MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

„A camera trapping study on medium-sized and large mammals, with a focus on predators of ground-breeding bird nests, across an elevational gradient in the Verwall Alps, Vorarlberg, Austria“

verfasst von / submitted by

Julia Ronja Elisabeth Paterno, BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2019 / Vienna 2019

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	A 066 879
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium Naturschutz und Biodiversitätsmanagement
Betreut von / Supervisor:	Dipl.-Biol. Dr. Christian H. Schulze

Mit Unterstützung von Bund und Europäischer Union

Bundesministerium
Nachhaltigkeit und
Tourismus

LE 14-20
Entwicklung für den Ländlichen Raum

Europäischer
Landwirtschaftsfonds für
die Entwicklung des
ländlichen Raums:
Hier investiert Europa in
die ländlichen Gebiete.

ACKNOWLEDGEMENTS

First, I'd like to thank my supervisor Christian Schulze for his support and his ongoing good ideas. Special thanks to Christian Kuehs from the Naturschutzverein "Verwall – Klostertaler Bergwälder", for a great amount of the organization done by him, his time and the great advice during field work and writing. Also Barbara Waringer was an indispensable support during the whole working progress. Thank you for all of your time, your shared knowledge, your constant support and proofreading. Furthermore, I'd like to thank Victoria Werner for her assistance in the field, her great support, critics and motivation. I'd also like to thank Nina Gallmetzer for great preparation of the raw data and providing maps. Furthermore, I'd like to thank Felix Meyer for sharing his equipment with me and thus making fieldwork much easier. I'd like to thank all the hunters and land owners in the area for their support. Thanks to Manuela Loretz from BH Bludenz for offering data. I'd also really like to thank my sister Sarah Paterno for numerous discussions, precious input and all of the shared time. Also thanks to Hansi Egger for various discussions, sharing his knowledge and inspecting the study sites with me. Special thanks to my mama Elisabeth Paterno for her ongoing awesome support, patience and time. And also for providing the car - field work would not have been possible without her. Special thanks also to my papa Hugo Richtig supporting me all my lifetime, for all his patience and understandings. Last but not least I'd like to thank all my friends for their precious support during my studies, for many great discussions, motivation and supporting my passion.

Thank you.

The project (**LE 14-20 / Antragsnr. 7.6.1a-I8-38/16 -** Vorhaben "Prädation von Bodenbrütern") was financially supported by the Federal Ministry for Sustainability and Tourism and the European Union in the framework of "Austria - Rural Development Programme (National)".

ABSTRACT

The aim of the present study was to improve the knowledge about occurring medium-sized and large mammals along elevational gradients in the Verwall Alps, Austria. Though, the focus was placed on mammalian predators of ground-breeding bird nests. Changes in species richness, composition and daily activity were assessed and shifts in predation risk for ground breeding bird nests evaluated. Therefore 100 artificial clutches equipped with camera traps were exposed along two elevational transects. Field surveys were conducted from May until September 2018 and nests remained in the field for a maximum duration of 26 days. Additionally, vegetation structure of the nest sites and abiotic variables were recorded. The following non-predator species could be detected: Red (*Cervus elaphus*) and Roe Deer (*Capreolus capreolus*), Chamois (*Rupicapra rupicapra*), Alpine Marmot (*Marmota marmota*), Snow Hare (*Lepus timidus*) and Domestic Horse (*Equus caballus*) and Cattle (*Bos primigenius Taurus*). Red Fox (*Vulpes vulpes*), Pine (*Martes martes*) and Beech Marten (*Martes foina*), Stoat (*Mustela erminea*), Polecat (*Mustela putorius*) and Badger (*Meles meles*), also Cattle and Corvids, were recorded as predators of the artificial nests. Their distribution was species-specific and depended on different variables, such as shrub height and distance to trails. Species composition of medium and large-sized mammals changed with increasing elevation and species richness and daily activity decreased. Predatory mammals in contrast showed no change in activity and richness. However, elevation was an important predictor for the risk of predation, as well as the distance to roads. The overall nest predation rate (36%) was relative low compared to previous studies, but predation pressure of ground breeding birds is a complex issue and detailed understanding of the different intricate interactions is a crucial for targeted management measures.

Keywords: clutch predation, mammalian predators, Mammalia, species richness, species composition, elevation, The Alps

ZUSAMMENFASSUNG

Die vorliegende Arbeit untersucht das Vorkommen großer und mittelgroßer Säuger entlang von Höhengradienten in der Verwallgruppe in Österreich, wobei der Fokus auf Nestprädatoren bodenbrütender Vogelarten gelegt wurde. Einerseits wurden Veränderungen im Artenreichtum, der Artenzusammensetzung und der täglichen Aktivität großer und mittelgroßer Säuger ermittelt, und andererseits die Veränderung des Prädationsdrucks erforscht. Für die Durchführung der Studie, wurden insgesamt 100 Kunstnester verwendet. Diese wurden, gemeinsam mit Fotofallen, entlang von zwei Höhengradienten in verschiedenen Untersuchungsgebieten zwischen Mai und September 2018 ausgebracht. Abhängig von der Expositionsdauer (max. 26 Tage) und der Prädation wurden sie regelmäßig in die nächste Höhenstufe versetzt. Zusätzlich dazu wurden verschiedene Vegetationsparameter und abiotische Variablen erhoben. Folgende Pflanzenfresser konnten dabei ermittelt werden: Rothirsch (*Cervus elaphus*), Reh (*Capreolus capreolus*), Gämse (*Rupicapra rupicapra*), Murmeltier (*Marmota marmota*), Schneehase (*Lepus timidus*), Hauspferd (*Equus caballus*) und Hausrind (*Bos primigenius Taurus*). Die vorkommenden Raubsäuger waren Rotfuchs (*Vulpes vulpes*), Baum- (*Martes martes*) und Steinmarder (*Martes foina*), Hermelin (*Mustela erminea*), Waldiltis (*Mustela putorius*) und Dachs (*Meles meles*). Allerdings waren auch Corviden und Kühe wichtige Prädatoren. Die Verbreitung der verschiedenen Arten, war von diversen Umweltfaktoren abhängig, wie zum Beispiel Höhe der Strauchschicht oder Nähe zu Wegen und Straßen. Die Artenzusammensetzung großer und mittelgroßer Säuger veränderte sich entlang des Höhengradienten und der Artenreichtum und die tägliche Aktivität nahmen mit zunehmender Höhe ab. Für Raubsäuger allein war dieser Zusammenhang nicht ersichtlich. Trotzdem zeigte sich, ein wichtiger Einfluss der Höhe auf das Pradationsrisiko, genauso wie die Distanz zu Wegen und Straßen. Insgesamt war die Prädationsrate (36%) verglichen mit ähnlichen Studien im unteren Bereich. Allerdings ist die Nestprädation bodenbrütender Vogelarten eine komplexe Angelegenheit und gezielte Managementmaßnahmen bedürfen einem detaillierten Verständnis der verschiedenen komplizierten Interaktionen.

Keywords: Nestprädation, Raubsäuger, Säugetiere, Artenreichtum, Artenzusammensetzung, Höhengradient, Alpen

Contents

1. INTRODUCTION

The biogeographical pattern of species richness decline from the equator to the poles is a well-established phenomenon. Latitudinal gradients in species richness have been reported for different taxa (Rohde 1992). When comparing elevational and latitudinal gradients, some similarities emerge. In fact, one could suppose that the elevational gradient just mirrors the latitudinal one (Rahbek 1995). However, Brown (2001) came to a different conclusion. He argues, that these gradients have not only similarities, but also numerous differences. While factors such as area, temperature and energy availability change continuously along both gradients, the seasonality of solar energy flux and related variables remains relatively constant along elevational gradients but changes significantly with latitude (Brown 2001).

These differences are also reflected in the distribution pattern of species richness. Numerous elevational studies came to the result of a hump-shaped curve for non-volant mammal species richness (e.g. Rahbek 1995; Geise et al. 2004; DeGregorio et al. 2016). Thus, there is a peak of species richness at intermediate elevations, contrastingly to the uniform pattern of species richness decline from equator to the poles. Brown (2001) mentioned two main explanations for the pattern of hump-shaped species richness depending to elevation. First, he explains it by the low tolerance of species to the comparable wide range of habitats depending on elevation (from sealevel to icebound peaks). Only few species would be able to suffer the entire range of environments. Hence he argues that there is an overlap of the range-limited species in the mid-elevations, what leads to a peak of species richness at intermediate elevations. Furthermore, he assumed a mid-elevation peak due to a higher productivity in this elevational range. Yet when the elevations, where species with different needs overlap correspond with the most productive part, there is an even higher peak in species richness (Brown 2001).

This peak at intermediate elevations may also occur for the activity of medium and large-sized mammals. There are rough conditions in higher elevations, since various abiotic factors change with increasing elevation (Körner 1999). Probably smaller species may occur more often in these areas than big ones, as this habitat provides less food sources and shelter. Small mammals need low amounts of food compared to their body-mass, but high in quality (Jarman 1974; Tershy 1992). Therefore the actions of smaller mammals may be more targeted and thus probably also lower in number. Big species in contrast, like e.g. the Red Deer (*Cervus elaphus*), may spend more time searching for food, since they feed on high amounts of low nutritive food (Jarman 1974; Tershy 1992), thus probably showing an increased activity. On this assumption, the activity of medium and large-sized mammals may decrease with increasing elevation.

Due to the habitat change from montane forest to high-elevational open grassland, there also may be a change in species composition depending to timberline. Since this transition zone is a natural edge, there may be an increased predation pressure due to an edge effect (Masoero et al. 2016). However, there could also be a higher predation probability along artificial, linear structures such as roads, since Carnivores often showed an increased use of them (e.g. Mahon et al. 1998; Bowman et al. 2010; Towerton et al. 2011). Pedersen et al. (2011) showed for example that some predator species depend strongly on human infrastructure. However, there are numerous additional factors influencing predator species distribution, such as prey-predator interactions, productivity or climate (Sandom et al. 2013). But also vegetation structure is an important factor, since Martens for example seem to avoid habitats without overhead cover (Hawley and Newby 1957; Pullianen 1981; Rondinini and Boitani 2002). Red Foxes (*Vulpes vulpes*) in contrast could be detected in various habitats in a study conducted in the Western Alps in Italy (Cagnacci et al. 2004). What is not surprising, since the Red Fox, as generalist, is very flexible in habitat choice and feeding preferences (Dell'Arte et al. 2007; Hartová-Nentvichová et al. 2010; Rosalino et al. 2010). The main food sources of Red Fox are rodents, fruits and plant material (Hartová-Nentvichová et al. 2010). But also (gallinaceous) birds and their eggs are taken, whenever possible (Hartová-Nentvichová et al. 2010).

Nesting failure caused by nest predation is considered to be one of the most important factors reducing the reproductive success for ground breeding birds (e.g. Jehl, JR. 1971; Angelstam et al. 1984; Steen and Haugvold 2009). However, there are many different interactions influencing the breeding success of birds.

The elevational distribution of mammalian predator species is a crucial for predicting elevational differences in predation risk of ground breeding bird species. For conservational management a basic knowledge about these relationships is essential.

The aim of the present study was to improve the knowledge about the occurring predator species across elevational gradients in the Verwall Alps, Austria. Hence, we assessed elevational changes in the occurrence of medium-sized to large mammal species, including mammalian predators, their relationship to environmental variables as well as their daily activity patterns.

The following hypothesis were tested:

I. *Is there a change in species richness of medium and large-sized mammal depending to elevation?*
We suggest that there is a decrease of species richness with increasing elevation. The elevational gradient probably mirrors the latitudinal one and it is well known that there is a decrease in species richness from the equator toward the poles (Rahbek 1995). Furthermore there seem to be a positive correlation of species richness and the productivity of an area (Waide et al. 1999; Sandom et al. 2013).

II. *Is there a change in activity of medium and large-sized mammals from mid-elevations to higher ones?*
We expect a higher activity in lower regions. In high elevations there are rough conditions. With increasing elevation, it gets colder, sun energy flux and precipitation are higher and the vegetation period is shorter (Körner 1999). Large and medium-sized mammals probably prefer more hospitable habitats with a higher availability of food sources and shelter.

III. *Is there a natural shift in species composition of medium and large-sized mammals depending to timberline?*
We suggest that there is a natural shift. Timberline marks an edge between montane forest and subalpine grassland, two very different biotope.

IV. *Witch environmental factors affect the distribution of mammalian predators?*
We expect that mammalian predators tend to use linear structures, like forest roads and hiking trails (e.g. Mahon et al. 1998; Bowman et al. 2010; Towerton et al. 2011). Also canopy cover or shrub height could be an important predictor for their distribution, as it represents concealment for them.

2. METHODS

2.1. Study area

The study was conducted in the Verwall Alps, a mountain range of the Central Eastern Alps, located at the border of the Austrian states Vorarlberg and Tyrol. The main part of the Verwall Alps is declared as the Natura 2000 area "Verwall". It is the biggest protected area of Vorarlberg with 120 km² and composed of the Important Bird Area "Verwall" and the FFH-protection area "Wiegensee" situated in it (LGBl. Nr. 56/2003; Metzler 2015).

Due to the geographical location and the great elevational range, there are a lot of different habitats in the region. These are vast shrubs of Dwarf Mountain Pine (*Pinus mugo*), Grey Alder (*Alnus incana)* and Alpine Rose (*Rhododendron sp*.), as well as cragged rock, bogs and lakes (Amt der Vorarlberger Landesregierung 2019). Norway Spruce *(Picea abies*) is the main tree species in the montane and low subalpine zone, with Grey Alder associations (*Alnetum incanae*) in the upper regions. In (low-) high subalpine regions Dwarf Mountain Pine and Alpine Rose shrubs are dominating (Kilian et al. 1994).

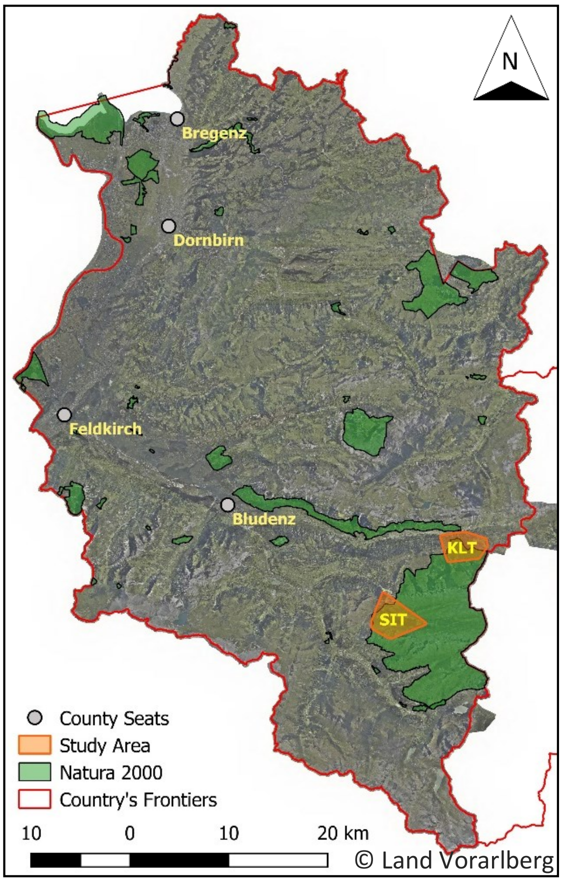


Figure 1: Map of Vorarlberg with the study stites marked in yellow (geodata altered after Land Vorarlberg 2019).

The survey was conducted in two different study areas within the Verwall Alps, one situated in the west of the Natura 2000 area, in the "Silbertal" and the other one at the northern border of the protected area, in the "Klostertal" (Figure 1). The two transects had similar sizes with 30.6 km² in Silbertal and 24.0 km² in Klostertal. The elevational gradient ranged from 1.200 to 2.200 m.a.s.l. and altogether there were two-thirds of the field surveys conducted in the Natura 2000 area.

2.2. Artificial nests

A total of 100 artificial ground nests were exposed from 24 May to 12 September 2018 to assess mammalian predator species occurring along the elevational gradients in the two sampling areas. Each of the nests contained six fresh brown domestic chicken eggs which were placed on the ground. In order to minimize human odor, the eggs were handled using fabric gloves (Whelan et al. 1994). Depending on plant cover height the nests were more or less hidden (Figure 2). The distance between each artificial clutch was at least 280 m air-line, but if possible more than 300 m. In each elevational belt (100 m) five artificial clutches were exposed (Figure 3).

Artificial clutches were exposed for a maximum of 26 days, but were controlled already after 13 days. If the clutches were found depredated already after 13 days, they were displaced. After the second control at day 26, the nests were displaced anyway, independent of predation. All points were recorded with a GPS device (Garmin GPSMAP 64s).

Figure 2: Examples for artificial clutches with different plant cover.

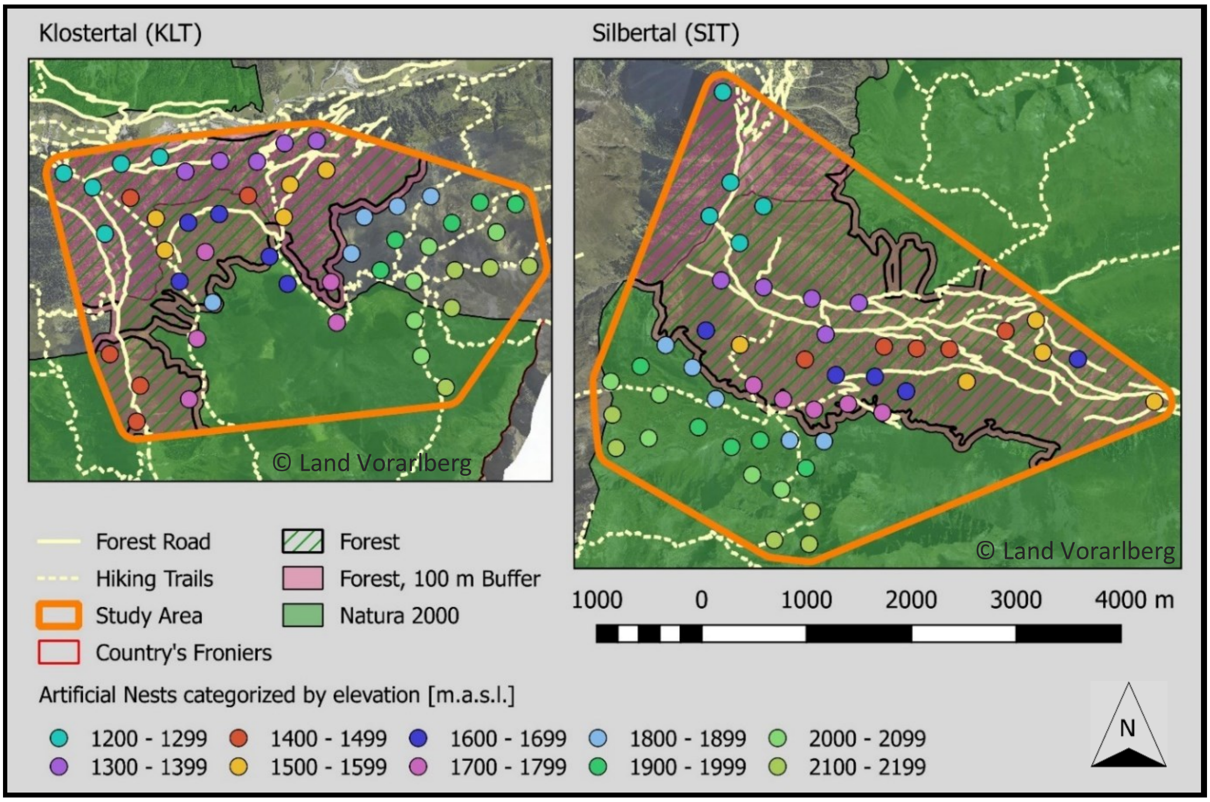


Figure 3: Map of the two study sites: Klostertal (KLT) and Silbertal (SIT) (geodata altered after (Land Vorarlberg 2019).

2.3. Camera trapping

There are differnet ways for detection of the predator species. One of them is the common method of camera trapping. It is used to identify elusive species, like nest-predators often are. Due to the increasing reliability and the wide range of use, studies using camera traps increased strongly in the last decade (e.g. Kelly and Holub 2008; Rowcliffe and Carbone C. 2008; Burton et al. 2015).

In the present study each artificial clutch was equipped with a camera trap (Cuddeback Long Range IR) fixed on a tree or a wooden plug (Figure 3). The cameras where installed ≤ 1.50 m (on trees) or ≤ 0.40 m (on plugs) above ground in a distance of ≤ 5 m to the nest with a picture focus on the artificial clutch. The trigger speed was 0.25 second, camera delay was always set to the mode "fast-as-possible", the zone control shutter was switched on the maximum view (wide angle setting) and the image size was adjusted to 5.11 Megapixel. 16 GB SD-Cards were used as storage medium and the cameras were powered by eight AA batteries.

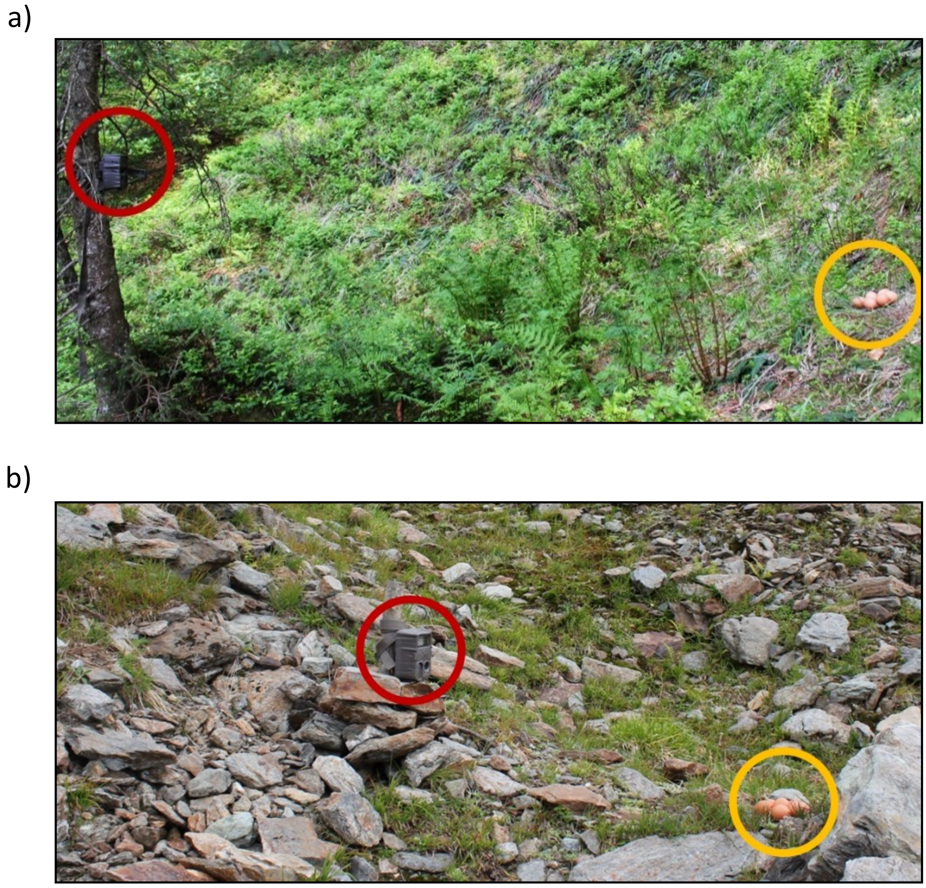


Figure 4: Experimental set-up (a) below and (b) above timberline, with red circles marking the cameras and yellow circles marking the clutches.

2.4. Environmental variables

Several environmental variables were recorded at each nest site (Table 1), such as the vegetation structure in a 20 m and a 1 m radius around the nest, the distance to trails, water bodies, forest clearings and managed huts. All values were estimated in the field, but for further calculations the distance to hiking trails and forest roads were calculated using ArcGIS (ESRI 2016). In contrast, for the distance to water bodies the estimated values were used, whenever possible, since small ponds and streams were not included in the available geodata. Whether an estimation in the field was not possible, because no water body could be seen, calculated values were used instead (using ArcGIS (ESRI 2016)). The amount of deadwood in a 20 m radius was noted, whereas deadwood was defined as lying or standing deadwood and rootstocks (height < 1.5m) and was counted if it had at least a diameter of 20 cm. The numbers of rootstocks as well as lying and standing deadwood were counted and the total cover was estimated. Furthermore, the number of anthills and the status of silvicultural use were noted in a 20 m and 1 m radius, at each site. Also abiotic variables like elevation, slope and the coordinates were recorded and each site was photographed.

Table 1: Environmental variables collected at each nesting site. B1… treetop cover of trees > 2/3 of the topheight and > 5 m, B2… treetop cover of trees < 2/3 of the topheight and > 5 m, Shrubs… all vegetation with a height of 1-5 m, Herbs… all vegetation with a height up to 1m.

<table>
<tr><th colspan="7">Abiotic factors</th></tr>
<tr><td>Site-ID</td><td>Date & Time</td><td>Coordinates</td><td>Slope [°]</td><td>Elevation [m.a.s.l.]</td><td colspan="2">Silvicutural use</td></tr>
<tr><th colspan="7">Biotic factors</th></tr>
<tr><th rowspan="2">Vegetation structure</th><th colspan="3">20 m Radius</th><th colspan="3">1 m Radius</th></tr>
<tr><th>cover [%]</th><th>height [m]</th><th>number</th><th>cover [%]</th><th>height [m]</th><th>number</th></tr>
<tr><td>B1</td><td>✓</td><td>✓</td><td>-</td><td>✓</td><td>-</td><td>-</td></tr>
<tr><td>B2</td><td>✓</td><td>✓</td><td>-</td><td>✓</td><td>-</td><td>-</td></tr>
<tr><td>Shrubs</td><td>✓</td><td>✓</td><td>-</td><td>✓</td><td>-</td><td>-</td></tr>
<tr><td>Herbs</td><td>✓</td><td>✓</td><td>-</td><td>✓</td><td>-</td><td>-</td></tr>
<tr><td>Blueberry (*Vaccinium myrtillus*)</td><td>✓</td><td>✓</td><td>-</td><td>✓</td><td>✓</td><td>-</td></tr>
<tr><td>Moss</td><td>✓</td><td>-</td><td>-</td><td>✓</td><td>-</td><td>-</td></tr>
<tr><td>Open ground</td><td>✓</td><td>-</td><td>-</td><td>✓</td><td>-</td><td>-</td></tr>
<tr><td>Boulders</td><td>✓</td><td>-</td><td>-</td><td>✓</td><td>-</td><td>-</td></tr>
<tr><td>Dead wood</td><td>✓</td><td>-</td><td>✓</td><td>-</td><td>-</td><td>-</td></tr>
<tr><td>Anthills</td><td>-</td><td>-</td><td>✓</td><td>-</td><td>-</td><td>✓</td></tr>
<tr><th colspan="7">Distance [m]</th></tr>
<tr><td>Nest - Camera</td><td>to Water bodies</td><td>to Forest clearings</td><td colspan="2">to Trails/ Forest roads</td><td colspan="2">to Managed huts</td></tr>
</table>

2.5. Data analysis

Nests were considered as predated if two or more eggs were broken or missing. In cases where only one egg was left, other causes than predation such as damage due to temperature changes or rock-fall could be supposed (Appendix 1). As there were no records showing a predator taking only one egg.

Predator species were identified by photographs (for examples see Appendix 4) or, if that was not possible, by marks at the nesting site and eggs respectively: Remaining eggs with peck marks indicated predation by birds. In this case the predator was classified as “Unknown Avian Predator”. If the predator species could not be detected, it was classified as “Unknown Predator”.
A distinguish between individuals of the same predator species was mostly impossible. However, we distinguished between juveniles and adults and between sexes, whenever possible. A determination of Red Fox individuals of same age without distinct features was not possible (Güthlin et al. 2014). Identification of Pine (*Martes martes*) and Beech Martens (*Martes foina*) by individual throat patches would have been easy (Stier 2012). But in most of the cases the throat patch could not be seen on the pictures. Though at least minimum and maximum values are available for the particular species. Whether the minimum value was bigger than one, the individuals were either of different age or different sex (Hooved Game species).
For further analysis only medium and large-sized mammals were included (Table 2). For determining activity of mammalian species a definition of events was made according to Forrester et al. (2016). They defined a new event when there were more than 60 seconds between two pictures (Forrester et

al. 2016). We needed to modify this definition, since the cameras used in the present study counted only minutes, but not seconds. We defined a new event with a minimum of two minutes between two pictures, to obviate the case that the camera just switched from one minute to the next. This definition was used for the non-predator species. The definition of events for mammalian predators was different: All records until the first photograph of predation were counted as mentioned before (≥ 2 min between two pictures), all following records were omitted to avoid biases caused by returning individuals due to their knowledge of food at a site.

To find the most important parameters for activity of mammals and the predation generalized linear models (GLMs, log- and logit-link function, function “glm”, R-package lme4, (Bates et al. 2015) and “glmulti”, R-package glmulti, (Calcagno V. 2013)) were fitted. To evaluate the degree of non-independence of factors, correlation matrices including potential predictor variables were calculated. Only variables with a correlation coefficient below 0.42 were included in the models (Appendix 1). The considered parameters were elevation, distance to trails and water bodies, shrub cover, herb height, Blueberry cover and height as well as boulder cover. The relevant parameters were different for the four calculated models, as can be seen in the results.

Further relationships between environmental variables and mammalian species were evaluated by a Canonical Correspondence Analysis (CANOCO, function “cca”, R-package CCA, (González and Déjean 2012)). Main parameters were elevation, distance to trails, canopy, shrub and boulder cover as well as silvicultural use. To get reliable results only species recorded at least at four sites were included.

Bray-Curtis dissimilarities were calculated by the function “vegdist” (R-package vegan (Oksanen et al. 2018)) to illustrate the species turnover of medium and large-sized mammals and predatory mammals respectively, and conduct a non-metric-multidimensional-scaling Plot (NMDS-Plot, function “ggplot”, R-package , ggplot2 (Wickham 2016)).

All statistical analyses were done with R (Version 3.5.1, R Core Team 2018) and R Studio (Version 3.5.1, RStudio Team 2016) using the following packages: CCA (González and Déjean 2012), ggplot2 (Wickham 2016), ggrepel (Slowikowski 2018), ggvegan (Simpson 2017), lme4 (Bates et al. 2015) and vegan (Oksanen et al. 2018). The maps shown in this thesis were generated using QGIS (QGis Development Team 2019).

Table 2: Medium and large-sized mammals including mammalian predator and domesticated species occurring in the Verwall Alps. Species abbreviations used in this thesis with their English and scientific counterparts. The check marks are showing the mammalian predator species.

Scientific name	English name	Abbreviations	Mammalian predator
Bos primigenius Taurus	Domestic Cattle	bostau	(✓)
Capreolus capreolus	European Roe Deer	capcap	
Cervus elaphus	Red Deer	cerela	
Equus caballus	Domestic Horse	equcab	
Lepus timidus	Snow Hare	leptim	
Marmota marmota	Alpine Marmot	marmam	
Martes foina	Beech Marten	marfoi	✓
Martes martes	European Pine Marten	marmar	✓
Meles meles	Badger	melmel	✓
Mustela erminea	Stoat	muserm	✓
Mustela putorius	Polecat	musput	✓
Rupicapra rupicapra	Chamois	ruprup	
Vulpes vulpes	Red Fox	vulvul	✓

3. RESULTS

3.1. Species richness without domesticated species

In Klostertal, there was a decrease from seven medium and large-sized species in the elevational belt of 1200 to only one above 2100 m.a.s.l. In Silbertal however, there was a rather constant number of species, with seven species between 1200 – 1299 m.a.s.l. and five between 2100 – 2199 m.a.sl. But there was also a loss at 1800 -1899 m.a.s.l., where only three species occurred. Finally looking at the predatory species there was quite a different pattern. The number of predator species was comparatively constant over the considered elevational range (Figure 5).

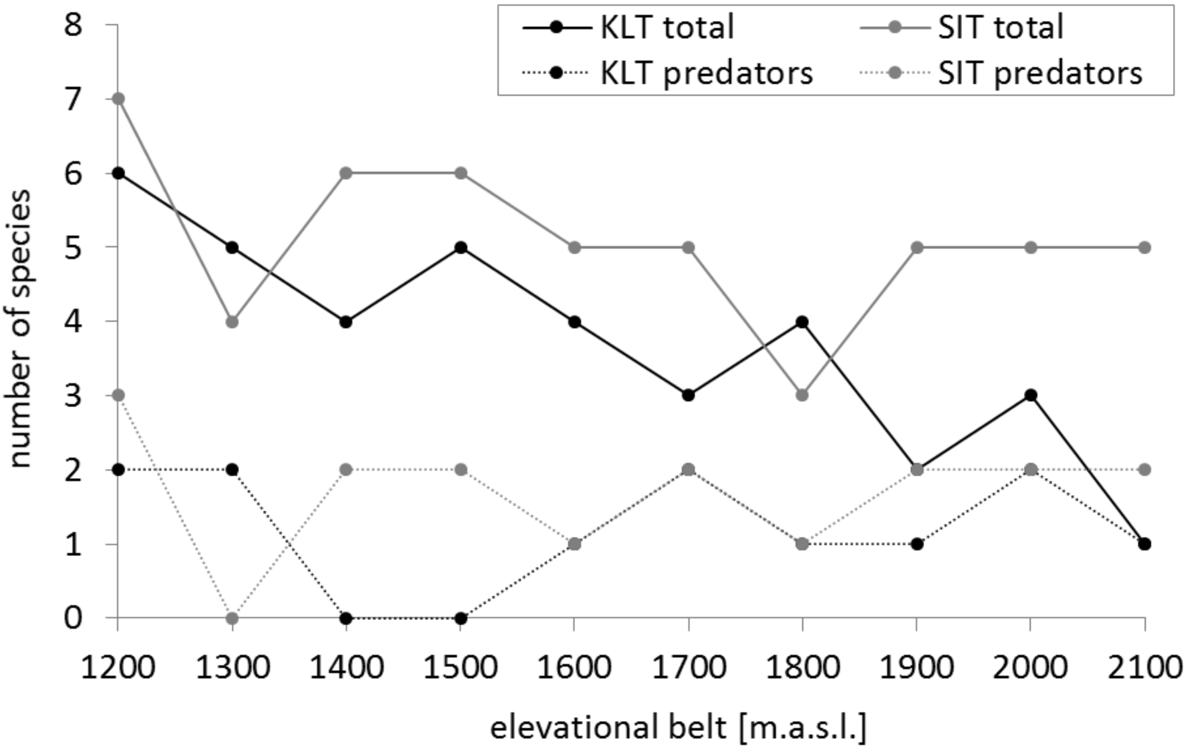


Figure 5: Change in the species richness of medium and large-sized mammals including predatory mammals (without Cattle and Horse) along two elevational gradients (KLT, SIT). The dotted lines show the number of mammalian predators.

3.2. Nest predation

Most predator species occupied similar elevational niches along both elevational transects (Figure 6). The biggest difference was shown by the Northern Raven (*Corvus corax*), whose elevational range differed completely between the two transects. The Red Fox had the widest range with records from elevations between 1226 to 2015 m.a.s.l. in Klostertal and 1473 to 2184 m.a.s.l. in Silbertal. Five of the six sightings of Red Fox above timberline (1800 m) were juvenile individuals, age determination was not possible for the sixth record. Considering its large elevational niche width, the absence of any nest predation caused by Red Foxes across the Silbertal transect is surprising. In Beech and Pine Marten a smaller distribution can be seen, ranging from 1205 to 1906 m.a.s.l. At Klostertal, no records of Beech Martens were made. There had been only three observations of Badgers (*Meles meles*), all of them at lower elevations, between 1285 and 1560 m.a.s.l. Contrastingly, Stoat (*Mustela erminea*) could only be recorded in higher regions between 1905 – 2183 m.a.s.l. in Klostertal and 1995 – 2096 m.a.s.l. in Silbertal. The Polecat (*Mustela putorius*) was only recorded once in Silbertal at 2190 m.a.s.l. Cattles (*Bos primigenius taurus)* were observed between 1740 and 1961 m.a.s.l. in Silbertal and 1778 and 2015 m.a.s.l. in Klostertal, respectively.

The topmost part of Figure 6 indicates the elevational distribution of the nest predation events. In total, combined for the two transects, 36% of the artificial clutches were predated. Similar figures of 34% and 38% were recorded at Silbertal and Klostertal, respectively. When not including nests predated or damaged by Cattles, the total proportion of predated nest was 31% for both transects, 32% for Silbertal and 30% for Klostertal. Hence, Cattles contributed 2% and 8% to the nest losses in Silbertal and Klostertal, respectively.

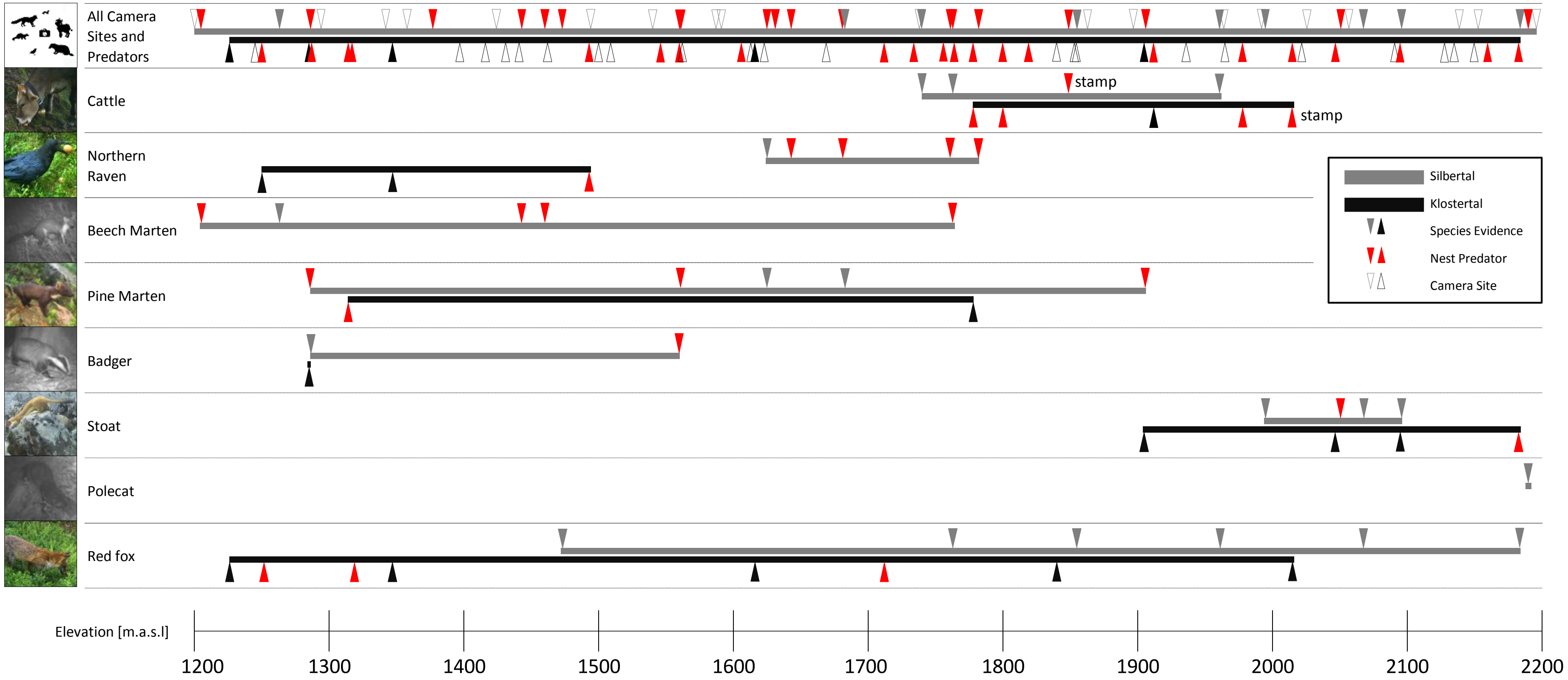


Figure 6: Distribution of predators along the two elevational gradients (KLT – Klostertal, SIT - Silbertal). The topmost part shows the elevational distribution of the artificial clutches/camera sites with red arrows marking predated nest sites. The rows below display the distribution of the particular predator species. The affiliation of observations to the different transects are indicated by different colors (grey, black). Red arrows marked with “stamp” show nest sites destroyed by trampling through Cattle (Pictures: LE-Projekt "Prädation von Bodenbrütern”).

A peak of predation at mid-elevations could be observed (Figure 7). Low and high elevations, on the other hand, showed less predation, independent of the transect. The lowest percentage of predated nests per elevational belt and transect was 20%. In Klostertal there was only one elevational belt where all predatory species could be fully identified (1400 m). In Silbertal in contrast in six of the ten belts a full identification of predatory species was possible. The ratio of Unknown Predation by birds was highest in the elevational belt of 1700 m in Silbertal. Predation by Northern Raven was four times higher in Silbertal than in Klostertal, were only one predation (= 20%, Figure 7) at an elevation of 1493 m.a.s.l. occurred (Figure 6). Comparing the two categories of clutch loss caused by Cattles there was a 20% higher ratio due to trampling than through targeted predation. The importance of Cattle for nest loss was restricted to the elevational belts 1700-2000 m (Figure 7). Only two clutch predations by Stoats were recorded between 2000 and 2200 m (Figure 6-7). In contrast, predation by Red Fox was restricted to low and mid-elevations (1200-1700 m) even though the species could be also recorded at much higher elevations. The Beech Marten had a similar predation pattern as the Red Fox, except in Klostertal, where no predation by Red Fox occurred. Pine Marten on the other hand had a somewhat higher elevational range of predation, between the belts of 1200-1900 m. The Badger only caused one clutch predation (Figure 6-7).

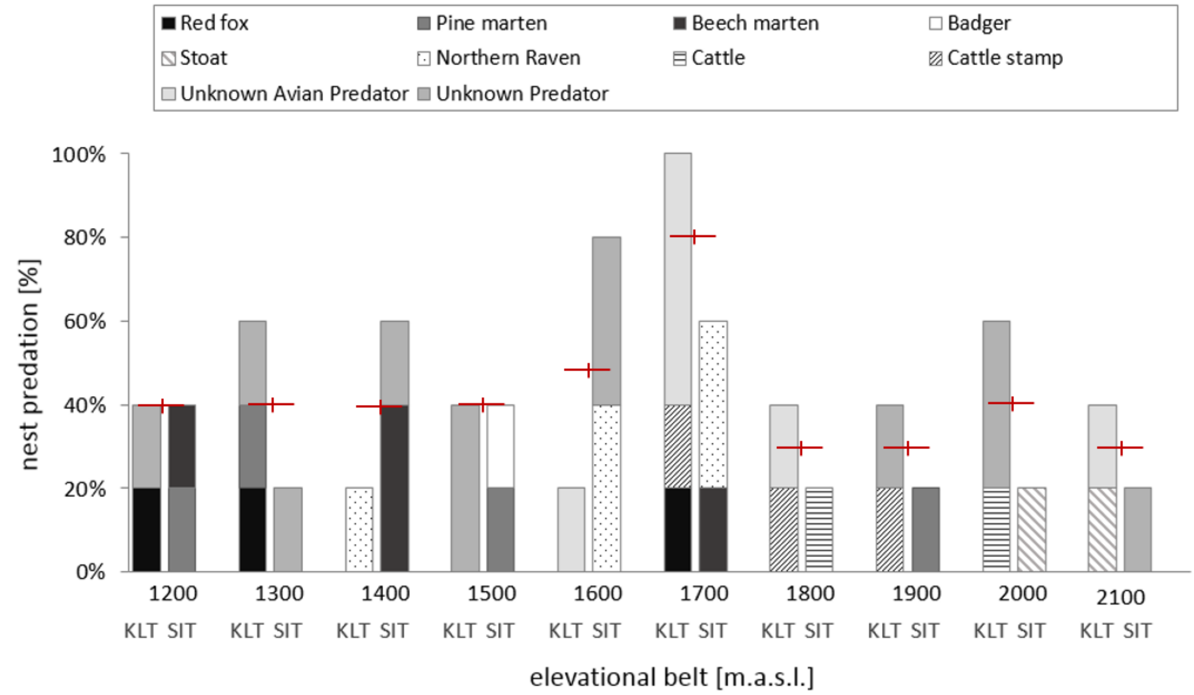


Figure 7: Nest predation (%) along two elevational gradients (KLT, SIT), indicating the contribution of different predator species. The different bars marked with KLT and SIT indicate the affiliation of observations to the two transects. Nest predation combined for the two transects is plotted by the red lines.

The ratio of mammalian predators in Klostertal was about a fourth (26%) of the total nest predation, half as much as in Silbertal (53%), whereas the ratio for both transects was more than one-third. Predation by Unknown Predator was 21% in Klostertal, 18% in Silbertal and 19% for both transects. The amount of nest losses by Cattle was more than three times higher in Klostertal (21%) as in Silbertal (6%) and 14% for both transects. Contrastingly, In Klostertal there were 5% and in Silbertal 24% predation by Northern Raven. Though the total rate of predation caused by birds was similar for the two transects, as well as for both of them together, with 31% for Klostertal, 24% for Silbertal and 28% for both transects (Figure 8).

The only important predictor for predation by mammalian predators, considered in this study, was the interaction term elevation x distance to trails, with a p-value short above significance (Table 3).

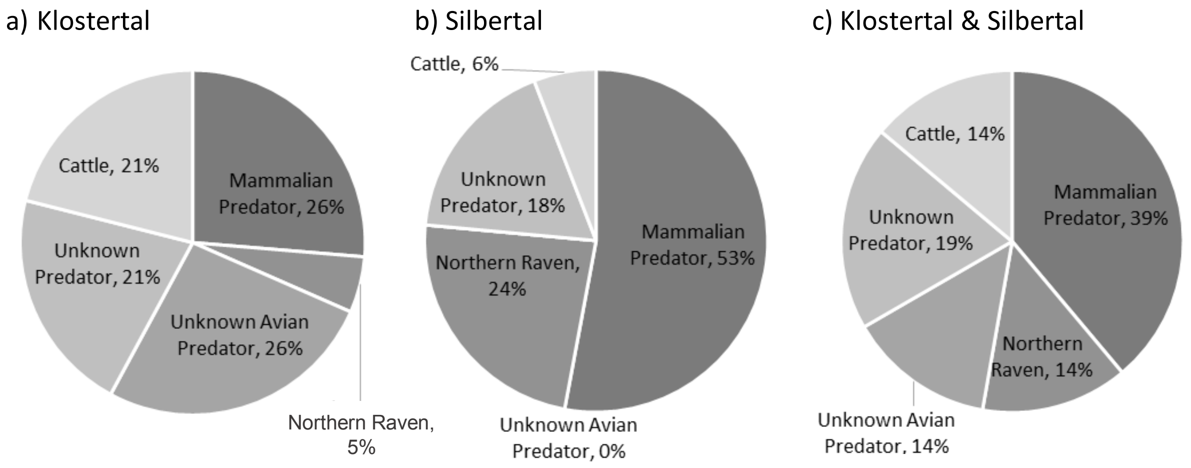


Figure 8: Contribution (%) of different predator groups to nest predation at (a) Klostertal, (b) Silbertal and (c) both study areas combined. The category Cattle includes the predation as well as nests stamped.

Table 3: GLM evaluating the effect of elevation and distance to trails on the predation of nest sites by mammalian predators.

Predation by mammalian predators				
Variable	*p-value*	*z-value*	*Estimate*	*D²*
Distance to Trails : Elevation	0.0959	-1.665	-2.593e-06	0.0358

3.3. Activity of mammals

3.3.1. Mammalian predators

There were two peaks of activity (i.e. number of events) in Klostertal: One in the elevational belt of 1300 m (five events) and the other one in the belt of 2000 m (six events). In Silbertal there were also peaks in high and low elevations, but the overall number of events was lower. The highest number was four events per belt (1200 and 2000 m) in Silbertal. In the mid-elevations there was a maximum of two events per belt in both transects. The highest number of events was caused by Stoat and Red Fox. All other species produced a maximum of two events per elevational belt (Figure 9).

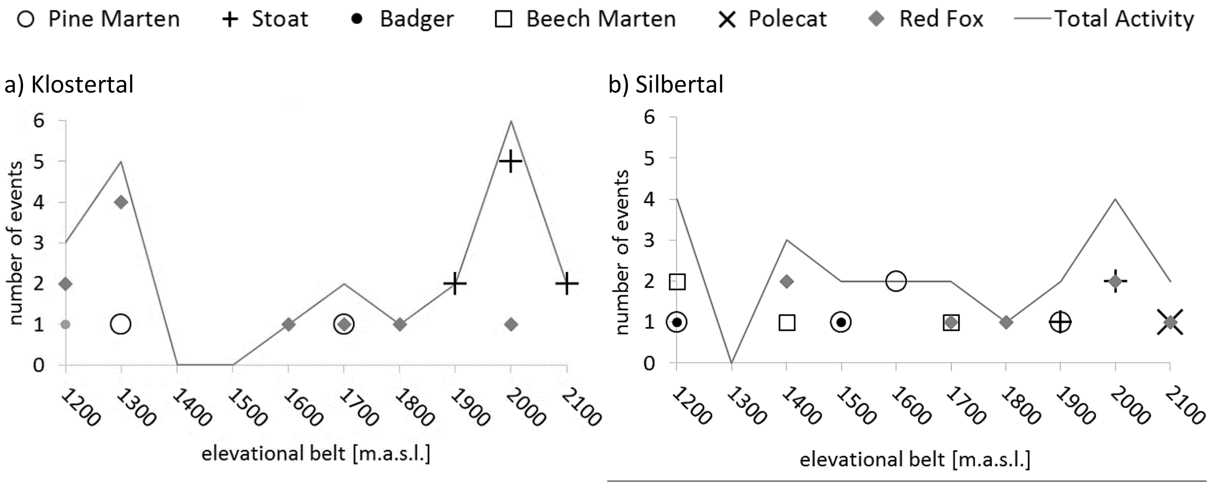


Figure 9: Change in the activity of mammalian predator species along two elevational gradients – (a) Klostertal and (b) Silbertal. The number of individuals of each species per 100 m elevational belt can be seen in Table 4.

The highest number of individuals was observed in the Stoat in the elevational belt of 2000 m with one or two individuals in Klostertal and one to three in Silbertal. The high number of events in this belt were also produced by the Red Fox, with at least one individual in each transect. The highest number of individuals of Red Fox were in Klostertal in the elevation between 1200 and 1399 m.a.s.l., where one to two individuals occurred per belt. The events in this belt in Klostertal were also caused by one Pine Marten. The high number of events in the elevational belt of 1200 m in Silbertal in contrast was caused by one Badger, one Pine Marten and one or two Beech Martens (Table 4).

Table 4: Number of individuals of mammalian predators categorized by 100 m elevational belts [m.a.s.l.] and transects.

Elevational belt [m.a.s.l.]	Red Fox		Badger		Beech Marten		Pine Marten		Stoat		Polecat	
	KLT	SIT	KLT	SIT	KLT	SIT	KLT	SIT	KLT	SIT	KLT	SIT
1200	1-2	-	1	1	-	1-2	-	1	-	-	-	-
1300	1-2	-	-	-	-	-	1	-	-	-	-	-
1400	-	1	-	-	-	1-2	-	-	-	-	-	-
1500	-	-	-	1	-	-	-	1	-	-	-	-
1600	1	-	-	-	-	-	-	1-2	-	-	-	-
1700	1	1	-	-	-	1	1	-	-	-	-	-
1800	1	1	-	-	-	-	-	-	-	-	-	-
1900	-	1	-	-	-	-	-	1	1	1	-	-
2000	1	≥ 1	-	-	-	-	-	-	1-2	1-3	-	-
2100	-	1	-	-	-	-	-	-	1	-	-	1

3.3.2. Medium and large-sized mammals without domesticated species

A trend of declining activity of medium and large-sized mammals could be observed with increasing elevation. In low and mid-elevations there were two peaks of activity in Silbertal. One at the elevational belt of 1300 m (28 events) and one at 1600 m (36 events). In these elevational belts there was a high number of Hoofed Game (Table 5). Contrastingly, the number of events of mammalian predators, was constantly low over the entire elevational range (Figure 10).

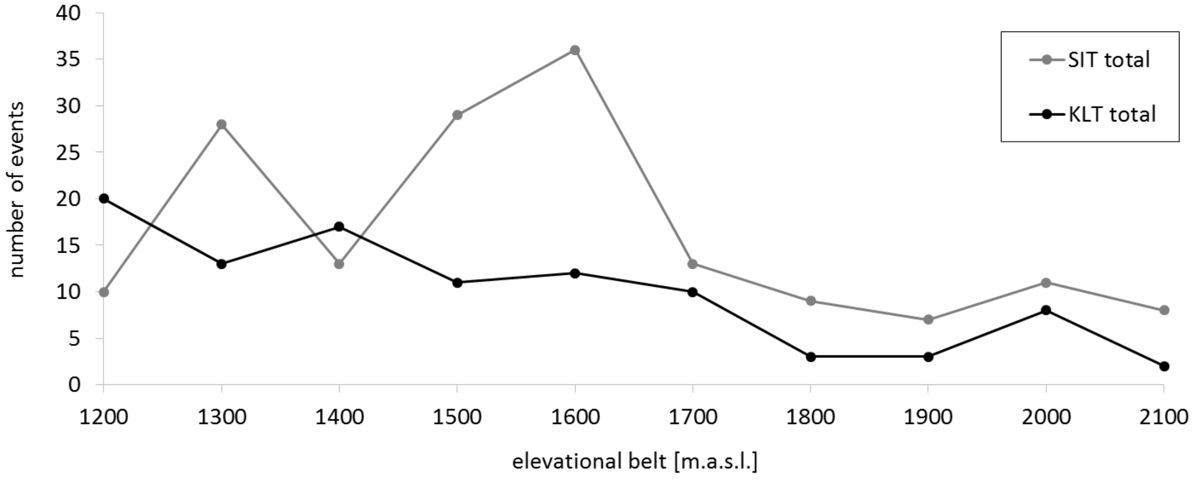


Figure 10: Change in the activity of medium and large-sized mammals including predatory mammals (without Cattle and Horse) along two elevational gradients (KLT, SIT – 100m belts). Number of individuals can be seen in Table 5 for medium and large-sized mammals and in Table 4 for predatory mammals.

Table 5: Number of individuals of medium and large-sized mammals (without mammalian predators as well as Cattle and Horse) separated by transect (KLT, SIT) and 100 m elevational belt [m.a.s.l.].

Elevational belt [m.a.s.l.]	Marmot		Snow hare		Red deer		Roe deer		Chamois	
	KLT	SIT	KLT	SIT	KLT	SIT	KLT	SIT	KLT	SIT
1200	-	-	-	-	1	1-3	≥ 2	1	≥ 4	1
1300	-	-	-	-	1	≥ 7	2-6	3-7	-	≥ 3
1400	-	-	-	-	4	≥ 1	≥ 4	≥ 4	2	1
1500	-	-	1	-	≥ 5	≥14	2-3	3-5	1	2
1600	-	-	1	2	-	≥ 15	3-4	2-6	≥ 7	-
1700	-	-	-	-	-	≥ 3	≥ 4	1-2	-	1
1800	-	-	1	-	-	2	1	-	-	≥ 2
1900	-	1	-	-	-	2	-	-	≥ 1	≥ 2
2000	-	≥ 1	-	1	-	-	1	-	≥ 1	≥ 5
2100	-	≥ 1	-	-	-	1	-	-	-	5

3.3.3. Effect of environmental variables

Elevation and boulder cover were the most important predictors for the occurrence and activity of medium and large-sized mammals. Especially for non-predator species there was a highly significant, negative correlation, but also for all medium and large-sized mammals there was a significant relationship. Also herbs height was a significant predictor. Predator species in contrast where not dependent on any of the considered variables (Table 6).

Table 6: GLMs evaluating the effect of elevation on the activity of different species communities. First the activity of medium and large-sized mammals without mammalian predators. Second including predator mammals. And third the activity of mammalian predators only. The green values indicate positive effects, the red values negative effects.

Events of medium and large-sized mammals without mammalian predators				
Variable	*p-value*	*z-value*	*Estimate*	*D^2*
Elevation	0.000133	-3.820	-3.130	0.2585058
Elevation, Quadratic Term	0.000248	-3.664	-2.662	
Distance to Trails	0.234562	1.189	9.312e-04	
Distance to Water Bodies	0.874039	0.159	7.982e-05	
Shrub, Cover	0.018579	-2.354	-1.140e-02	
Herbs, Height	0.164952	1.389	6.299e-01	
Blueberry, Cover	0.334768	-0.965	-3.713e-03	
Blueberry, Height	0.318043	-0.998	-1.189e-01	
Boulder, Cover	0.003370	-2.932	-1.643e-02	
Events of medium and large-sized mammals including mammalian predators				
Variable	*p-value*	*z-value*	*Estimate*	*D^2*
Elevation	0.0211	-2.306	-1.5326370	0.2142576
Elevation, Quadratic Term	0.0104	-2.561	-1.5539252	
Distance to Trails	0.1857	1.323	0.0008823	
Distance to Water Bodies	0.7477	0.322	0.0001613	
Shrub, Cover	0.0311	-2.155	-0.0093732	
Herbs, Height	0.2293	1.202	0.5114310	
Blueberry, Cover	0.8182	-0.230	-0.0007996	
Blueberry, Height	0.2097	-1.254	-0.1473896	
Boulder, Cover	0.0302	-2.167	-0.0098230	
Events of mammalian predators				
Nullmodel had the best fit				D^2 -8.4723e-16

3.4. Species distribution

Only a minor number of species apper to depend directly on elevation (CANOCO, Figure 11). The strongest connection to elevation had the Horse (*Equus caballus*). Distance to trails in contrast was an important predictor for the Stoat. The Chamois (*Rupicapra rupicapra)* was strongly linked to boulder cover. Though shrub height was also an important factor for the Chamois as well as for the Beech Marten. Canopy cover and silvicultural use were crucial predictors for the Red and the Roe Deer (*Capreolus capreolus*) while the silvicultural use also played an important role for the distribution of the Snow Hare (*Lepus timidus*). The Red Fox and the Pine Marten are plotted close to the center of ordination suggesting they were linked to all the considered factors. Only the Cattle was not clustered at any of the variables.

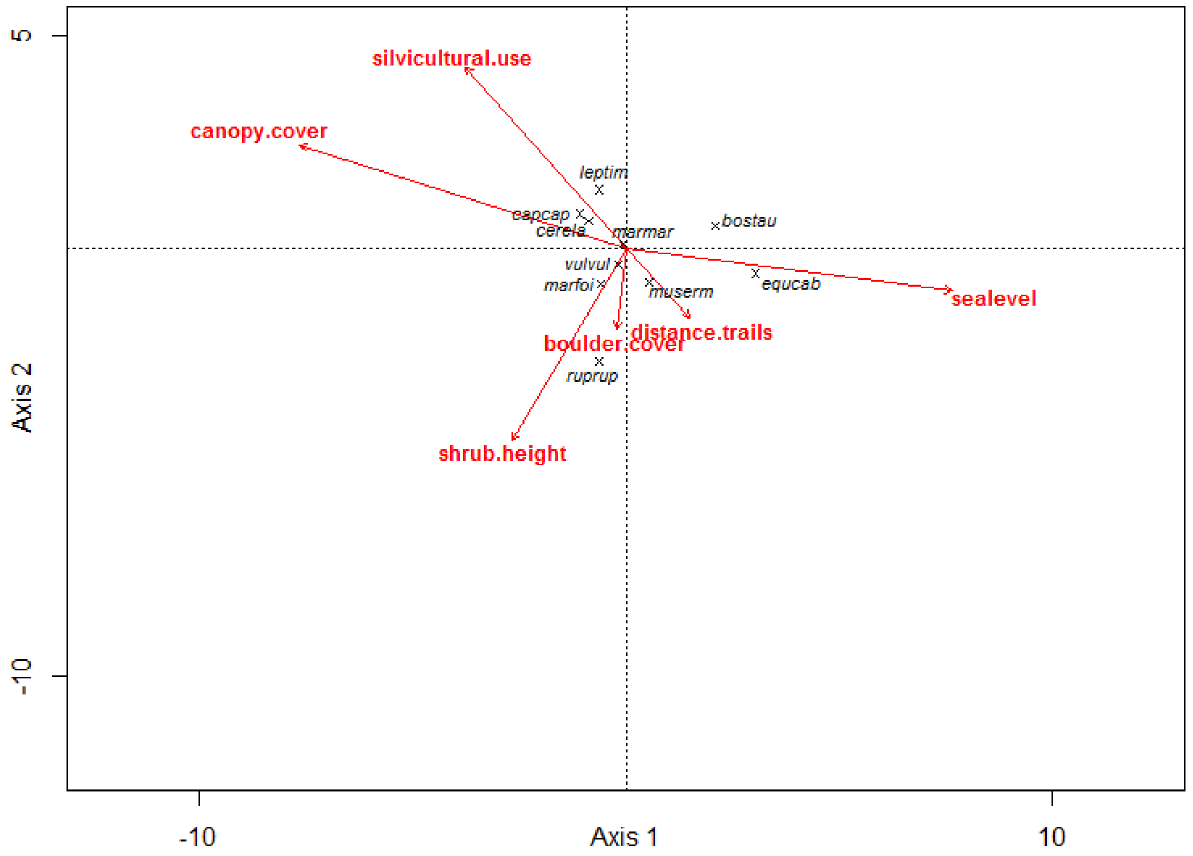


Figure 11: Canonical correspondence analysis (CANOCO) for medium and large-sized mammals and six environmental variables (elevation, distance to trails, canopy cover, silvicultural use, shrub height and boulder cover). Only species recorded at least at four sites were included. Species abbreviations are listed in Table 2 (Methods).

3.4.1. Elevational change in species composition

The similarity relationships of mammal assemblages recorded in different elevational belts are illustrated in the NMDS plots in Figure 12 a & b. There can be seen a smooth transition from the lower to the upper regions for medium and large-sized mammals as well as predatory mammals. Correlation analyses between elevation and the extracted dimension 1 values indicated a distinct relationship between elevation and species composition (Spearman rank correlations; all medium and large-sized mammals: rs = 0.67, p = 0.001224; for predator species: rs = 0.72, p = 0.0004239).

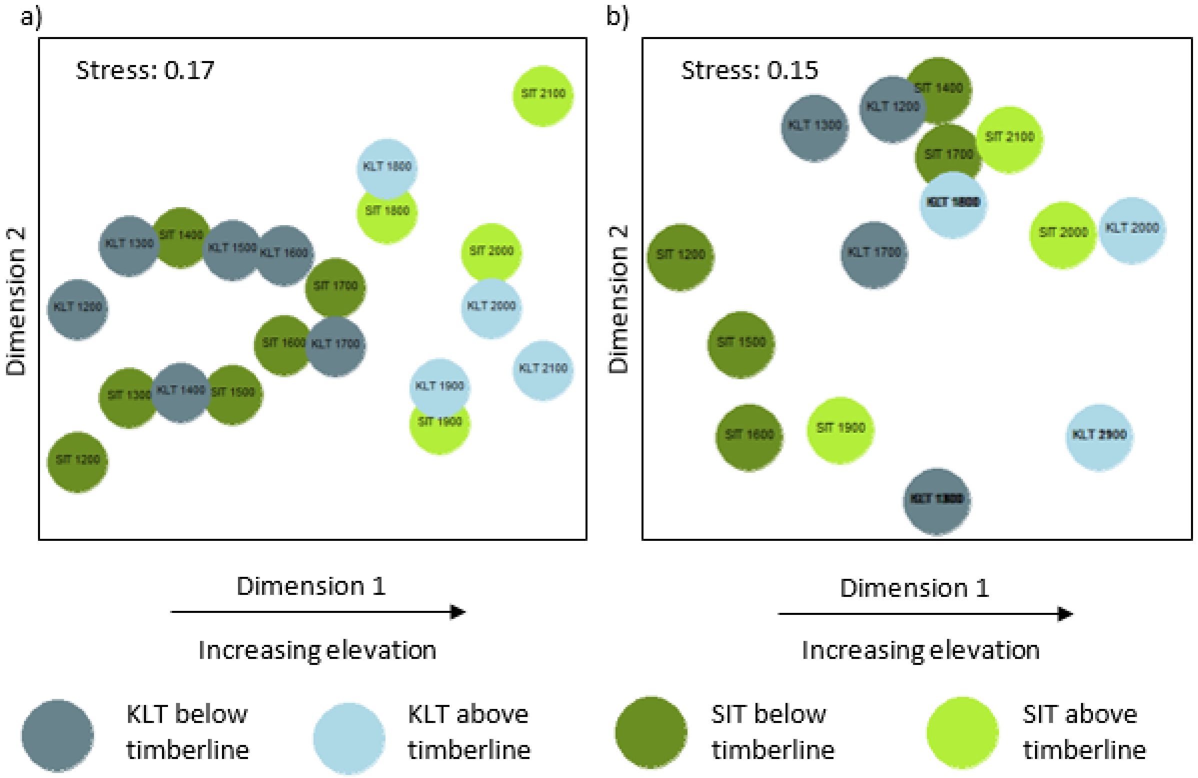
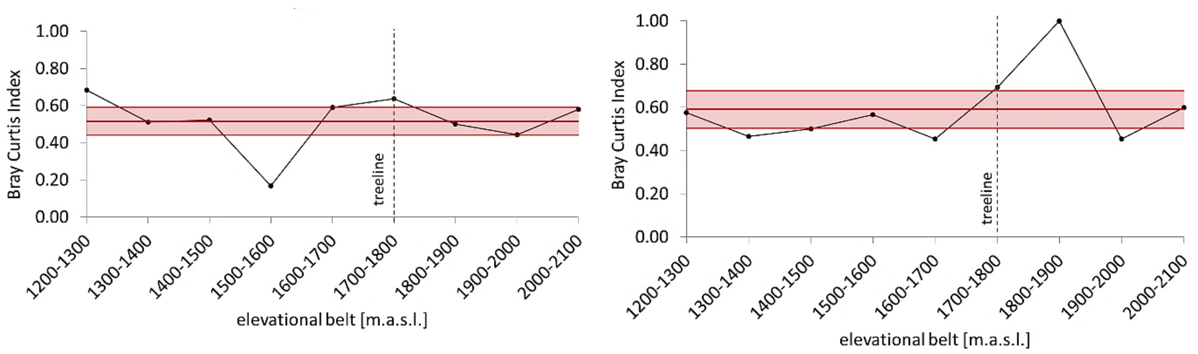


Figure 12: Two-dimensional non-metric multidimensional scaling (NMDS) ordinations based on Bray-Curtis dissimilarities for (a) all medium and large-sized mammal species composition and (b) mammalian predator species composition along the elevational gradients (100 m belts). The affiliation of observations to the different transects, as well as their location to the timberline (1800 m.a.s.l.), are indicated by different colors. For mammalian predators there were three elevational belts (SIT 1300 m, KLT 1400 & 1500 m) excluded from the calculations, since there were no species recorded.

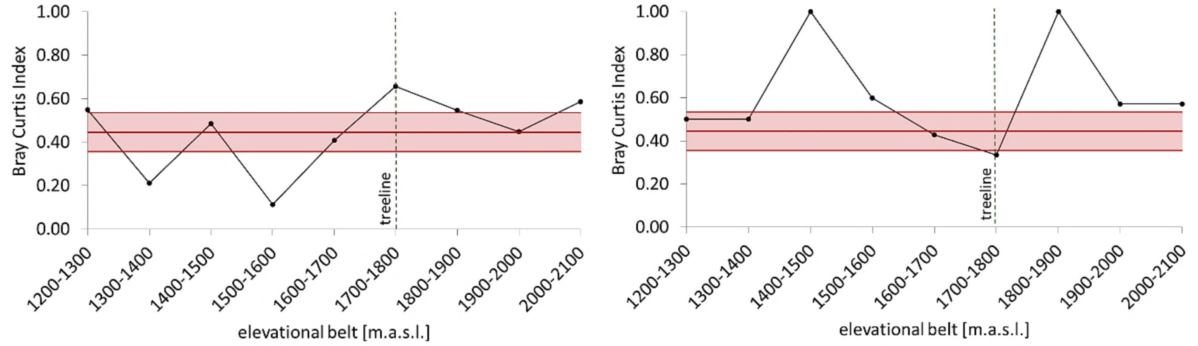
3.4.2. Species turnover without domesticated species

When comparing the Bray-Curtis dissimilarities between neighboring elevation belts, there was a peak at the transition between the belts of 1700 to 1800 and 1800 to 1900 in both sampling areas for medium and large-sized mammals and predatory mammals, respectively. The Bray Curtis Index for all of them was above 0.64, also outside the confidence interval for the mean similarity of species assemblages. In Silbertal there was an additional peak at the transition between the belts of 1200 to 1300 m. For mammalian predators there were two total shifts in species composition one at the transition between the belts of 1400 to 1500 m and the other one between the belts of 1800 to 1900 m.



a) SIT - Medium and large-sized mammals

b) KLT - Medium and large-sized mammals



c) KLT & SIT - Medium and large-sized mammals

c) KLT & SIT – Predator mammals

Figure 13: Species turnover across an elevational gradient (100 m belts) quantified by Bray Curtis Dissimilarities. For (a) medium and large-sized mammals in Silbertal, (b) medium and large-sized mammals in Klostertal, (c) the combination of these two (medium and large-sized mammals in Klostertal and Silbertal) and (d) mammalian predators in Klostertal and Silbertal. The domesticated species Cattle and Horse, were not included in the calculations. The red central line represents the mean similarity of species assemblages and the red outer lines the upper and lower 95% confidence intervals.

4. DISCUSSION

The species richness of medium and large-sized mammals declined with increasing elevation, especially in Klostertal. Given that only high and mid-elevations were considered, this result confirms the theory of a hump-shaped pattern of species richness with a high richness in mid-elevations and a lower richness in high-elevations (e.g. Rahbek 1995; Geise et al. 2004; DeGregorio et al. 2016). A similar pattern was recorded for the species activity, which also declined in medium and large-sized mammals from mid- to high-elevations. Ferreira de Pinho et al. (2017) came to similar results in their elevational study, conducted in two protected areas of a mountain range in Brazil. They found a minimum of species richness and activity in higher elevations. Forested areas in contrast had the most intense use and a high species richness. Due to the low activity and species richness in rupestrian habitats, Ferreira de Pinho et al. (2017) concluded that less productive areas tend to have a lower species richness (Waide et al. 1999; Sandom et al. 2013).

These declining trends in species richness and activity with increasing elevation could not be detected for mammalian predator species. There were rather two peaks of activity in low- and high-elevations, however the daily activity was low in all elevations. Due to a quite low number of observations in the high-elevations the data are not reliable for analyzing true changes in predatory species activity. Also the occurring change in species composition, depending to timberline is based on unreliable data.

This change in species composition depending to timberline could also be seen for medium and large-sized mammals, where more reliable data was available, since more species were recorded. Due to the analysis based on Bray-Curtis dissimilarities on presence/ absence data, a continuous change of species assemblages could be detected. Md. Nor (2001) for example found a distinct grouping in low and highland communities for non-volant small mammals.

Species turnover in space and time is a well-studied pattern, however its understanding is still a challenging issue for researchers (Baselga 2010; Jackson and Sax 2010). There have been several studies analyzing species turnover and its possible drivers, especially for birds (Järvinen and Ulfstrand 1980; Rahbek 1997; Herzog et al. 2005). A close relationship between birds and vegetation is known, although elevation could also be an important predictor for their distribution (Jankowski et al. 2013). Such a tight bounding to vegetation is also given for other taxa and changes of species composition may depend on habitat changes. Thus the sharp change in habitat structure from montane forest to high-elevational open grassland probably was an important cause of species turnover in the present study.

In this transition zone also a higher predation rate could be observed, than below and above the timberline, thus indicating an edge effect. Masoero et al. (2016) also showed an increased predation risk close to the timberline. With growing distance to forest, the expected survival rate rose. Although Lathi (2001) reported that only for 24 % of 54 study sites an habitat edge effect on nest predation could be recorded, this may not be necessarily relevant for the timberline. Angelstam (1986) hypothesized that the occurrence of an edge effect is associated with a steep gradient in productivity. The transition zone between the montane forest belt and open grasslands at higher elevations represents such a steep gradient, from a high productive forest to a low productive grassland.

However, there are also various edges along artificial structures such as roads. Several previous studies have shown an increased use of trails and roads for Carnivores (Mahon et al. 1998; Bowman et al. 2010; Towerton et al. 2011), since locomotion is easier there. Due to this increased use, a higher predation pressure may occur near roads. In our study the total predation rate was influenced by a combination of elevation and distance to trails. But, more than 40% of the nests had a distance of less than 50 m to roads or hiking trails and only 23 of the 100 nests were more than 150 m away, in contrast. Thus, these results have to be interpreted carefully, since the distance to trails was not standardized.

Due to the lower predation rates below and above timberline, the overall predation rate (36%) was at the lower limit, compared to most other previous studies using artificial nests. The mean predation rates of previous studies differed strongly. Büttner (2012) showed a mean rate of 25.8% for artificial nests, whereas other studies came to much higher predation rates up to 80% (Whelan et al. 1994; Thompson 2007; Pedersen et al. 2009; Masoero et al. 2016).

Recent predation rates for real Capercailie and Black Grouse nests, based on Mayfield estimations (Mayfield 1975) were between 66–74% predation in Capercailie and 46-49% in Black Grouse. These rates strongly increased during the last forty years. From the mid-seventies to the recent past there was an increase of clutch predation of 47–55% in Capercailie and 33–36 % in Black Grouse (Jahren 2012).

The predation rate often differs between natural and artificial nests (Major and Kendal 1996). On the one hand there is the conclusion of a more intense predation of artificial nests (Salonen and Penttinen 1988; MacIvor et al. 1990). But on the other hand there are also studies representing a higher predation pressure for natural nests (George 1987; Willebrand and Marcström 1988; Roper 1992). Gottfried and Thompson (1978) in contrast showed no difference in predation rates. Major and Kendal (1996) got an average predation rate of 59% for artificial clutches and 49% for real clutches comparing different studies. And in 14 of 20 comparable studies there was a higher predation rate of artificial nests (Major and Kendal 1996).

Comparing artificial and real nests there is also a difference in the main predator species. Willebrand and Marcström (1988) came to the conclusion that artificial nests were depredated mainly by avian. Natural nests in contrast were mainly depredated by mammals (Willebrand and Marcström 1988). MacIvor et al. (1990) came to similar results, with a higher predation rate of artificial nests by American Crows (*Corvus brachyrhynchos*) and a lower predation rate by Red Fox.

Our study shows a mean predation of 39% by mammalian predators and 28% by avian predators, demonstrating a trend indicated by some previous studies (Storch 1991; Sálek et al. 2004; Storch et al. 2005). But there are also studies demonstrating quite the opposite (Angelstam 1986; Buler and Hamilton 2000).

The main predator species may depend to habitat type and visibility of the nest amongst other things (Pedersen et al. 2011). Corvids seem to be more important predators in agricultural areas than mammals and vice versa in forested areas (Andrén 1992). While avian predators use visual cues to find the nest, mammalian predators mostly rely on olfactory cues for nest location (Picozzi 1975; Whelan et al. 1994; Rangen et al. 2000). Therefore, mammalian predators may detect nests by chance, where avian predators can locate them targeted by sight.

In our study there were probably different odors present, which are not present at natural nests, thus probably attracting mammalian predators. Human odor for example could be attracting (Harriman et al. 2007), rejecting (MacIvor et al. 1990) or neutral (Ortega et al. 1997) for mammalian predators. Real clutches in contrast provide odors of adult birds and the parental activity can lead to a higher or a lower predation risk. Predators may on the one hand follow parent birds to locate the nest but on the other hand there may be a higher protection through nest defense of the adults (Major and Kendal 1996). Overall nesting success of ground breeding birds depends on different factors. Some of them probably are predator-specific, as Angelstam (1986) and Hannon and Cotterill (1999) showed for example the importance of predator abundance and community structure. But also the nesting habitat could be an important factor, as mentioned before (Pedersen et al. 2011; DeGregorio et al. 2016).

Different predator species depend on various habitats. Some of them are generalists, like the Red Fox, which is utilizing a wide range of different habitats. Others are more specialized and strongly depend on particular resources. The habitat use of species can be affected by numerous factors, like for example food availability, climatic factors or interspecific interactions (Pianka 1969; Pullianen 1981; Cagnacci et al. 2004), but also shelter is an important predictor. Some species are more vulnerable than others, especially in open habitats.

Smaller animals probably have a higher predation risk by avian predators, than bigger ones, like the Red Fox or the Badger for example. Consequently, different avoiding strategies evolved. The fur of the Martens as well as the Polecat are (dark-) brownish in contrast to the subnivean habit of the Stoat during winter. This adaption makes them probably less vulnerable in open habitats. Martens in contrast could be seen easily on the white snow, thus avoiding habitats without overhead cover (Hawley and Newby 1957; Pullianen 1981; Rondinini and Boitani 2002).

Pine and Beech Marten are habitat generalists with a high flexibility in their diet. But in areas where both species occur, the Beech Marten swerves to more rocky and open areas as well as urban areas, while the Pine Marten primarily selects coniferous and mixed deciduous forests (Prigioni et al. 2008). In absence of Pine Marten, Beech Marten occupies higher quality forest habitats (Virgós et al. 2000; Virgós and García 2002). This pattern could also be seen in our study. While Pine Marten seemed to depend to numerous considered factors, thus indicating to be a generalist, Beech Marten was mostly correlated shrub height. Furthermore, there was no evidence of Beech Marten in Klostertal, and records of Pine Marten were very low in contrast to Silbertal. This pattern could probably be explained by the higher abundance of Red Fox at lower elevations of Klostertal (in Silbertal Red Fox occurred only in elevations above 1473 m.a.s.l.) as previous studies reported an intraguild predation of Marten by Red Fox (e.g. Lindstroem et al. 1995).

The Red Fox is very flexible in habitat choice and feeding preferences (Dell'Arte et al. 2007; Hartová-Nentvichová et al. 2010; Rosalino et al. 2010). This well-established phenomenon could be supported by our study, since individuals could be detected in all elevational belts. Its distribution was slightly affected by shrub height and boulder cover. Most of the individuals above timberline were juveniles and therefore probably searching for a new territory. The total numbers of individuals were probably lower than they could be expected in comparable areas, since there have been cases of mange again and again in the past decade (Greber 2013; Ammann 2014; pers.comm, Markus Dönz (03.07.2018)).

Another generalist considered in this study is the Badger. There were just few records of this species in both transects and only one predation in total. Prigioni et al. (2008) described the Badger more as forager (Neal 1986) than as predator. Generally the Badger is an opportunistic food generalist mainly relying on fruits, cereals and invertebrates, like for example earthworms (Virgós et al. 2004; Balestrieri et al. 2005; Rosalino et al. 2005). As there is evidence for nest trampling before the Badger depredated the nest in our study, it could be assumed that it was probably attracted by the strong smell of the broken eggs, but cannot be classified as true nest predator.

The Stoat in contrast is a specialized predator, with rodents as its main prey (Martinoli et al. 2001). Its elevational distribution in the present study was limited to elevations above the timberline and furthermore correlated with distance to trails. Thus propably avoiding intraguild predation by Red Fox (Latham 1952; Dell'Arte et al. 2007).

There also was one record of a Polecat at an elevation of 2190 m.a.s.l. This record was remarkable, since they generally prefer flat landscapes and dales (Blandford 1987). The proximity to a lake and some small streams probably provided enough food sources and thus the area may represent a suitable habitat (Blandford 1987).

Additionally to the generally known mammalian predator species, Cattles were responsible for nest losses in our study area. In total there were five nests destroyed by Cattle, two of them by trampling and three of them were depredated. A study in the UK about nest trampling came to the result that a higher livestock density produces a higher probability of nest trampling (Sharps et al. 2017). However, they also concluded that livestock grazing could have positive effects to ground breeding birds, since they keep the vegetation low and thus increase the availability of suitable nesting sites (Sharps et al. 2017).

Looking at the overall predation there was a high rate by unknown predator, 19% in total. This could have many reasons. One of them could be a bias with the cameras, since there were a couple of eggs with signs indicating predation caused by birds, but no photographs documenting the predation event. Probably also small mammals were not ever recorded. But most of them would not even be able to break quail eggs (Haskell 1995), which are generally smaller than the used eggs. Therefore, we can assume that small mammals are not relevant as predators in the present study.

Most of the considered predator species strongly rely on rodents, such as voles (Lanszki et al. 2007). However, cyclic fluctuations in vole populations (Stenseth 1999; Zub et al. 2012; Korpela et al. 2013) can force predators to shift to alternative prey (Angelstam et al. 1984). This alternative prey are often tetraonids and their clutches as well as hares and squirrels (Lanszki et al. 2007).

As summarized by Pedersen et al. (2011) nesting success of ground breeding birds depends on various factors, such as habitat composition, abundance, community structure and foraging behavior of predators, and the availability of alternative prey (Pedersen et al. 2011). In our study also roads had an impact to the risk of predation, therefore building of new roads should be avoided. All in all predation pressure of ground breeding birds is a complex issue and before management measures will be implemented, a detailed understanding of the different, intricate interactions should be achieved.

5. REFERENCES

Ammann, C. (2014): Entsorgung von toten Füchsen. Vorarlberger Jägerschaft. Available online at www.vjagd.at/entsorgung-von-toten-fuchsen/, checked on 14.03.19.

Amt der Vorarlberger Landesregierung (2019). Available online at https://naturvielfalt.at/schutzgebiet/verwall/, checked on 3/19/2019.

Andrén, H. (1992): Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. In *Ecology* 73 (3), pp. 794–804.

Angelstam, P. (1986): Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. In *Oikos* 47 (3), pp. 365–373.

Angelstam, P.; Lindström, E.; Widén, P. (1984): Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. In *Oecologia* 62 (2), pp. 199–208.

Balestrieri, A.; Remonti, L.; Prigioni, C. (2005): Diet of the eurasian badger (*Meles meles*) in an agricultural riverine habitat (NW Italy). In *Hystrix* 15 (2).

Baselga, A. (2010): Partitioning the turnover and nestedness components of beta diversity. In *Global Ecology and Biogeography* 19 (1), pp. 134–143.

Bates, D.; Maechler, M.; Bolker, B.; Walker, S. (2015): Fitting linear mixed-effects models using lme4. In *Journal of Statistical Software* 67 (1), pp. 1–48.

Bellebaum, J.; Boschert, M. (2003): Bestimmung von Predatoren an Nestern von Wiesenlimikolen. In *Vogelwelt* 124, pp. 83–91.

Blandford, P. R. S. (1987): Biology of the polecat *Mustela putorius*: A literature review. In *Mammal Review* 17, pp. 155–198.

Bowman, J.; Ray, J. C.; Magoun, A. J.; Johnson, A. S.; Dawson, F. N. (2010): Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. In *Canadian Journal of Zoology* 88, pp. 454–467.

Brown, J.H (2001): Mammals on mountainsides: elevational patterns of diversity. In *Global Ecology and Biogeography* 10 (1), pp. 101–109.

Buler, J. J.; Hamilton, R. B. (2000): Predation of natural and artificial nests in a southern pine forest. In *The Auk* 117 (3), pp. 739–747.

Burton, A.; Neilson, E.; Moreira, D.; Ladle, A.; Steenweg, R.; Fisher, J. et al. (2015): REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. In *Journal of Applied Ecology* 52, pp. 675–685.

Büttner, W. (2012): Habitatnutzung von Prädatoren des Birkwildes im NSG Lüneburger Heide zur Abschätzung des Prädationsdruckes in Birkwildhabitaten. Master Thesis. Universität für Bodenkultur Wien. Department für Integrative Biologie.

Cagnacci, F.; Meriggi, A.; Lovari, S. (2004): Habitat selection by the red fox *Vulpes vulpes* (L. 1758) in an alpine area. In *Ethology Ecology & Evolution* 16 (2), pp. 103–116.

Calcagno V. (2013): glmulti: Model selection and multimodel inference made easy. Version R package version 1.0.7. Available online at https://CRAN.R-project.org/package=glmulti.

DeGregorio, B. A.; Chiavacci, S. J.; Benson, T. J.; Sperry, J. H.; Weatherhead, P. J. (2016): Nest predators of North American birds: Continental patterns and implications. In *BioScience* 66 (8), pp. 655–665.

Dell'Arte, G. L.; Laaksonen, T.; Norrdahl, K.; Korpimäki, E. (2007): Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. In *Acta Oecologica* 31 (3), pp. 276–281.

ESRI (2016): ArcGIS Desktop. Release 10.5. Redlands, CA: Environmental Systems Research Institute.

Ferreira de Pinho, F.; Ferreira, G. B.; Paglia, A. P. (2017): Influence of vegetation physiognomy, elevation and fire frequency on medium and large mammals in two protected areas of the Espinhaço Range. In *Zoologia* 34 (Suppl), pp. 1–11.

Forrester, T.; O'Brien, T.; Fegraus, E.; Jansen, P. A.; Palmer, J.; Kays, R. et al. (2016): An open standard for camera trap data. In *Biodiversity Data Journal* 4.

Geise, L.; Pereira, L. G.; Bossi, D.E.P.; Bergallo, H. G. (2004): Pattern of elecational distribution and richness of non volant mammals in Itatiaia National Park and its surroundings, in Southeastern Brazil. In *Brazilian Journal of Biology* 64, pp. 1–15.

George, T. L. (1987): Greater land bird densities on island vs. mainland: Relation to nest predation level. In *Ecology* 68 (5), pp. 1393–1400.

González, I.; Déjean, S. (2012): CCA: Canonical correlation analysis. R package version 1.2. Available online at https://CRAN.R-project.org/package=CCA.

Gottfried, Bradley M.; Thompson, Charles F. (1978): Experimental analysis of nest predation in an old-field habitat. In *The Auk* 95 (2), pp. 304–312.

Greber, N. (2013): Fuchsräude im Vormarsch. In *Vorarlberger Jagdzeitung* (Juli/ August).

Güthlin, D.; Storch, I.; Küchenhoff, H. (2014): Is it possible to individually identify red foxes from photographs? In *Wildlife Society Bulletin* 38 (1), pp. 205–210.

Hannon, S. J.; Cotterill, S. E. (1999): No evidence of short-term effects of clear-cutting on artificial nest predation in boreal mixedwood forests. In *Canadian Journal of Forest Research* 29 (12), 1900-1910.

Harriman, V.; Pitt, J. A.; Lariviere, S. (2007): Do repugnant scents increase survival of ground nests? A test with artificial and natural duck nests. In *Canadian Field-Naturalist* 121 (2), pp. 150–154.

Hartová-Nentvichová, M.; Šálek, M.; Červený, J.; Koubek, P. (2010): Variation in the diet of the red fox (*Vulpes vulpes*) in mountain habitats: Effects of altitude and season. In *Mammalian Biology* 75 (4), pp. 334–340.

Haskell, D. G. (1995): Forest fragmentation and nest predation: Are experiments with japanese quail eggs misleading? In *The Auk* 112 (3), pp. 767–770.

Hawley, V. D.; Newby, F. E. (1957): Marten home ranges and population fluctuations. In *Journal of Mammalogy* 38 (2), pp. 174–184.

Herzog, S. K.; Kessler, M.; Bach, K. (2005): The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. In *Ecography* 28 (2), pp. 209–222.

Jackson, S. T.; Sax, D. F. (2010): Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. In *Trends in Ecology & Evolution* 25 (3), pp. 153–160.

Jahren, T. (2012): Nest predation in capercaillie and black grouse. - increased losses to red fox and pine marten. Master Thesis. Hedmark University College. Faculty of Applied Ecology and Agricultural Sciences.

Jankowski, J. E.; Merkord, C. L.; Rios, W. F.; Cabrera, K. G.; Revilla, N. S.; Silman, M. R. (2013): The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. In *Journal of Biogeography* 40 (5), pp. 950–962.

Jarman, P. J. (1974): The social organisation of antelope in relation to their ecology. In *Behaviour* 48 (1-4), pp. 215–267.

Järvinen, O.; Ulfstrand, S. (1980): Species turnover of a continental bird fauna: Northern Europe, 1850-1970. In *Oecologia* 46 (2), pp. 186–195.

Jehl, J. R., JR. (1971): Patterns of hatching success in subarctic birds. In *Ecology* 52 (1), pp. 169–173.

Kelly, M. J.; Holub, E. L. (2008): Camera trapping of carnivores: Trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. In *Northeastern Naturalist* 15 (2), pp. 249–262.

Kilian, W.; Müller, F.; Starlinger, F. (1994): Die forstlichen Wuchsgebiete Österreichs: Forstliche Bundesversuchsanstalt, Waldforschungszentrum (FBVA-Berichte, 82).

Körner, C. (1999): Alpine plant life - Functional plant ecology of high mountain ecosystems. 1st ed.: Springer Verlag Berlin Heidelberg.

Korpela, K.; Delgado, M.; Henttonen, H.; Korpimäki, E.; Koskela, E.; Ovaskainen, O. et al. (2013): Nonlinear effects of climate on boreal rodent dynamics: mild winters do not negate high-amplitude cycles. In *Global Change Biology* 19 (3), pp. 697–710.

Land Vorarlberg (2019): VoGIS. Available online at vogis.cnv.at, checked on 2/22/2019.

Lanszki, J.; Zalewski, A.; Horváth, G. (2007): Comparison of red fox *Vulpes vulpes* and pine marten *Martes martes* food habits in a deciduous forest in hungary. von, 2007, Band 13, Ausgabe 3. In *Wildlife Biology* 13 (3), pp. 258–271.

Latham, R. M. (1952): The fox as a factor in the control of weasel populations. In *The Journal of Wildlife Management* 16 (4), pp. 516–517.

Lathi, D. C. (2001): The "edge effect on nest predation" hypothesis after twenty years. In *Biological Conservation* 99, pp. 365–374.

Lindstroem, E.; Brainerd, S.; Helldin, Jo; Overskaug, K. (1995): Pine marten - red fox interactions: A case of intraguild predation? In *Annales Zoologici Fennici* 32 (1), pp. 123–130.

MacIvor, L.; Melvin, S. M.; Griffin, C. R. (1990): Effects of research activity on piping plover nest predation. In *Journal of Wildlife Management* 54 (3), pp. 443–447.

Mahon, P. S.; Banks, P. B.; Dickman, Ch. R. (1998): Population indices for wild carnivores: a critical study in sand-dune habitat, south-western Queensland. In *Wildlife Research* 25, pp. 11–22.

Major, R. E.; Kendal, C. E. (1996): The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. In *Ibis* 2 (138), pp. 298–307.

Martinoli, A.; Preatoni, D. G.; Chiarenzi, B.; Wauters, L. A.; Tosi, G. A. (2001): Diet of stoats (*Mustela erminea*) in an alpine habitat: The importance of fruit consumption in summer. In *Oecologica* 22 (1), pp. 45–53.

Masoero, G.; Maurino, L.; Rolando, A.; Chamberlain, D. (2016): The effect of treeline proximity on predation pressure: an experiment with artificial nests along elevational gradients in the European Alps. In *Bird Study* 63 (3), pp. 395–405.

Mayfield, H. F. (1975): Suggestions for calculating nest success. In *The Wilson Bulletin* 87 (4), pp. 456–466.

Md. Nor, S. (2001): Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. In *Global Ecology and Biogeography* 10 (1), pp. 41–62.

Metzler, H. W. (2015): Gebietsführer Europaschutzgebiete Verwall und Wiegensee: Naturschutzverein Verwall - Klostertaler Bergwälder.

Neal, E. (1986): The natural history of badgers. London & Sydney: Croom Helm.

Oksanen, J.; Blanchet, F. G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlinn, D. et al. (2018): vegan: Community ecology package. R package version 2.5-3.

Ortega, C. P.; Ortega, J. C.; Rapp, C. A.; Vorisek, S.; Backensto, S. A.; Palmer, D. W. (1997): Effect of research activity on the success of american robin nests. In *The Journal of Wildlife Management* 61 (3), pp. 948–952.

Pedersen, Å. Ø.; Yoccoz, N. G.; Ims, R. A. (2009): Spatial and temporal patterns of artificial nest predation in mountain birch forests fragmented by spruce plantations. In *European Journal of Wildlife Research* 55 (4), pp. 371–384.

Pedersen, Å.Ø.; Asmyhr, L.; Pedersen, H. Ch.; Eide, N. E. (2011): Nest-predator prevalence along a mountain birch - alpine tundra ecotone. In *Wildlife Research* 38 (6), p. 525.

Pianka, E. R. (1969): Sympatry of desert lizards (*Ctenotus*) in Western Australia. In *Ecology* 50 (6), pp. 1012–1030.

Picozzi, N. (1975): Crow predation on marked nests. In *The Journal of Wildlife Management* 39 (1), pp. 151–155.

Prigioni, C.; Balestrieri, A.; Remonti, L.; Cavada, L. (2008): Differential use of food and habitat by sympatric carnivores in the Eastern Italian Alps. In *Italian Journal of Zoology* 75 (2), pp. 173–184.

Pullianen, E. (1981): A transect survey of small land carnivore and red fox populations on a subarctic fell in Finnish Forest Lapland over 13 winters. In *Annales Zoologici Fennici* 18 (4), pp. 270–278.

QGis Development Team (2019): QGIS Geographic Information System: Open Source Geospatial Foundation Project.

R Core Team (2018): R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available online at https://www.R-project.org/.

Rahbek, C. (1995): The elevational gradient of species richness: A uniform pattern? In *Ecography* 18 (2), pp. 200–205.

Rahbek, C. (1997): The relationship among area, elevation, and regional species richness in neotropical birds. In *The American Naturalist* 149 (5), pp. 875–902.

Rangen, S. A.; Clark, R. G.; Hobson, K. A. (2000): Visual and olfactory attributes of artificial nests. In *The Auk* 117 (1), pp. 136–146.

Rohde, K. (1992): Latitudinal gradients in species diversity: The search for the primary cause. In *Oikos* 65 (3), pp. 514–527.

Rondinini, C.; Boitani, L. (2002): Habitat use by beech martens in a fragmented landscape. In *Ecography* 25 (3), pp. 257–264.

Roper, J. J. (1992): Nest predation experiments with quail eggs: Too much to swallow? In *Oikos* 65, pp. 528–530.

Rosalino, L.; Sousa, M.; Pedroso, N.; Basto, M.; Rosario, J.; Santos, Mj; Loureiro, F. (2010): The influence of food resources on red fox local distribution in a mountain area of the Western Mediterranean. In *Vie et milieu* 60 (1), pp. 39–45.

Rosalino, L. M.; Loureiro, F.; Macdonald, D. W.; Santon-Reis, M. (2005): Dietary shifts of the badger (*Meles meles*) in mediterranean woodlands: an opportunistic forager with seasonal specialisms. In *Mammalian Biology* 70 (1), pp. 12–23.

Rowcliffe, J. M.; Carbone C. (2008): Surveys using camera traps: are we looking to a brighter future? In *Animal Conservation* 11 (3), pp. 185–186.

RStudio Team (2016): RStudio: Integrated development environment for R. Boston, MA: RStudio, Inc. Available online at http://www.rstudio.com/.

Sálek, M.; Svobodová, J.; Bejcek, V.; Albrecht, T. (2004): Predation on artificial nests in relation to the numbers of small mammals in the Krusné hory Mts, the Czech Republic. In *Folia Zoologica* 53 (3), pp. 312–318.

Salonen, V.; Penttinen, A. (1988): Factors affecting nest predation in the Great Crested Grebe: Field observations, experiments and their statistical analysis. In *Ornis Fenn.* 65, pp. 13–20.

Sandom, C.; Dalby, L.; Flojgaard, C.; Kissling, W. D.; Lenoir, J.; Sandel, B. et al. (2013): Mammal predator and prey species richness are strongly linked at macroscales. In *Ecology* 94, pp. 1112–1122.

Sharps, E.; Smart, J.; Mason, L. R.; Jones, K.; Skov, M. W.; Garbutt, A.; Hiddink, J. G. (2017): Nest trampling and ground nesting birds: Quantifying temporal and spatial overlap between cattle activity and breeding redshank. In *Ecology and Evolution* 7 (16), pp. 6622–6633.

Simpson, G. L. (2017): ggvegan: 'ggplot2' plots for the 'vegan' package. R package version 0.0-9.

Slowikowski, K. (2018): ggrepel: Automatically position non-overlapping text labels with ggplot2. R package version 0.8.0. Available online at https://CRAN.R-project.org/package=ggrepel.

Steen, J. B.; Haugvold, O. A. (2009): Cause of death in willow ptarmigan *Lagopus l. lagopus* chicks and the effect of intensive, local predator control on chick production. In *Wildlife Biology* 15 (1), pp. 53–59.

Stenseth, N. Chr. (1999): Population cycles in voles and lemmings: Density dependence and phase dependence in a stochastic world. In *Oikos* 87 (3), pp. 427–461.

Stier, N. (2012): Zur Populationsökologie des Baummarders (*Martes martes* L., 1758) in Nordost-Deutschland. Wildtierforschung in Mecklenburg-Vorpommern. Band 1. Mecklenburg-Vorpommern.

Storch, I. (1991): Habitat fragmentation, nest site selection, and nest predation risk in capercaillie. In *Ornis Scandinavica* 22 (3), pp. 213–217.

Storch, I.; Woitke, E.; Krieger, S. (2005): Landscape-scale edge effect in predation risk in forest-farmland mosaicsof Central Europe. In *Landscape Ecology* 20, pp. 927–940.

Tershy, B. R. (1992): Body size, diet, habitat use, and social behavior of balaenoptera whales in the Gulf of California. In *Journal of Mammalogy* 73 (3), pp. 477–486.

Thompson, F. R. (2007): Factors affecting nest predation on forest songbirds in North America. In *Ibis* 149, pp. 98–109.

Towerton, A. L.; Penman, T. D.; Kavanagh, R. P.; Dickman, Ch. R. (2011): Detecting pest and prey responses to fox control across the landscape using remote cameras. In *Wildlife Research* 38 (3), p. 208. DOI: 10.1071/WR10213.

LGBl. Nr. 56/2003 (9/30/2003): Verordnung der Landesregierung über das Europaschutzgebiet (Natura 2000 Gebiet)"Verwall".
Source: https://www.ris.bka.gv.at/GeltendeFassung.wxe?Abfrage=LrVbg&Gesetzesnummer=20000871, checked on 2/22/2019.

Virgós, E.; García, F. J. (2002): Patch occupancy by stone martens *Martes foina* in fragmented landscapes of central Spain: the role of fragment size, isolation and habitat structure. In *Acta Oecologica* 23 (4), pp. 231–237.

Virgós, E.; Mangas, J. G.; Blanco-Aguiar, J. A.; Garrote, G.; Almagro, N.; Viso, R. P. (2004): Food habits of european badgers (*Meles meles*) along an altitudinal gradient of mediterranean environments: a field test of the earthworm specialization hypothesis. In *Canadian Journal of Zoology* 82 (1), pp. 41–51.

Virgós, E.; Recio, M. R.; Cortés, Y. (2000): Stone marten (*Martes foina,* Erxleben 1777) use of different landscape types in the mountains of central Spain. In *Zeitschrift fur Saugetierkunde* 65 (6), pp. 375–379.

Waide, R. B.; Willig, M. R.; Steiner, C. F.; Mittelbach, G.; Gough, L.; Dodson, S. I. et al. (1999): The relationship between productivity and species richness. In *Annual Review of Ecology and Systematics* 30, pp. 257–300.

Whelan, C. J.; Dilger, M. L.; Robson, D.; Hallyn, N.; Dilger, S. (1994): Effects of olfactory cues on artificial-nest experiments. In *The Auk* 111 (4), pp. 945–952.

Wickham, H. (2016): ggplot2: Elegant graphics for data analysis: Springer-Verlag New York. Available online at ggplot2.org.

Willebrand, T.; Marcström, V. (1988): On the danger of using dummy nests to study predation. In *The Auk* 105 (2), pp. 378–379.

Zub, K.; Jędrzejewska, B.; Jędrzejewski, W.; Bartoń, K. (2012): Cyclic voles and shrews and non-cyclic mice in a marginal grassland within european temperate forest. In *Acta Theriologica* 57 (3), pp. 205–216.

6. APPENDIX

Appendix 1: Correlation coefficients of different variables considered for the generalized models evaluation effects of variables on species activity of medium and large-sized mammals. Critical values are marked red. Bold variables were included in the glms. Abbreviations: B1… treetop cover of trees > 2/3 of the topheight and > 5 m, B2… treetop cover of trees < 2/3 of the topheight and > 5 m, Shrubs… all vegetation with a height of 1-5 m, Herbs… all vegetation with a height up to 1m.

	Elevation	**Distance to Trails**	**Distance to Water bodies**	Silvi-cultural use	B1 cover	B1 height	B2 cover	B2 height	**Shrubs cover**	Shrubs height	Herbs cover	**Herbs height**	**Blueberry cover**	**Blueberry height**	Moss cover	Open-ground cover	**Boulder cover**	Dead-wood cover
Elevation	1																	
Distance to Trails	0.41055605	1																
Distance to Water bodies	-0.13098004	-0.11367700	1															
Silvi-cultural use	-0.64539559	-0.36250922	0.11125679	1														
B1 cover	-0.74406462	-0.26742702	0.07264160	0.55021005	1													
B1 height	-0.89116955	-0.35718223	0.10385140	0.66598689	0.80494464	1												
B2 cover	-0.36329514	-0.17175718	0.18183163	0.27271966	0.12039939	0.36812860	1											
B2 height	-0.47551268	-0.25877520	0.00926293	0.42815921	0.28259292	0.52405054	0.52959714	1										
Shrubs cover	-0.07202170	0.05929493	-0.09929994	-0.16521202	-0.06576997	-0.06124701	0.17028891	0.03278044	1									
Shrubs height	-0.53411515	-0.26911101	-0.02846375	0.31799181	0.37729996	0.49624008	0.28392679	0.29507841	0.31227153	1								
Herbs cover	0.60840002	0.18832778	-0.13790994	-0.35627219	-0.52316860	-0.56781835	-0.22643113	-0.24466120	-0.15421422	-0.25964973	1							
Herbs height	-0.16452807	-0.16446255	-0.00602435	-0.02210549	-0.01505780	0.16137641	0.12779325	0.23767126	0.06921291	0.06750742	-0.02277055	1						
Blueberry cover	-0.18783168	-0.20527062	0.14258119	0.01481027	0.03961982	0.19833027	0.10261370	0.03221523	-0.10659446	0.03816165	-0.38077863	0.30911215	1					
Blueberry height	-0.05648898	0.00012409	-0.09683425	0.10440419	0.18436154	-0.02705271	-0.06813628	-0.10597516	-0.04709493	0.10043374	-0.12383464	0.01202071	-0.08495853	1				
Moss cover	-0.51085147	-0.15854303	0.09091119	0.44521431	0.43831572	0.52202662	0.27414687	0.36219851	-0.07966133	0.26913341	-0.47335045	-0.12423712	-0.08047094	0.27908373	1			
Open-ground cover	-0.51925619	-0.14960459	0.08070602	0.39211271	0.56132486	0.42056741	0.01590549	0.09470037	-0.09203961	0.20369004	-0.35023609	-0.27809124	-0.24594896	-0.03780525	0.23457632	1		
Boulder cover	0.13067292	0.07106271	0.02880604	0.03442297	-0.17404975	-0.15857294	0.15199207	0.04405487	-0.20225663	-0.19879195	-0.13696017	-0.12998985	-0.31384889	0.20734622	0.21877750	-0.06879249	1	
Dead-wood cover	-0.46347156	-0.15052051	0.12009204	0.45045845	0.45102187	0.44046096	0.29294959	0.19864129	-0.09454077	0.21805075	-0.26274170	-0.17064017	-0.06799905	0.00526522	0.43151912	0.38991474	0.02409713	1

Appendix 2: Overview of nesting sites with unknown predator species. Background colors are indicating whether the event was counted as predation or not, depending on the number of broken eggs. Red … predation (more than one eggs damaged or lost), green … no predation (only one egg damaged or lost). An overview of the nesting sites can be seen in Appendix 3.

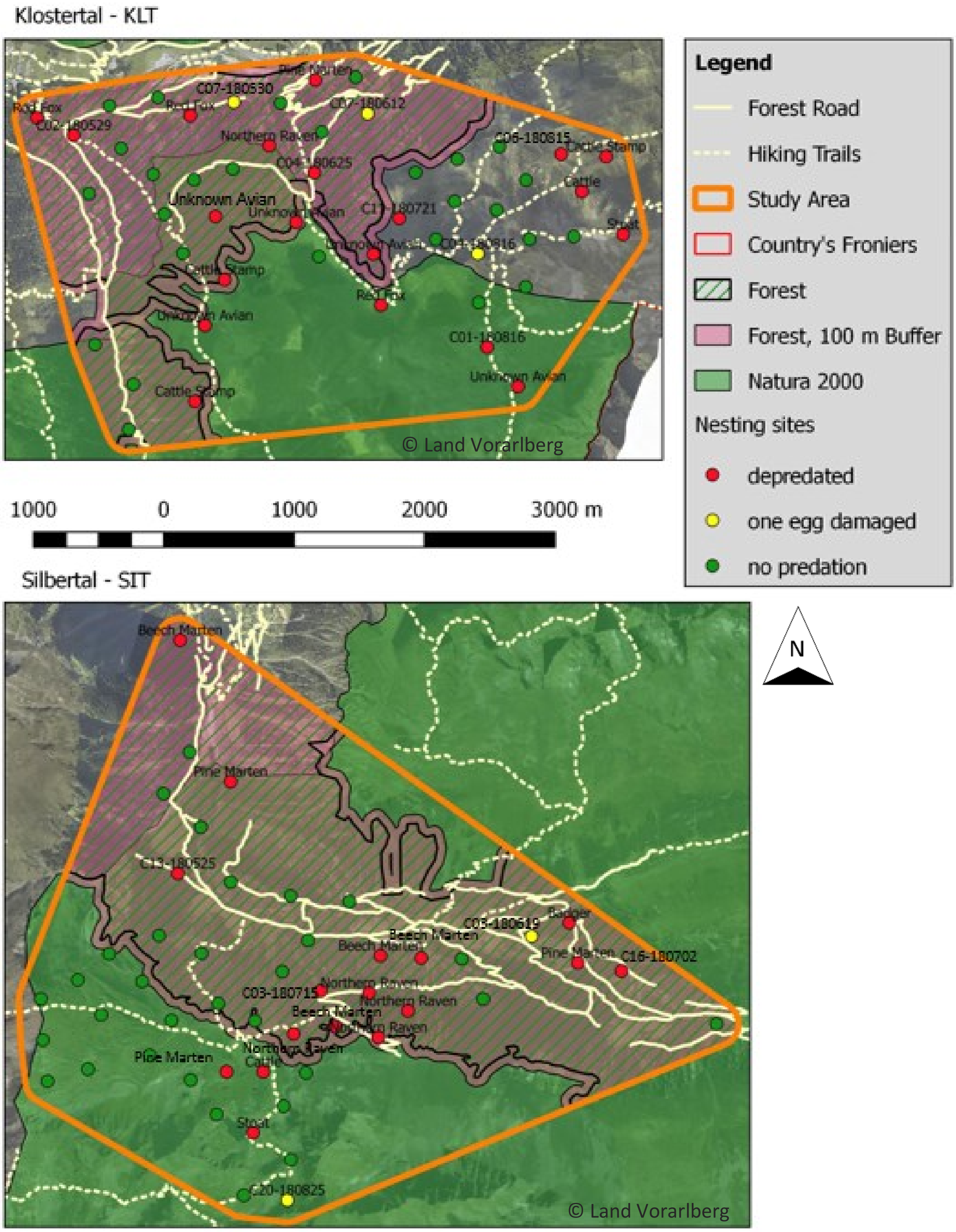
Transect	Site - ID	Elevation [m.a.s.l.]	Predator suspicion	Signs in the field	Comments pictures	Pictures
KLT	C02-180529	1287	Bird or Squirrel	hen's egg lies on a stump, remaining egg shell indicates bird predation	Squirrel was often near the eggs	
KLT	C07-180530	1314	-	one egg opened and contents mostly removed, fife eggs undamaged	-	
KLT	C07-180612	1546	Stamped by Red Deer, and predation afterwards by another species?	one egg opened and contents removed, fife eggs undamaged, one of them lying two meters from the nest	-	

KLT	C04-180625	1560	-	remaining egg shell of one egg three meters below the nest, not a bit of the other five eggs	-	
KLT	C06-180815	1912	-	-	-	
KLT	C04-180816	2047	-	one egg opened and contents removed, fife eggs undamaged	-	

KLT	C01-180816	2095	-	-	-	
SIT	C03-180715	1625	Stamped and afterward Northern Raven?	There were remaining egg shells in the nest and also some below the nest (1.5 – 4 m)	After 11 days in the field predation by Northern Raven, but one egg was already broken before. Maybe stamped.	
SIT	C13-180525	1377	Stoat	Remaining egg shells of two eggs near the nest, one of them hidden in a small “moss cave” showing three holes (1-2 mm) counterpart of the opening, probably the marks of canine tooth (≤ 8mm -> Stoat (Bellebaum and Boschert 2003))	-	

SIT	C03-180619	1473	Environmental cause, afterwards maybe Squirrel	Five eggs remaining undamaged, egg shell rests 12 m below the nest (with yolk rest), eggshell mostly intact, probably rolled away and afterward predation by Squirrel	-	
SIT	C16-180702	1631	-	-	-	
SIT	C20-180825	2190	Environmental cause	one egg opened, egg white rests on the ground	-	

Appendix 3: Map of the artificial nesting sites in the two study areas. The different colors indicate the predation status of the nests, with red dots showing predated sites (labeled with predator or Site-ID, when predator was unknown), yellow dots showing nesting sites where only one egg was damaged or lost (labeled with Site-ID) and green dots showing nesting sites where no predation occurred (no labeling), geodata altered after (Land Vorarlberg 2019). Further information to the nesting sites where only one egg was broken or lost and sites with Unknown Predator can be seen in Appendix 2.



Appendix 4: Photos of the nesting sites.


5/24/2018 10:37 PM

Beech Marten feeding on hen’s eggs


6/20/2018 8:15 PM

Pine Marten feeding on hen’s eggs


6/9/2018 3:56 PM

Adult Red Fox at a nesting site


9/8/2018 9:30 PM

Juvenile Red Fox feeding on hen’s eggs


9/3/2018 11:32 PM

Juvenile Red fox with mange


7/2/2018 3:01 AM

Badger feeding on hen’s eggs

Stoat trying to open a hen’s egg

Stoat trying to open a hen’s egg

Cattle feeding on hen’s eggs

Cattle feeding on hen’s eggs

Northern Raven feeding on hen’s eggs

Polecat at a nesting site


7/3/2018 6:51 AM

Squirrel trying to open a hen’s egg


8/16/2018 3:53 AM

Rodent probably trying to open a hen’s egg


6/21/2018 9:09 PM

Male Red Deer inspecting a nest


7/20/2018 7:28 AM

Female and juvenile Red Deer


6/14/2018 4:19 PM

Male Roe Deer


7/1/2018 10:39 AM

Juvenile Roe Deer


7/20/2018 5:54 AM

Male Chamois


8/31/2018 3:57 PM

Juvenile Chamois


8/23/2018 1:57 PM

Alpine Marmot


7/18/2018 1:49 AM

Snow Hare


6/10/2018 11:14 PM

Garden Dormouse


9/9/2018 5:57 PM

Horses

Great Spotted Woodpecker (Dendrocopus major)

Northern Wheatear (Oenanthe oenanthe)

Alpine Chough (Pyrrhocoray graculus)

Black Redstart (Phoenicurus ochruros)

Male Black Grouse

Female Black Grouse