestingly, the *aspect* seemed not to influence bat activity in his study but a significant influence of *easterness* (gradient east – west) and of a combined effect of *easterness* and *northerness* on bat activity was found. However, *northerness* (gradient north – south) did not show any significance. The highest activity was found at eastern slopes. Since in Central Europe the western slopes are exposed to the strongest weather conditions, a preference of eastern slopes may enable hunting under more moderate weather conditions. The avoidance of strong wind (complicates flying) and heavy rain (attenuates echolocation calls) by selecting the foraging habitat based on its hillside enables hunting for a longer period of time, even when the weather is not ideal.

Especially the *humidity* influenced Greater Mouse-eared Bat activity during the fieldwork: The range of echolocation calls is the highest at low air humidity since absorption is small (O'Donnell, 2010). Furthermore, also a slight effect depicted *air temperature* with a higher

bat activity at warmer days. Since the costs of thermoregulation to maintain body condition are lower and usually more insects are abundant, bat activity might be higher at warmer temperatures (Catto et al., 1996; Wolbert et al., 2014). *Wind velocity* and *precipitation* did not show an effect on Greater Mouse-eared Bat activity since the fieldwork was only carried out during good weather conditions. However, these weather conditions would certainly have had an effect on Greater Mouse-eared Bats if they had not been deliberately avoided (O'Donnell, 2010).

Unexpectedly, the *total forest size*, the *relative forest size* and also the *target forest size* seemed not to influence Greater Mouse-eared Bat activity strongly since they all are no part of the model. If checked individually, the relative forest size (proportion of forest in a range of 300 m) was more important for *M. myotis* than the total forest size. This suggests that Greater Mouse-eared Bats hunted preferably surrounded by forest than close to the forest border, whereby the immediate vicinity played a bigger role than the total size of the forest. These findings may be linked with the vegetation structure at forest borders, where normally a dense shrub layer occurs and might explain why the variable does not explain further variation of the model. The target forest size improved the model slightly (within subsample A) but not enough to exceed the simpler one. Nevertheless, a higher bat activity was found at bigger areas of suitable forest. Therefore, it can be suggested that Greater Mouse-eared Bats do not need huge connected woodland since they are able to hunt at different foraging areas per night with a distance of around 500 m apart from each other (Rudolph et al., 2009) but the bigger the forest patches displaying suitable forest structure the better. Also *homogeneous* areas were preferred what suggests, that the hunting habitat should not be too small-scaled.

The variable *recording hours per night* adjusted for different night durations and for the failure of batloggers. The longer the duration of recordings per night the bigger the chance for Greater Mouse-eared Bats to be captured on the batlogger, what was reflected in a higher bat activity. The last variable explaining variation of Greater Mouse-eared Bat activity is the *distance* from the roost to the foraging habitat, whereby less bat activity was found at sampling sites further away. It is suggested that *M. myotis* will select foraging habitats closer to the maternity roost to save energy through short routes if suitable habitats are available but still are able to fly longer distances if needed (Rudolph et al., 2009).

Forest situation in Switzerland

But what happens if no longer suitable hunting habitats are reachable for Greater Mouse-eared Bats? Different studies showed that *M. myotis* also hunts in open landscapes like recently mown meadows or orchards (Arlettaz, 1996; Pereira et al., 2002; Rey, 2004; Zahn et al., 2006). The question that arises is whether Greater Mouse-eared Bats could forage exclusively outside the forest if the latter would no longer exhibit good hunting habitats. Like Arlettaz (1996) indicated in his paper, it probably depends on prey abundance at the meadows and orchards, since they mainly hunted outside the forest in summer, when mole crickets, cockchafers and European crane flies were abundant. But especially in spring and during cold weather it seemed that forests offer better condition for hunting than open landscapes due to a more temperate climate (Zahn et al., 2006). Additionally, the abundance of insects in agricultural land is questionable in times when there is talk of 75% insect decline (Hallmann et al., 2017). Therefore, it seems difficult if the Greater Mouse-eared Bats would have to forgo forests as foraging areas.

However, the suitable foraging areas this study defined as single-layered pure deciduous or mixed forests containing at least young timber, a closed canopy, free flight space and hardly any shrub layer, are scarce across vast parts of Switzerland. This situation was visible through the own experiences during field work and the difficulty to find suitable sampling sites; but also through the very few predictions of the classifications model in many places. In general, the model predictions to simplify the search for suitable sampling sites were consistent with the situation in the field. Suitable sampling sites were more often located on areas which were also predicted as suitable by the classification model. Also, the model was able to differentiate clearly between suitable sampling sites (respectively less suitable sampling sites) and not suitable sampling sites. Though, the predictions were complicated by the fact that the classification models based on constantly updated LiDAR data due to ongoing measurements until 2023. This had the consequence that some areas of Switzerland were calculated with newer data, whereby other regions have possibly altered more since the LiDAR data collection. Especially in regions with a high level of silvicultural activity, big forest changes appeared to be possible in a short time what led to unprecise model predictions. However, the basic impression of only few old beech forests and suitable mixed forests left seemed to be confirmed throughout Switzerland, whereby the remaining ones

could be mainly found in the North of Switzerland (canton Schaffhausen). Additionally, many of the forests with closed canopies and open ground were often marked, probably for timber harvesting in near future. The intensified logging probably occurs due to the guidelines to substantiate the Forest Policy 2020 (Bundesamt für Umwelt, 2013) whereby light forests are intended.

Since the aim of brightening up the forests is amongst others a diverse herbaceous layer, the influence of ground vegetation on Greater Mouse-eared Bat activity should be further investigated. The results of this study showed that the herbaceous layer seemed not necessarily to be a disadvantage for *M. myotis* but especially the impact of the type of herbaceous layer is unclear. Moreover, since the *degree of herbaceous layer* was an important indicator for suitable foraging habitat in many studies (Güttinger, 1997; Zahn et al., 2005), the findings of this study, which depicted the ground vegetation as unimportant, should be examined more closely.

To make sure that the explored suitable forest structures are as assumed species-specific for Greater Mouse-eared Bats, other bat species will be tested equally in a follow-up project. Due to the recording method using batloggers, all bat species which used echolocation calls near the sampling site have been recorded and can be analysed similarly in regard to the forest variables. This investigation will determine whether the found preference for a specific type of forest structures is unique for Greater Mouse-eared Bats and if other bat species show different patterns in terms of favoured foraging habitat.

With the new insights of important vegetation structures for Greater Mouse-eared Bats, the classification model can be improved and will enable to identify suitable forest throughout Switzerland. This will help to locate the important foraging areas more easily and to preserve them against extensive forest tending. Moreover, the model predicting the commuting corridors can be enhanced by including the quality of the target forests, what will strengthen the validity of the predicted commuting corridors. With the two models the protection of the total Greater Mouse-eared Bat habitat including maternity roost, commuting corridors and foraging habitat will be simplified and facilitated.

Conclusion

The conservation of Greater Mouse-eared Bats in Switzerland is of great significance, since they belong to the most threatened bat species based on their habitat selection and are listed as vulnerable on the Swiss Red List (Bohnenstengel et al., 2014). This study focused on the identification of the preferred hunting areas of *M. myotis* to enable a complete consideration and protection of their habitat. Different forest variables predicting a higher Greater Mouse-eared Bat activity could be defined, whereby results of previous studies (Güttinger, 1997; Rudolph et al., 2009; Zahn et al., 2005) were confirmed in principal: Suitable foraging areas were primarily constituted of single-layered pure deciduous or mixed forests with a closed canopy, a free flight space and hardly any shrub layer. Furthermore, forests with older trees were preferred. Since Greater Mouse-eared Bats show a typical gleaning behaviour and a free flight space without shrub or herbaceous layer was assumed to be important, it is even more interesting that in this study the degree of herbaceous layer as well as the type of herbaceous layer did not seem to influence Greater Mouse-eared Bat activity. These findings should be investigated more closely in further studies, especially because light forests with a diverse herbaceous layer are intended to be promoted in the future (Bundesamt für Umwelt, 2013). Since Greater Mouse-eared Bats are dependent – at least for certain times of the year (Zahn et al., 2006) – on foraging in single-layered forests with a closed canopy and no shrub layer, timber harvesting and brightening is likely to destroy suitable foraging habitat and therefore endangers the Greater Mouse-eared Bats even more. With the gained insights on preferred forests structures of this study, it will be possible to locate suitable forests more easily by the adjusted classification model. The preservation of these forests against extensive forest tending and habitat change will help to protect the Greater Mouse-eared Bats.

Acknowledgements

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Appendix

Appendix I

Explanation of the habitat variables describing the study site

(1) GPS

Measurement of GPS data at the location of the batlogger.

Stand related recording in the field with Garmin GPSMAP 62st and verified with swisstopo (map.geo.admin.ch, Bundesamt für Landestopografie). GPS data was entered in batlogger before recording to incorporate in meta-data.

(2) Elevation

Measurement of elevation in meters above sea level at the location of the batlogger.

Stand related recording in the field with Garmin GPSMAP 62st and verified with swisstopo (map.geo.admin.ch, Bundesamt für Landestopografie).

(3) Aspect

Measurement of the aspect if the relief is an upper slope, middle slope or foot slope. If the slope is ≤ 10% or if the interpretation area is situated on an edge, on a hilltop, in a depression or on a plain, the aspect is not determinable. The categories north, northeast, east, southeast, south, southwest, west and northwest were recorded.

Stand related recording in the field with Garmin GPSMAP 62st and verified with swisstopo (map.geo.admin.ch, Bundesamt für Landestopografie). Origin and classification according to LFI4 (Düggelin, 2019).

(4) Slope

Measurement of the slope if the relief is an upper slope, middle slope or foot slope. The average slope within the 12.5 m radius sampling site was determined.

Stand related recording in the field with Bosch GLM 80 Professional laser rangefinder. Variable is referring to LFI4 (Düggelin, 2019) and adapted to this research project.

(5) Target forest size

Measurement of the area of connected forest patches categorised as "suitable" beyond the 12.5 m radius sampling site (total area of assumed suitable sampling site). If the area is too large for measurement, the target forest size was qualitatively estimated.

Stand related estimation in the field with Bosch GLM 80 Professional laser rangefinder. The variable was specially created for this research project.

(6) Free flight space

Record of the height of the free airspace as fly zone for bats measured from 0.5 m to the first tree or shrub layer which inhibited a free flight.

Stand related estimation in the field with Bosch GLM 80 Professional laser rangefinder. The variable was specially created for this research project.

(7)   Forest form

The forest form defines the basic type of forest resulting from application of a chosen management system.

- **High forest:** forest composed of standards (generative propagation).
- **Even-aged high forest regenerated by area-wise cut:** stands generated by cuts in the group-selection system, including strip-cuts, shelterwood cuts, clear cuts or afforestations. Area-wide regeneration (areal and temporal order). – in the following termed "high forest with area-wise cut".
- **Plenter forest** (uneven-aged high forest): Regeneration spread over large areas and sheltered permanently by mature stand; all tree dimensions present on small area (selection of single trees) or all stages of development (selection of groups of trees or selection type forest in the mountains).
- **Coppice forest**: Tree originating from vegetative propagation. Coppice forest can develop naturally (e.g. after rockfall).
- **Coppice with standarts:** Combination of high forest and coppice forest; standards generally in the upper layer and coppice regrowth in medium and lower layer (coppice layer).
- **Special forms:** Selvas and plantations.

Stand related recording in the field. Origin and classification according to LFI4 (Düggelin, 2019), few classes combined.

(8)   Stand structure

The stand structure describes the vertical structure of the reference stand and is defined by the proportion of the different layers. The minimum degree of cover is 20% for each layer.

- **Single-layered:** Crowns of the trees forming the stand extend into the upper layer, horizontal crown closure, uniform stands. Degree of cover in the medium layer and lower layer is <20% for each of them.
- **Multi-layered:** Two or more uniform layers, upper layer is mostly open and clearly distinct from the medium and lower layers. The degree of cover for the medium layer and lower layers >20%.

- **All-aged/all-sized**: Trees and shrubs forming stands with several indistinct layers. Horizontal closure exists only for groups of trees. Trees of the lower and medium layers can grow into the upper layer.
- **Clustered**: Crowded groups of trees, trees and shrubs within a group have different heights, are one-sided and low-branched. (For example, clusters of trees near the timber-line or on wooded pastures).

Stand related recording in the field. Origin and classification according to LFI4 (Düggelin, 2019).

(9) Degree of mixture

To determine the proportion of basal area of conifers and deciduous trees in the reference stand. Percentage qualitatively estimated of the sampling site.

- 91–100% conifers   = Pure coniferous forest
- 51– 90% conifers   = Mixed coniferous forest
- 11– 50% conifers   = Mixed deciduous forest
- 0– 10% conifers   = Pure deciduous forest

Stand related estimation in the field. Origin and classification according to LFI4 (Düggelin, 2019).

(10) Stage of stand development

To assess the stage of stand development as a function of the dominating diameter at breast height (dbh). Ddom = mean dbh of the strongest trees of the reference stand.

- Young growth/thicket ddom < 12 cm
- Pole wood ddom = 12–30 cm
- Young timber ddom = 31–40 cm
- Medium timber ddom = 41–50 cm
- Old timber ddom > 50 cm
- Mixed Trees belonging to different diameter classes, where no diameter class dominates or groups with different stages of stand development varies over at least three diameter classes.

Stand related recording in the field. Origin and classification according to LFI4 (Düggelin, 2019).

(11) Relief

Relief with a minimum size equal to or larger than the sampling site.

- **Plain, flat area:** Slope ≤10%: Plain, plateau, terrace, valley floor.
- **Top, upper slope:** Convex forms, predominantly water running off: Hilltop, crest, ridge, spur, edge of plateau and terrace.
- **Middle slope:** Sloped area, lateral inflow and outflow ± equal: Middle slope, debris cones, alluvial cones, screes.
- **Foot slope, depression:** Concave forms, predominantly water inflow: Foot slope, lower slope, slope depression, depression, cirque, gully, gorge.
- **Undeterminable:** No clear allocation to 1 to 4 possible, e.g. landslip with widely varying and alternating slopes and aspects.

Stand related recording in the field. Origin and classification according to LFI4 (Düggelin, 2019).

(12) Abiotic

Percentage of abiotic structures (stone, rock) with a minimum size of approximately 10 cm (driving obstacle) within the sampling site.

Stand related estimation in the field. The variable was specially created for this research project.

(13) Degree of herbaceous layer

Degree of herbaceous layer within the sampling site up to 0.5 m. Assessed were all ferns, grasses, herbs, tall forbs and dwarf shrubs but no mosses or foliage.
Gradual estimation of the percentage coverage of the ground vegetation.

Stand related estimation in the field. Origin according to LFI4 Variable but instead of a classification it was gradually estimated.

(14) Type of herbaceous layer

Rough recording of the plant species of the ground vegetation (under 0.5 m) and categorization the most abundant species into one of the six groups starting with number 1 (short plants, predicted as small obstacles for bats) to number 6 (large plants, predicted as big obstacles for bats).

1. Clover (*Trifolium* sp.), ivy (*Hedera* sp.)
2. Grass (*Poaceae* sp.)

3. Ramson (*Allium ursinum*), woodruff (*Galium odoratum*), common periwinkle (*Littorina littorea*)
4. Fern (*Polypodiopsida* sp.), little trees
5. Small bramble bush (*Rubus* sp.)
6. Large bramble bush (*Rubus* sp.), small firs (*Abies* sp.)

Stand related estimation in the field. The variable was specially created for this research project.

(15) Degree of shrub layer

The degree of shrubs and young trees within the sampling site, consisting of all woody species from approx. 0.5 m to 3.0 m in height, including the branches of higher trees and shrubs between these limits. Gradual estimation of the percentage coverage of the shrub layer.

Stand related estimation in the field. Origin according to LFI4 Variable but instead of a classification it was gradually estimated.

(16) Degree of crown cover (canopy)

The degree of crown cover gives the ratio between the total area and the area covered by the canopy. It does not matter whether the gaps are concentrated in the canopy or diffusely distributed over the stand. Gradual estimation of the percentage coverage of the canopy.

Stand related estimation in the field. Origin according to LFI4 Variable but instead of a classification it was gradually estimated.

(17) Homogeneous/heterogeneous

Estimation if the study area is homogeneous or heterogeneous in relation to the general impact influenced by forest type, stand structure, ground-, shrub-, crown cover, size of airspace etc.

Stand related estimation in the field. The variable was specially created for this research project.

(18) Weather data (Air temperature, humidity, precipitation and wind velocity)

The average of air temperature, humidity, precipitation and wind velocity per night measured from 21.00 to 06.00 o'clock. Air temperature and the relative humidity were measured 2 m above ground, precipitation and wind velocity as a sum of ten minutes.

Weather data from CLIMAP-net (Bundesamt für Meteorologie und Klimatologie MeteoSchweiz).

(19) Total forest size

Area of connected woodland in km^2.

The variable was specially created for this research project. Calculation of the area in ArcGIS (ArcGIS Desktop 10.7, Version 10.7.0.10450) using data from the large-scale topographical landscape model of Switzerland swissTLM^{3D} (Version 1.7).

(20) Relative forest size

The relative forest size was calculated as the ratio of forest to non-forest of an area of 300 m radius (area of around 0.28 km^2) around a batlogger.

The variable was specially created for this research project. Calculation of the percentage in ArcGIS (ArcGIS Desktop 10.7, Version 10.7.0.10450) using data from the large-scale topographical landscape model of Switzerland swissTLM^{3D} (Version 1.7).

(21) Distance

Straight-line distance in kilometres from the roost to the sampling site (location of a batlogger).

The variable was specially created for this research project. Distance calculated in ArcGIS (ArcGIS Desktop 10.7, Version 10.7.0.10450) using GPS data of the batloggers and roosts.

Appendix II

Table 13: Selection criteria for the verification of Greater Mouse-eared Bat calls.

	Identified species	Filter	Verification or disable
1		0 calls in sequence	disabled
2	Not *M. myotis*		disabled
3	1st *M. myotis*	• 10 calls in the sequence • 95% CI-test passed	verified
4	1st *M. myotis*	• > 5 calls in the sequence • < 3 species identified • 95% CI-test passed	verified
5	1st *M. myotis*		Remaining sequences checked manually for *M. myotis*
6	1st *Nyctalus leisleri* 2nd or 3rd *M. myotis*		Sequences checked manually for *M. myotis*
7	1st *Eptesicus* sp.[13] 2nd or 3rd *M. myotis*		Sequences checked manually for *M. myotis*
8	1st *Vespertilio murinus* 2nd or 3rd *M. myotis*		Sequences checked manually for *M. myotis*
9	2nd or 3rd *M. myotis*		Remaining sequences checked manually for *M. myotis*
10	1st *Pipistrellus pipistrellus* 2nd or 3rd *M. myotis*		Sequences checked manually for *M. myotis*
11	1st *Pipistrellus pipistrellus*	• > 3 calls in the sequence • Only 1 species identified • 95% CI-test passed	disabled
12	1st *Pipistrellus pipistrellus* 2nd or 3rd not *M. myotis*		disabled
13		All remaining sequences checked manually for *M. myotis*	

[13] *Eptesicus serotinus* and *Eptesicus nilssonii*

Appendix III

Table 14: Complementary information about the data sources.

Data source	Data type	Source scale	Year of measurement	Source
LiDAR	Airborne Light Detection and Ranging data	• Point density: at least 5 pts/m^2, mean value 15-20 pts/m^2 • Position accuracy: 20 cm • Height accuracy: 10 cm	Ongoing until 2023	Projekt landwirtschaftliche Nutzflächen LWN (Swisstopo) In individual cases supplemented with cantonal flights
LFI4	Acquisition of condition and changes of Swiss forests like forest form and stand structure	Perimeter: whole Switzerland	2009 - 2017	WSL, 2019: Schweizerisches Landes-forstinventar LFI, Daten der Erhebung 2009/17 (LFI4). Christoph Düggelin. 18.01.2019
WGM	Degree of mixture of Swiss forests	• 25 x 25 m raster resolution • perimeter: whole Switzerland	2017	WSL, 2017: Schweizerisches Landes-forstinventar LFI. Datenbankauszug vom 28.04.2017. Christian Ginzler. Eidg. Forschungsanstalt WSL, Birmensdorf.
DTM25_L2	Digital Elevation Model	25 meters	1994	Bundesamt für Landestopografie swisstopo (Art. 30 GeoIV): 5704 000 000
swissTLM^{3D}	3D Vector Dataset	Various	2012 - 2019	Bundesamt für Landestopografie swisstopo (Art. 30 GeoIV): 5704 000 000
CLIMAP-net (Bundesamt für Meteorologie und Klimatologie MeteoSchweiz)	Weather data of almost 1000 weather stations	250 different parameters	ongoing	MeteoSchweiz
Map viewer map.geo.admin.ch	Map of Switzerland	Various		geodata © swisstopo

Appendix IV

Table 15: Complementary information about the figure sources.

Figure	Source	Date
Cover picture "Suitable sampling site of a forest in Beggingen"	Photographed by Katja Rauchenstein.	Recorded on 17.06.2019
Cover picture "Greater Mouse-eared Bat" (silhouette)	Photographed by Dietmar Nill. Image downloaded from https://www.flickr.com/photos/dietmarnill/5117636000 and edited to a silhouette.	Recorded on 18.10.2010 Downloaded on 09.10.2019
Fig. 1: The distribution of the 18 selected study locations (maternity roosts of *M. myotis*).	ArcGIS (ArcGIS Desktop 10.7, Version 10.7.0.10450) Background image: Relief of DEM/DHM (50 m resolution) © 2019 Bundesamt für Landestopografie swisstopo (Art. 30 GeoIV): 5704 000 000	Produced on 19.09.2019
Fig. 2: Examples of sampling sites.	Photographed by Katja Rauchenstein	Recorded on 02.07.2019 (Embrach) 18.06.2019 (Lipperswil)
Fig. 3: Field design with four triplets of sampling sites (suitable, less suitable, not suitable) in the forests around the maternity roost *of M. myotis* in Burgdorf. The classification models 1, 2 and 3 predicted sampling sites of different suitability. The circle defines the sampling area of 5 km around the roost.	ArcGIS (ArcGIS Desktop 10.7, Version 10.7.0.10450) Background image: Swissimage (25 cm resolution) © 2019 Bundesamt für Landestopografie swisstopo (Art. 30 GeoIV): 5704 000 000	Produced on 03.09.2019
Fig. 4: Batlogger A with information sign and microphone mounted on a pole in Eichberg.	Photographed by Katja Rauchenstein	Recorded on 10.06.2019 (Eichberg)
Fig. 5: Predictions of the classification model 1 for suitable forests.	ArcGIS (ArcGIS Desktop 10.7, Version 10.7.0.10450)	Produced on 15.11.2019
Fig. 6: Each pixel displays the sum of the nine contiguous pixels whereby as suitable predicted pixels counted 1, the others 0.	ArcGIS (ArcGIS Desktop 10.7, Version 10.7.0.10450)	Produced on 15.11.2019
Fig. 7 – Fig. 19	© 2009-2019 RStudio, Version 1.2.5001	Produced on 24.10.2019

Appendix V

Affidavit

I hereby declare that the thesis with title

Forests suitable for Greater Mouse-eared Bat's (Myotis myotis) foraging

has been composed by myself autonomously and that no means other than those declared were used. In every single case, I have marked parts that were taken out of published or unpublished work, either verbatim or in a paraphrased manner, as such through a quotation.

This thesis has not been handed in or published before in the same or similar form.

Zurich, 10.01.2020