Scale-dependent resource selection by Alpine ibex (*Capra ibex*) in summer

Bachelor of Science Thesis

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Declaration

This thesis was written in the faculty of environment and natural resources of the University of Freiburg, in the department of biometry and environmental analysis from the 12th of June to the 12th of September 2015 under supervision of Dr. Simone Ciuti.

I, Milena Zurmühl, hereby declare, that I am the sole author and composer of my thesis and that no other sources or learning aids, other than those listed, have been used. Furthermore, I declare that I have acknowledged the work of others by providing detailed references of said work.

Furthermore, I certify that this thesis or any part of it has not been a subject of another examination procedure.

Place, date

Signature

Acknowledgment

I would like to thank Simone Ciuti for supervising my thesis, giving me useful advice and taking the time to discuss my concerns and problems with me.

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Abstract

As not every habitat unit provides the adequate mixture of environmental conditions, animals often have to face a certain trade-off between several factors when selecting their habitats. Thereby, the main drivers, which need to be weighed against each other, are mostly food, safety and reduced exposure to unfavourable climate conditions.

To find out how male ibex select their habitat and which seasonal decisions they make when confronted with the trade-off between the named factors, their resource selection behaviour has been observed in Gran Paradiso National Park (Western Italian Alps) during the growing season (May-October) of the years 2010 and 2011.

The analysis was carried out on two different scales by means of resource selection functions (RSFs). The large scale was defined by the home range size of the whole population, which was determined by the calculation of a minimum convex polygon (MCP 100%). The smaller scale was described by the areas which male ibex could reach within a month. To consider that habitat use patterns vary also in time, both daily and seasonal parameters were included in the analysis.

And in fact seasonal dependent selection patterns could be clearly detected for both scales. Among the different spatial scales however, only slight differences could be noticed. Over all, the trade-off between reducing the exposure to unfavourable climate conditions, especially to heat, and maximizing the energy input by foraging high quality food played the key role in the resource selection of male ibex. Most of the other environmental parameters seemed to only be selected in consequence to the seasonal dependent weighting of those factors. Additionally it was clearly shown that male ibexes rather react in expectations of the maximum air temperature values than in consideration of to the actual conditions, which indicates a certain predictive capability in terms of imminent temperature conditions. Regardless of the food quality and the highest temperature values male ibex preferred areas with high forage quantity. The reduction of predation risk however did not seem to have a huge impact on the resource selection of those animals.

1. Introduction

The investigation of the relationship between organisms and their environment is an integral part of ecology. Therefore, resource selection studies are carried out to enhance the understanding of such complex phenomena. A preference for a certain resource is determinable when it is used disproportionately to its availability in the environment (Johnson 1980). A number of studies already showed that when selecting a habitat, animals often have to deal with several internal and external factors. External drivers are mostly environmental conditions, like the climatic situation or the quantity and quality of available forage. Internal factors, which potentially influence the resource selection of animals, could i.a. be the migratory behaviour of an animal or its mating spur. In a study of Scandinavian brown bears (*Ursus arctos*), for instance, the complex relationship between internal and external factors was investigated. Thereby it was show that their individual movement patterns were mainly driven by the internal factor of reproductive status and that especially females had to face trade-offs to guarantee the security of their cups (Martin et al. 2013). In case of African elephants (*Loxodonta Africana*), however, it could be detected that their habitat selection first of all is determined by the external factor of available water sources trading off other resources, like forage, in order to stay close to areas providing a sufficient water supply (de Knegt et al. 2011).

For large herbivores it was shown that in most of the cases the main driver of their resource selection results from a trade-off between food quality and exposure to potential predators (e.g. Anderson et al. 2005). Thereby, especially for females and young individuals the reduction of predation risk plays a key role in their selection behaviour, like it was detected in a study of seasonal range selection in bighorn sheep (Festa-Bianchet 1988). Also for alpine ibex (*Capra ibex*) an increased importance of predator risk reduction was determined for females but as well for young males (Grignolio et al. 2007a). Further analysis additionally discovered that the vigilance behaviour, at least among ibex, is not only affected by the sex and the age of an animal, but also depends on the dimension of the group it is staying in (Brivio et al. 2014). Accordingly, animals in larger groups are at lower risk of predation, so the reduction of the exposure to potential predators is of minor importance for their behaviour than for animals in smaller groups.

Besides the distribution of high quality forage and the predation risk among the available habitat units, also the respective exposure to unfavourable climate conditions is a main driver of the resource selection of large herbivores (van Beest et al. 2012). As shown by Parrini et al. (2003), both cool air temperature values and wind have a direct impact on mammals, mostly entailing a loss in condition. However also high air temperature values can cause stress for animals, especially for heat-sensitive species

like the alpine ibex (van Beest et al. 2012), which already experiences heat discomfort when temperatures exceed 15-20°C (Aublet et al. 2009).

The habitat choice of an animal thus results from an individual weighting of the respective costs and benefits of a habitat unit. It, however, may vary not only with an animal's sex and age but also with the season and the time of the day (Godvik et al. 2009).

The aim of this study was to disentangle the main trade-off between food quality, thermoregulation and predation risk, which male alpine ibex have to face in their efforts to maximize both their survival and reproductive success. Thereby, also its different effects on their selection behaviour shall be examined throughout the growing season (May-October), meaning the time of the year, when plant growth takes place.

To analyse resource selection behaviour of ibex, it was decided to use the common method of resource selection functions (RSF). According to Manly et al. (2002, S. 14), they are defined as a "*function of characteristics measured on resource units such that its value for a unit is proportional to the probability of that unit being USED*" by a species. As the shown preference of a certain resource is thereby dependent on the respective availability in the environment (Johnson 1980), both its variation in time and space were considered by analysing the resource selection at different levels.

Based on prior studies (i.a. Aublet et al. 2009, Bon et al. 2001, Brivio et al. 2014, Grignolio et al. 2007a, Scillitani et al. 2013), the trade-off between high food quality, which they need to maximize their energy intake, and the reduced exposure to high air temperatures is expected to play a key role in the resource selection of male alpine ibex. Therefore, it is assumed that in spring they mainly chose their habitats in regard to high class forage, whereas in summer, when the air temperature values increase, they primarily decide to stay at the cooler places. In this respect, it shall additionally be tested, whether current air temperature values or their daily maxima are more crucial for the resource selection behaviour of male ibex, to test the hypothesis of Aublet et al. (2009, S. 245) that "ungulate [...] behaviour is not simply a function of current [air] temperature, but can be modified by the expectations of [later on] conditions [...]". Based on the fact that ibex are strongly heat sensitive animals and are less affected by cool temperatures, it was assumed that, in contrast to most mammals, they show rather a preference for windy areas instead of sheltered locations to reduce the operative temperature conditions (Aublet et al. 2009). As this analysis is limited to the behaviour research of male individuals, the reduction of predation risk was not expected to be essential for their habitat choice. However, it was supposed that they still show a certain selection pattern in regard to this depending on the group size. Ibex in small groups or solitary individuals were assumed to show stronger preference for places close to refuge areas than animals in big groups, since they are more exposed to possible predators (Brivio et al. 2014).

2. Materials and methods

2.1 Material

2.1.1 Study area and population

Study area – The study took place in the Valsavaranche Valley, a part of the Gran Paradiso National Park (GPNP: 45° 35' N, 7° 12' E) in north-western Italy. The area covers 1700ha and has an altitudinal range of 1700-3300m above sea level (Grignolio et al. 2007b). The bottom of the valley is dominated by larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) woods and pastures. Above the tree line, in the more common areas used by ibex, the area mainly contains rocks, screes, meadows and grassland. Since 2006 the presence of a wolf pack (*Canis lupus*) has been confirmed in the National Park (Palmegiani et al. 2013). Their main prey, however, was alpine chamois, followed by red deer (Palmegiani et al. 2013). Alpine ibex were only secondary in diet, representing 8% of wolf diet in summer and 14% in winter, on average (Palmegiani et al. 2013). Predation by golden eagles (*Aquila chrysaetos*) is, according to Grignolio et al. (2007a, S. 1489), "*limited and focused only on young ibex a few month of age*". Other relevant predators like lynx (*Lynx lynx*) have not been recorded in this area for about a century (Brivio et al. 2015). Hunting is not allowed in the National Park (Brivio et al. 2014).

Population – The population in Gran Paradiso National Park is the "*only surviving natural population of alpine ibex*" (Grignolio et al. 2007a, S. 1489) and has been intensively monitored since 1999 (Brivio et al. 2014). Every year, animals were captured and marked for a long-term study on ethology, ecology and sanitary conditions of this population (Brivio et al. 2014). As described in Brivio et al. (2015), the captures and markings were executed by a team of rangers and the park veterinarian using a sex-specific dose of xylanzine and ketamine for chemical immobilisation. After the capture, they collected biometric data and took biological samples (Brivio et al. 2015). The age of an animal was identified by counting the annuli on their horns as explained by Ratti und Habermehl (1977) and finally the ibex were marked with different coloured ear tags (Brivio et al. 2014). During the period of data collection in the years 2010 and 2011, 70 marked ibex were observed in the study area, 59 of them males and 11 females.

2.1.2 Data collection

2.1.2.1 Ibex data

Ibex observation data – The ibex data used for this research was collected by Francesca Brivio (University of Sassari, Italy) in 2010 and 2011, each year during the growing season from the beginning of May to the end of October, in total 166 days. Therefor certain transects (see Appendix Map A.1) were continuously walked twice a day, mostly between 5-10am and 4-8pm, looking everywhere around for ibex groups. These were defined as one or more animals of the same species within 50 meters of each other. When sighting a group, the group size was recorded and their composition, that is to say their sex and age classes, were estimated using binoculars. Besides this the group's location was determined using the observer's position extracted from a GPS waypoint (Garming CSx60), the sighting distance, meaning the direct distance between the observer and the centre of the group, measured with a Leica 7x42 laser rangefinder. Additionally, the time and the date were noted as well as any marked individual present in the group. To avoid counting the same group or individual twice, transects were walked quite fast taking into consideration that groups of ibex move slowly and infrequently. Besides this, the marked individuals were additionally used to identify different groups throughout one walk. In total 1675 ibex groups were observed during the study period, each assigned to a certain group-ID.

For the analysis this group-based data was changed into an individual based dataset using all the recorded positions of marked ibexes which were then referred as "USED" locations. The loss of 203 data points by means of keeping only the ibex observation data of marked individuals was accepted for more precise information about the sex and age of the animals. The group size was kept as a possible predictor in resource selection analyses. And also the group-ID was retained to save the information about which individuals where seen together in the same group.

As there are big differences in ibex behaviour depending on the sex (Grignolio et al. 2007a), the original data, which included both the data of females and males, has been split for separate analyses. Due to temporal limitations only the resource selection of male ibex (i.e., the vast majority of the individuals observed during this research) could be investigated in this thesis.

Ibex telemetry data – In order to define AVAILABILITY at the proper scale in resource selection analysis, information about the movement behaviour of male ibex were required. Since the observation frequency of the marked animals was not constant over time and varied among the individuals, the chance of using telemetry data, collected a few years after this study mainly for activity analyses, was used to get more accurate information about the movement ranges of ibex. The dataset contains location data recorded from 10 male ibex, which were captured and fitted with GPS collars (GPS PRO Light collar, Vectronic Aerospace GmbH). Moreover they were equipped with an activity sensor measuring the activity in two axes based on the actual acceleration experienced by the collar (Brivio et

al. 2015). The male ibex were all captured between the 7th of May and the 28th of June in 2013 by telenarcosis. The first 7 days after the capture, the collar was set to record the position every two hours. After that it was changed into one record every 7 hours for the rest of the year. Due to technical problems, only for two males (collar ID 12228 and 12335) there were long data series available (see Appendix Table A.1). The other dataset are limited, only containing time series in which the GPS radiocollar worked properly. Furthermore, one collared ibex (collar ID 12229) died on the 4th of October 2013. However as for this study only the data from May to October was decisive, the monthly movement ranges could be averaged using the data of at least three individuals.

2.1.2.2 Environmental data

To describe the environmental variability of the study area throughout the observation period several parameters, which were assumed to influence the resource selection of ibex, have been taken into account for the analysis.

The meteorological data for this study was mostly recorded by the meteorological station at Pont. It is situated about 6000 m south-south-westerly from the study area at an elevation of 1951 m above sea level (a.s.l.). The relevant parameters, i.e. solar radiation, air temperature, wind speed and wind direction, were recorded hourly (24h/day) and most of the data was used directly as an input for the resource selection function (RSF). Only for the air temperature data, 15 (17 in 2011) ibuttons (1 record per hour) were placed additionally in the study area (see Appendix Map A. 2), to get more precise information about the actual and maximal air temperature values. However, their data was fragmentary providing measurements only for about 70-80% of the study period. (In case of the two additional ibuttons of 2011 it was even less.) The values of the wind direction, originally indicated in degrees, were cosine-transformed to deal with the circularity of this variable.

In addition to the meteorological data, several other parameters were extracted from data layers describing the environmental variability of the study area (Table 1).

Туре	Name	Description
Terrain	DEM (ELEVATION)	Digital Elevation Model (m)
	ASPECT	cosine-transformed (N-S)
	SLOPE	° rise
	TRI	Terrain Ruggedness Index (m)
Forage quality	NDVI	Normalized Difference Index (16-days-composite)
Land use	MEADOWS AND GRASSLAND	meadows, meadows/pasture, grassland
	WOODS AND BUSHES	larch and Swiss stone pine woods, pioneer woods, invasive bushes, bushes

Table 1: Data layers. Description of the data layers and their characteristics to describe the resource selection of male ibex in summer

	SCREES AND ROCKS OTHERS	rocks, screes, river banks abandoned crop fields, urban are- as/infrastructure
Predation risk	DIST_HIKING_TRAILS	Distance to hiking trails (m)
	DIST_REFUGE_AREAS_45	Distance to refuge areas defined by a slope > 45 (m)
	DIST_REFUGE_AREAS_30	Distance to refuge areas defined by a slope > 30 (m)
Microclimate	SECTOR	hydro-geographic sectors (1-5)

Elevation, aspect, slope and ruggedness – The elevation data for this study area was taken from a Digital Elevation Model (DEM) with a spatial resolution of 10m, provided by Regione Autonoma Val d'Aosta. Based on that, the aspect and the slope were generated in ArcMap 10.1, a GIS-software product from ESRI. As the aspect was calculated in degrees, it was subsequently cosine-transformed to take the circularity of this variable into account. Due to the fact, that the heterogeneity of an area is an important variable for predicting the habitats selected by species (Koehler, G.M. and Hornocker, M.G. 1989; Fabricius, C. and Coetzee, K. 1992), the ruggedness of the area was also considered. Therefore, the terrain ruggedness index (TRI), a DEM-derived index which was calculated using the DOCELL code developed by Riley et al. (1999), was taken as a measure.

NDVI – The Normalized Difference Vegetation Index (NDVI), a global vegetation indicator that strongly correlates with the above ground net primary productivity (Pettorelli et al. 2007), was also considered as a possible parameter influencing the resource selection of ibex. It is derived from satellite-based data using the ratio of red light (RED) and near-infrared light (NIR) reflected by the vegetation (NDVI = [NIR - RED] / [NIR + RED]; Hamel et al. 2009). The NDVI was chosen as a possible predictor for the RSF because, as Pettorelli et al. (2011, S. 16) noted, it "can be used to assess temporal aspects of vegetation development and quality". This correlation between the NDVI and the quality of vegetation was detected by Hamel et al. (2009), who discovered that the NDVI is a main driver in predicting the annual variation in timing of peak faecal crude protein in mountain ungulates, which, according to her, is a good indicator of vegetation quality. In addition, there are many other studies which proved that NDVI is an efficient and significant predictor of large herbivores' movements and migration patterns (e.g. Mueller et al. 2008; Boone et al. 2006; Pettorelli et al. 2005). The NDVI data, which was used for this study, was provided by the Earth Resources Observation and Science Center (EROS) and was acquired by the moderate-resolution imaging spectroradiometer (MODIS) on board of the AQUA satellite. It has a spatial resolution of 250m and due to measurement errors caused by cloud covers the daily NDVI records were taken to compute a 16-day-composite.

Land use – The land use categories are extracted from a land use map obtained from Gran Paradiso National Park. It is based on aerial survey and consequent validation on the ground. For the analysis, the land use types were simplified to four main categories (see Table 1).

Refuge areas – Based on several publications (Fox et al. 1992; Ruckstuhl und Neuhaus 2001; Kohlmann et al. 1996), the refuge areas were defined as the zones in the study area with a slope > 45° and a land use type of rocks and screes. They were created in ArcMap 10.1 by intersecting the land use layer with the slope layer. Additionally also a second refuge area layer was generated, using all sites with a slope of over 30° while keeping the land use type of rocks and screes, to test the definition of these zones.

Hiking trails – Furthermore the distance to the nearest hiking trails and the frequency, in which the nearest hiking trail was used, were considered as possible predictors for the habitat selection of male ibex. The data of the hiking trails was therefor provided by the National Park.

Hydro-geographic sectors – The hydro-geographic sectors (see Appendix Map A. 3) describe areas with certain microclimates, as suggested by local wildlife managers. They were defined using a geomorphological approach considering the watersheds, the peaks and the bottoms of the secondary valleys.

2.2 Methods

All pre-calculations and the analysis were carried out using the statistic program R 3.2.0. (https://www.r-project.org/)

2.2.1 Predicting air temperature data

In order to discover whether the maximum or the hourly air temperature is more crucial for male ibex in their habitat selection, both possibilities needed to be tested as input variable for the resource selection function (RSF), to see which one explains more of the selection behaviour of male ibex.

2.2.1.1 Predicting hourly air temperature data

The air temperature data, which was included in the RSF as a possible predictor, was pre-calculated by means of an interpolation model, which predicted the air temperature values for the whole study area considering certain spatial and temporal features. As the data to fit this interpolation model was taken from the ibutton stations, at first the missing air temperature values in these datasets had to be filled to ensure a good interpolation over time.

Therefore, for every ibutton the incomplete dataset was used as the response variable (y) to fit a linear model (LM) (1), calculating the parameters estimates (β_i) for every explanatory variable (X_i) to predict the missing values, considering a certain error term (ϵ).

(1) $\mathbf{y} = \beta_0 + \beta_1 \cdot \mathbf{X}_1 + \beta_2 \cdot \mathbf{X}_2 + \ldots + \beta_n \cdot \mathbf{X}_n + \varepsilon$

In this case the air temperature values of the ibutton stations (y) were predicted depending on the time (X_1) , the Julian date (X_2) and the year (X_3) as well as on the air temperature data recorded at the weather station at Pont (X_4) , as it was strongly correlated with the fragmentary measured datasets of the ibuttons. The few missing values in the weather station's data were filled by respectively calculating the mean of the air temperature values one hour before and one hour after the time when no value was measured.

As the correlation between the time, respectively the Julian date, and the air temperature data was not expected to be a linear correlation, but a cubic (in case of time) and a squared one (in case of Julian date), the two parameters were correspondently included in the LM. Furthermore two interactions were considered in the model, to take into account that the range of air temperature during a day may differ among the Julian date, as well as that the trend of the air temperature depending on the Julian date may differ across the years.

In case of the weather station data, a linear correlation with the ibutton data was assumed, since the temperature profiles showed similar patterns among those measuring points. However, a certain time lag was detected between the meteorological station and the ibutton stations, which is probably due to differences in elevation between the weather station and the ibuttons sampling points. Therefore the ibutton datasets were temporally shifted, to accomplish the best possible correlation between each ibutton and the weather station for an improvement of the prediction model. After fitting the model with the shifted data and calculating the missing values, the whole datasets were shifted back, to not manipulate the actual time of the daily temperature patterns. As the i-button datasets were also strongly correlated among each other, in some cases the completed dataset of another i-button (X_4) was used to fit the prediction model instead of the weather station data.

In short, the modelling approach used either data from the meteorological station or from another ibutton sampling point in order to accomplish the best predictive model providing the best replacement for not available data in ibuttons series.

For every model, either including the weather station data or a completed ibutton dataset as a predictor, a stepwise algorithm repeatedly dropping and adding one of the parameters was executed (using the step-function of the stats-package implemented in R), to respectively get the best models according to the Akaike information criterion (AIC). The final models were subsequently evaluated in terms of their predictive ability. Therefore for every model the R² value, indicating the variance of the recorded ibutton data explained by the predicted data, was calculated as a measure.

Using these finally selected and validated models, the air temperature data of the ibutton datasets were completed by predicting the missing values. By means of this procedure, information about the air temperature conditions during the study period became available at every ibutton station.

In the next step this ibutton data was interpolated to have the predicted temperature values for each pixel of the study area at any time and date of the season. Therefore, the completed air temperature

datasets as well as some spatial data of the ibutton stations were taken to fit a temperature interpolation model calculating the hourly air temperature values depending on the time, the Julian date and the year as well as on the elevation and the hydro-geographic sectors of the ibutton stations. Both the aspect and the radiation, which were also assumed to influence the air temperature values, were, however, disregarded to avoid the risk of losing the parameters for the final resource selection analysis due to collinearity problems. For interpolation a generalized additive model with integrated smoothness estimation (GAM) was chosen (mgcv-package in R), assuming a Gaussian distribution of error.

The GAM basically extends the GLM through the possibility of replacing the linear predictors (X_i) with a smooth function of the parameters $s_i(X_i)$, so it allows also for non-linear responses to these variables (2).

(2) $y = \beta_0 + s_1(X_1) + s_2(X_2) + \beta_1 X_3 + \ldots + s_n(X_n) + \varepsilon$

The smooth function can be estimated by any scatterplot smoother, which can be for example a local average estimate like the running mean or the running median (Hastie, T. and Tibshirani, R. 1986). However, for some covariates (see X_3) still a linear fit can be forced (Hastie, T. and Tibshirani, R. 1986).

In case of the interpolation model a smooth function was calculated for the time as well as for the Julian date of each year and also for the included interaction between the time and the Julian date. The year and the hydro-geographic sector however were integrated in the model as factors, which is why no smooth function was calculated for them. For the elevation, which was expected to have a squared correlation at the most, two ways of including the parameter in the model were compared, both accounting for the risk of overfitting by using the GAM. In one way a smooth term for the elevation was included; however, it was only allowed to fit a squared correlation by setting the basis dimension to represent the smooth term for this variable to 3, which was the minimum possible. In the other way the model was forced to fit the squared correlation by adding the squared effect of the parameter as a line-ar predictor.

Hence, two different models had to be validated. Starting with these full models, in each case one of the parameters or one of their interactions was stepwise omitted, checking for an improvement of the model according to the AIC. After getting the best two models, subsequently their predicting ability was evaluated by cross validation. Therefor a sample of 80% of the data was taken to predict the remaining 20% and their correspondence was evaluated by means of the R² value. This procedure was repeated 50 times. Subsequently the respectively calculated R² values were averaged and compared among the two possible models. The one with the highest predictive ability was finally chosen to interpolate the hourly air temperature values for every pixel of the study area.

Due to including the elevation and the time as predictors, the interpolation model had a spatial resolution of 10m and a temporal resolution of hours.

2.2.1.2 Predicting maximum air temperature data

The input values of the maximum air temperature for the RSF were also computed by an interpolation model. Again, the data of the ibutton stations was used to fit the model. The datasets of the maximum air temperature were therefore calculated for each day at each ibutton station based on the completed datasets of hourly air temperature values.

Also in this case, a generalized additive model with integrated smoothness estimation (GAM) was used for interpolation. The only difference to the air temperature interpolation model was the removal of the time as a predictor. Due to smaller datasets (compared to the hourly air temperature), additionally a generalized additive mixed model (GAMM) was fitted also using the mgcv-package of R. The mixed model also describes the relation between the response and the independent variables, but by including a random effect it allows the coefficients to vary depending on a grouping variable, which in this case was the ibutton-ID. For every model type again the two different ways of including the elevation as a predictor were tested.

Hence, there were four different full models which had to be validated. In each case the best model was selected again by a stepwise omission of one of the parameters or one of their interactions, testing for a model improvement according to the AIC. Subsequently, the four best models were also validated by means of a cross validation. Again, 80% of the data were sampled and used to predict the remaining 20%. In case of the maximum air temperature this procedure was repeated 500 times to get the average predictive ability of every possible model. The final best model to interpolate the maximum air temperature was then chosen according to the mean of the calculated R² values.

As the maximum air temperature interpolation model also included elevation as one of the parameters its spatial resolution was 10m.

2.2.2 Resource selection analysis

The resource selection analysis was executed for two different spatial extents, to consider the variation of habitat use patterns with scale (Mayor et al. 2009; Bowyer und Kie 2006).

The large scale was defined by the home range size of the whole population of marked ibex (see Appendix Map A. 4). As an approximation for it a minimum convex polygon including all the observation points of marked ibex (MCP 100%) was calculated by means of the program "Geospatial Modelling Environment (GME)". It is a widely accepted method in the analyses of home range, which provides the maximum habitat area of a specific species (Ryan et al. 2006).

The smaller scale was described on an individual level by creating a buffer around every ibex observation point including only those areas that male ibex can reach within a month. Considering that their movement behaviour varies with time (Scillitani et al. 2012) the radius of the buffer describing the AVAILABLE areas was determined on a monthly basis. In order to define these reachable areas, the telemetry data providing accurate information about the movement behaviour of male ibex was used. Therefore, the 75% quantile of the maximal monthly covered distances was calculated for every collared male ibex. The average values were subsequently taken to define the radius of the buffer for every month (see Table 2). The 75% quantile was thereby used because it is not as susceptible to outliers as the absolute maximum.

Table 2: Radius of the buffer defining the monthly AVAILABILITY (described by the 75%-quantile of the monthly moved distances of male ibex)

May	June	July	August	September	October
400.2143	1358.137	1363.814	785.6982	1179.451	1016.209

Although the habitat use patterns do not vary only with the spatial scale but also with the temporal scale (Mayor et al. 2009; Bowyer und Kie 2006), the resource selection of male ibex was only investigated for one time period using all the observation data collected from May to October in 2010 and 2011. Nevertheless, the daily and seasonal differences in resource selection of animals were taken into account by including temporal parameters in the analysis. To properly describe the changes during a day, both the actual time and also the part of the day divided in dawn, daylight and dusk, were considered as possible predictors. For the depiction of the seasonal differences in resource selection, the Julian date, the month and also the 16 day periods, in which the NDVI data was collected, were taken into consideration.

As design for the resource selection analysis the USED/AVAILABE respectively presence/pseudoabsence design was chosen instead of the second most common presence/absence design (Boyce 2006). This was done due to the problem of defining certain sites of the study area as unused or absent of ibex. In the USED/AVAILABE design, however, a sample of resource units which were detected to be USED by an animal (= 1) through observations, are compared with a sample of AVAILABLE landscape locations (= 0) which could have been used by the species (Boyce et al. 2002). Thereby the domain of AVAILABLE sites depends on the chosen study scale which has to be considered when creating the datasets of available resource units.

To define the AVAILABLE locations on the large scale, at first a number of 10.000 random points were generated inside the MCP and the values of the different data layers were extracted to the points. As the NDVI and air temperature values change during the study period, the time, Julian date and year of the observations had to be assigned to the random points to calculate the respective AVAILABLE values. Besides this also the data of the individuals, which was necessary for the analysis as well, needed to be allocated to these points. Therefor for each ibex observation a certain number of random points were sampled out of the 10.000 random landscape locations and its time, Julian date and year were assigned to them as well as the individual data of the specific observed ibex and the size of the group it was seen in. Additionally, every ibex observation and its corresponding random points got the same number, as a so called stratum-ID, so the AVAILABLE data could be easily matched with the USED data having the same temporal and individual features.

For the smaller scale the 10.000 landscape locations were also taken as a basis to sample a certain number of random points, which subsequently got the necessary data assigned. However, for each individual the AVAILABLE locations were only sampled out of the random points situated within the corresponding created buffer.

In order to understand the minimum number of available random points required to characterize the available environment properly, a simulation was designed and carried out by running a simple RSF model with only the air temperature as predictor. The number of USED points (=1) was thereby kept constant, while the number of AVAILABLE (= 0) points varied, testing different amounts of random points. This was done to verify when the parameter's estimate for air temperature in the RSF was stable, and thus to define the minimum number of random points per observation point required to fit the more complex RSFs.

The actual resource selection behaviour of male ibex was investigated by means of a resource selection function (RSF) with an exponential structure (3) which gives the relative probability of selection (w(x)) for each resource unit depending on the values of its environmental parameters (x_i) (Manly et al. 2002).

(3) RSF = w(x) = exp($\beta_1 X_1 + \beta_2 X_2 + ... + \beta_n X_n$)

The coefficients (β_i) of this function were estimated by means of a logistic regression with a binary dependent variable (USED=1/0) indicating the USED and AVAILABLE data. Therefor a generalized mixed model (GLMM) (4) was fitted using the lme4-package implemented in R.

(4) USED = $\beta_0 + \beta_1 X_1 + \beta_2 X_2 + ... + \beta_n X_n + u_m Z_m$

By choosing the mixed model also random components (random effects (Z_i) and their estimates (u_i)) could be added, which allowed adjustment for autocorrelation and pseudo-replication (Boyce 2006) by grouping interdependent samples. This way it could be considered that in some cases several marked individuals were observed in the same group and were thus not independent (Z_i = group-ID). Additionally, the dependency among observations of the same individual could be taken into account as well as it could be ensured that the USED data of every ibex is only compared to the appendant AVAILABLE data with the same temporal and individual data. This was achieved by adding the stratum-ID nested in the individual-ID as a second random effect (Z_2) to the model.

To avoid collinearity among the covariates of the model, the variables which were considered to be problematic were tested by means of a correlation matrix calculation based on the Pearson correlation coefficient r_p . Additionally, the Variance Inflation Factor (VIF) was calculated to check for multicol-linearity among the parameters. Only uncorrelated, independent ($|r_p| \le 0.7$ and VIF < 3) variables were analysed together in a model.

The better predictor out of two collinear variables was chosen based on assessments of their biological meaningfulness in respect to the trade-off, which male ibex have to face in their resource selection. In

the event of uncertainty, the better predictor was evaluated by means of a random forest calculation (randomForest-package of R), which ranks the importance of the parameters based on a certain number (n=500) of randomly generated decision trees.

As one aim of this study was to find out whether the actual or the maximum air temperature values were more important for the resource selection of male ibex in summer, both possibilities had to be tested. So it was decided to run two GLMMs, each including either one of them as a predictor, to avoid collinearity among to variables of the same model ($r_p = 0.7$).

Hence, for every scale two model selections had to be executed. As there were proportionally too many possible parameters to fit the models with the available amount of data, in each case a preselection based on a random forest rank of all the possible predictors was carried out. Subsequently, a backward selection was executed for each model, respectively starting with the biggest possible and stepwise omitting all the parameters and interactions which didn't contribute towards the model based on Wald statistics (p > 0.05). The AIC value was hence irrelevant for the model selection, however, it was calculated for every intermediate model as it is a good "measure of the appropriateness of alternative models" according to Boyce et al. (2002, S. 283). For the final validation of the two different mixed models of each scale, additionally their marginal (R^2m) and the conditional R^2 value (R^2c) were calculated (using the MuMIn-package in R). The marginal value is a measure for the variance explained only by the fixed effects of a mixed model whereas the conditional R² value evaluates the variance explained by both, the fixed and random effects. The best model to estimate the coefficients of the parameters for the RSF was finally chosen for each scale based on both the AIC and the R² values. To test its performance, a 5-fold cross validation according to Boyce et al. (2002) was executed. The Spearman-rank correlation was thereby used as a measure to evaluate its predictive ability (Boyce et al. 2002).

3. Results

3.1 Predicting air temperature data

3.1.1 Predicting ourly air temperature data

Almost all of the final models (see the structure in Appendix Table A. 2), fitted to calculate the missing air temperature values in the ibutton datasets, showed a pretty high predictive ability with an adjusted R² value of > 0.90. Only for the ibuttons 7.LevMezzo (adjusted R² = 0.82) and 7b.LevMezzo-New (adjusted R² = 0.78) it was worse. The AIC values, however, varied much among the models between 3612.1 (for ibutton 14.PianaInferno) and 25953.9 (for ibutton 4.LevMezzo).

Comparing the two best possible models to interpolate the hourly air temperature (see Table 3) differing in the way of including the elevation as a predictor, the model containing a smooth estimation for this parameter performed distinctly better (AIC = 725385.8; $R^2 = 0.684$) then the one comprising the squared effect as a linear predictor ($\Delta AIC = 10572.8.6$; $R^2 = 0.660$). Hence, it was taken as the final interpolation model for hourly air temperature.

Table 3: Interpolation model for hourly air temperature values. Evaluating interpolation models with different model structures (β_i = estimates of factors or predictors with linear correlation; s_i =smooth functions) by means of their AIC value (Δ AIC= difference between the best and the other given model) and the average R² value (ac(R²) = mean of R² values calculated by cross validation).

Model type	Model structure	$\Delta \operatorname{AIC}$	av(R ²)
GAM	$y = \beta_0 + \beta_1 \text{sector} + \beta_2 \text{year} + s_1(\text{elevation}) + s_2(\text{time}) + s_3(\text{julian}_\text{date}, \text{time}) + s_4(\text{julian}_\text{date}, \text{by} = \text{year})$	0	0.684
GAM	$y = \beta_0 + \beta_1 \text{sector} + \beta_2 \text{year} + \beta_3 \text{elevation} + \beta_4 \text{elevation}^2 + s_1(\text{time}) + s_2(\text{julian_date, time}) + s_3(\text{julian_date, by} = \text{year})$	10572.8.6	0.660

3.1.2 Predicting maximum air temperature data

For the maximum air temperature interpolation model also two models differing in the way of including the elevation were compared for each model type (see Table 4), the GAM and the GAMM. In the case of the GAM, again the model containing a smooth estimation for the elevation resulted in lower AIC and higher R² values. For the mixed model, however, no considerable differences could be detected (see Table 4).

Although the mixed models showed a slightly higher predicting ability ($R^2 = 0.591$) than the GAM ($R^2 = 0.589$), it was decided to take the simpler model, due to the fact that the increase of the model complexity did not cause a significant predicting improvement and also to stay consistent with the interpolation model of the hourly air temperature.

Table 4: Interpolation model for maximum air temperature values. Evaluating interpolation models with different model structures (β_i = estimates of fixed effects either included as factors or as a predictors with linear correlation; s_i =smooth functions of fixed effects, u_i =estimates of random effects) by means of their AIC value (Δ AIC= difference between the best and the other given model) and the average R² value (ac(R²) = mean of R² values calculated by cross validation).

Model type	Model structure	ΔΑΙϹ	av(R ²)
GAM	$y = \beta_0 + \beta_1 \text{sector} + \beta_2 \text{year} + s_1(\text{elevation}) + s_2(\text{julian}, \text{by} = \text{year})$	0	0.589
GAM	$y = \beta_0 + \beta_1 \text{sector} + \beta_2 \text{year} + \beta_3 \text{elevation} + \beta_4 \text{elevation}^2 + s_1(\text{julian}, \text{by} = \text{year})$	972.1	0.514
GAMM	$y = \beta_0 + \beta_1 \text{sector} + \beta_2 \text{year} + s_1(\text{elevation}) + s_2(\text{julian}, \text{by} = \text{year}) + u_1 \text{Ibutton_ID}$	0	0.591
GAMM	$y = \beta_0 + \beta_1 \text{sector} + \beta_2 \text{year} + \beta_3 \text{elevation} + \beta_4 \text{elevation}^2 + s_1(\text{julian}, \text{by} = \text{year}) + u_1 \text{Ibutton_ID}$	4.6	0.591

3.2 Resource selection analysis for male ibex

3.2.1 Resource selection on the large scale

Minimum amount of random points – Considering the results of the carried out simulation (see Appendix Figure A. 1), the data of AVAILABILITY for the large scale was created with 15 random points per observation point.

Collinearity and multicollinearity –To avoid collinearity and multicollinearity among the predictors of the models, for the following problematic parameter pairs ($r_p \ge 10.71$) the better one was chosen. Between the DEM and the NDVI it was decided to take the vegetation index instead of the elevation, considering it to be biologically more meaningful and taking into account that the effect of elevation already is partly integrated by means of the air temperature interpolation. For the rest of the problematic parameter pairs the random forest rank had to be used as decision guidance. So finally the refuge areas defined by a slope > 45° were favoured over the ones defined by a slope > 30° ($r_p = 0.7$) as well as the slope was taken for the analysis instead of the TRI ($r_p = 0.9$) because it happened to explain more of the data's variability. Also, it was decided to take the Julian date instead of the month or the 16 days period ($r_p > 0.9$) and the time instead of the part of the day ($r_p = 0.9$) as temporal parameters describing the seasonal and daily differences in resource selection of animals.

After omitting the named parameters no further problem in terms of mulitcollinearity was detected (VIF < 3).

Model selection – In the preselection of both models (one including the air temperature and one including the maximum air temperature as a predictor) the age, the frequency in which the hiking trails have been used, the time and the land use were removed from the model as the least important parameters. In the subsequent backward selection also the solar radiation and its interaction with the aspect were omitted. In case of the model including the hourly air temperature as a predictor, additionally the interaction between the Julian date and the air temperature data was left out as it was non-

significant. In both cases the model, favoured by the backward selection, also had the lowest AIC value. Both calculated R² values were equal in case of each selected model, which means that the random effects did not contribute to explain the variance of the data. Comparing these models, the one including the maximum air temperature as a predictor performed much better with an AIC of 16901.69 and R² values (R²m/R²c) of 0.5279, than the one containing the hourly data (Δ AIC = 274.91, R²m/R²c = 0.4441). Hence, it was used as the final model to calculate the parameters' estimates for the RSF at the large scale (see Table 5). The Spearman rank 5-fold cross-validation of this model indicated a good predictive fit for each fold of the data ($\rho_1 = 0.988$, $\rho_2 = 0.988$, $\rho_3 = 0.976$, $\rho_4 = 0.976$, $\rho_5 = 0.976$).

Table 5: Resource selection at the large scale. General linear mixed model coefficients (β), standard error (SE), Wald statistics (z) and probability values (p) comparing USED with AVAILABLE locations within the home range of the entire population of marked ibex (MCP) in the study area in the years 2010 and 2011.

Variable	β	SE	Z	р
scale(MAX_TEMPERATURE)	-0.22608	0.03423	-6.606	< 0.001
scale(MAX_TEMPERATURE)^2	-0.09623	0.03200	-3.007	0.003
scale(NDVI)	-0.13333	0.03275	-4.071	< 0.001
scale(NDVI)^2	-0.55025	0.03179	-17.307	< 0.001
scale(SLOPE)	-0.13945	0.03324	-4.196	< 0.001
scale(SLOPE)^2	-0.25423	0.02304	-11.036	< 0.001
scale(cos(ASPECT))	0.00041	0.02072	0.020	0.984
<pre>scale(cos(ASPECT))^2</pre>	-0.07597	0.02844	-2.671	0.008
scale(log(DIST_HIKINGTRAIL))	-0.62554	0.02870	-21.794	< 0.001
<pre>scale(log(DIST_HIKINGTRAIL))^2</pre>	-0.08779	0.01100	-7.982	< 0.001
scale(DIST_REFUGEAREA)	0.28369	0.03526	8.046	< 0.001
scale(DIST_REFUGEAREA)^2	-0.28667	0.03009	-9.528	< 0.001
scale(GROUP_DIM)	0.00856	0.03425	0.250	0.803
scale(GROUP_DIM)^2	-0.02177	0.01701	-1.280	0.201
<pre>scale(cos(WIND_DIRECTION))</pre>	0.01707	0.02071	0.824	0.410
<pre>scale(cos(WIND_DIRECTION))^2</pre>	0.01270	0.02846	0.446	0.655
scale(WIND_SPEED)	0.00956	0.03174	0.301	0.763
scale(WIND_SPEED)^2	-0.01220	0.01238	-0.985	0.324
scale(JULIAN)	-0.14885	0.03118	-4.774	< 0.001
scale(JULIAN)^2	-0.13140	0.03442	-3.818	< 0.001
<pre>scale(log(DIST_HIKINGTRAIL))*scale(GROUP_DIM)</pre>	-0.07528	0.01950	-3.860	< 0.001
<pre>scale(DIST_REFUGEAREA)*scale(GROUP_DIM)</pre>	-0.28893	0.02692	-10.733	< 0.001
scale(MAX_TEMPERATURE)*scale(NDVI)	-0.66806	0.03973	-16.816	< 0.001
<pre>scale(cos(ASPECT))*scale(cos(WIND_DIRECTION))</pre>	0.07646	0.02067	3.699	< 0.001
<pre>scale(cos(ASPECT))*scale(WIND_SPEED)</pre>	-0.07025	0.02207	-3.183	0.001
<pre>scale(cos(WIND_DIRECTION))*scale(WIND_SPEED)</pre>	-0.01845	0.02025	-0.911	0.362
<pre>scale(MAX_TEMPERATURE)*scale(JULIAN)</pre>	-0.14947	0.03545	-4.216	< 0.001
scale(NDVI)*scale(JULIAN)	-0.51781	0.03449	-15.013	< 0.001
<pre>scale(SLOPE)*scale(JULIAN)</pre>	0.18231	0.03006	6.064	< 0.001
<pre>scale(cos(ASPECT))*scale(JULIAN)</pre>	-0.08300	0.02124	-3.907	< 0.001
scale(log(DIST_HIKINGTRAIL))*scale(JULIAN)	-0.07863	0.02078	-3.784	< 0.001

scale(DIST_REFUGEAREA)*scale(JULIAN)	-0.33508	0.03159	-10.606	< 0.001
<pre>scale(cos(ASPECT))*scale(cos(WIND_DIRECTION))</pre>	-0.05672	0.02001	-2.835	0.005
*scale(WIND_SPEED)				

Resource selection – The strongest driver of the resource selection of male ibex at a large scale was the interaction between the maximum air temperature and the NDVI (see Figure 2). If the maximum air temperature was low, ibex clearly selected areas with a high vegetation index. In case of increased values however they mainly preferred areas with lower NDVI values. As seen in Figure 2 the relative probability of selection is in both cases very high, which demonstrates the strong influence of this pattern on the general resource selection of male ibexes.

Both the NDVI and the maximum air temperature showed also a significant variation in their selection depending on the Julian date. For the selected NDVI it was even stronger than for the temperature data (see Table 5). As shown in Figure 1, in spring the ibex tend to mainly choose areas with a high vegetation index, whereas its selected values evidently decrease over the season. In case of the maximum air temperature conditions, they only went for warmer places in the beginning of the growing period. During the rest of the year they clearly went for the coolest available locations (see Figure 1).

Another crucial factor for the resource selection was the distance to the refuge areas. Also in this case the ibex showed a significant variation in their selection behaviour of this parameter over time (see Table 5). In spring they clearly preferred areas further away (~ 350m), whereas they exhibited a slighter preference for location in shorter distance over the rest of the season (see Figure 1). In general, especially the solitary male ibex selected the areas far away from the refuge areas whereas larger groups of ibex tend to stay at places closer to them (see Figure 3).

Besides these findings, male ibex exhibited a clear selection of habitats close to the hiking trails with only slight differences in the importance as a driver among the different group sizes (see Figure 3) and over the seasons (see Figure 1).

In case of strong winds from the south, they obviously preferred to stay in north-faced aspects (see Figure 4). Apart from that the male ibex didn't show any strong selection pattern in terms of the aspect (see Figure 1).

On view to the slope they mainly selected areas of medium steepness, showing a slight preference for flatter terrain in spring (~ 20°) and steeper terrain in autumn (~ 40°) (see Figure 1).



Figure 1: Relative selection probability depending on the Julian date for a) aspect, b) slope, c) distance to hiking trails, d) distance to refuge areas, e) maximum air temperature and f) NDVI at the large scale considering the respective availability



Figure 2: Relative selection probability of NDVI depending on maximum air temperature conditions at the large scale



Figure 3: Relative selection probability for the distance to the hiking trails (left) and the distance to the refuge areas (right) depending on the group size at the large scale.



Figure 4: Relative selection probability for the aspect depending on the wind direction in case of low wind speed (left) and high wind speed (right) at the large scale

3.2.2 Resource selection on the small scale

Minimum amount of random points – Considering the results of the carried out simulation (see Appendix Figure A. 2), the data of AVAILABILITY for the small scale was created with 13 random points per observation point.

Collinearity and multicollinearity – For the small scale the same parameter pairs were problematic due to high correlation as at the large scale. Although the DEM wasn't as highly correlated to the NDVI $(r_p = -0.7)$, still only one of those parameters could be included in the analysis. Hence, only the NDVI was taken as a predictor. According to the random forest ranking of the other strongly correlated variables, the same parameters happen to be better predictors for both, the predictors describing the environmental variability and the ones describing temporal changes. In contrast to the larger scale, however, the hourly air temperature and the time were too strongly correlated ($r_p = 0.7$), to be both included in the model. As according to the random forest rank the air temperature explained more variability, in case of the model including the hourly temperature values, the effect of time was omitted whereas it was kept as an input variable for the RSF for the one including the maximum values.

Also at the finer scale no further problem in terms of mulitcollinearity was detected (VIF < 3) after omitting the named parameters.

Model selection – Again both models needed to be simplified by a pre-selection of the most important parameters. Based on the random forest rank of each model again the age, the frequency in which the hiking trails have been used, the land use and, in case of the model including the maximum air temperature, the time had to be left out, so the models could converge properly. In the subsequent backward selection, in each case, also the radiation and its interaction with aspect were removed from the model as well as the interaction of the respective air temperature parameter and the Julian date. Again, the models favoured by the backward selection also showed the lowest AIC. In contrast to the large scale, this time the random effects clearly contribute to explain the variance of the data ($R^2m \ll R^2c$). Giving both the AIC and the R^2 values, the model including the maximum air temperature (AIC = 19267.89, $R^2m = 0.119$, $R^2c = 0.674$) again happens to perform better than the one containing the hourly air temperature ($\Delta AIC = 84.93$, $R^2m = 0.117$, $R^2c = 0.673$), which is why it was finally chosen to calculate the parameters' estimates for the RSF at the small scale (see Table 6).

According to the Spearman rank 5-fold cross validation the model had a good predictive fit, with a correlation index for every fold of $\rho_1 = 0.952$, $\rho_2 = 0.939$, $\rho_3 = 0.915$, $\rho_4 = 0.976$ and $\rho_5 = 1.000$.

Table 6: Resource selection at the small scale. General linear mixed model coefficients (β), standard error (SE), Wald statistics (z) and probability values (p) comparing USED with AVAILABLE locations within the monthly reachable areas of male ibex.

Variable	β	SE	Z	р
scale(MAX_TEMPERATURE)	-0.09198	0.02670	-3.445	< 0.001
scale(MAX_TEMPERATURE)^2	0.02893	0.01815	1.594	0.111
scale(NDVI)	0.12423	0.02703	4.596	< 0.001
scale(NDVI)^2	-0.19048	0.01844	-10.332	< 0.001
scale(SLOPE)	-0.06318	0.03228	-1.957	0.050
scale(SLOPE)^2	-0.22402	0.02242	-9.993	< 0.001
scale(cos(ASPECT))	-0.06126	0.01993	-3.074	0.002
<pre>scale(cos(ASPECT))^2</pre>	-0.09079	0.02733	-3.323	< 0.001
<pre>scale(log(DIST_HIKINGTRAIL))</pre>	-0.65375	0.02996	-21.825	< 0.001
<pre>scale(log(DIST_HIKINGTRAIL))^2</pre>	-0.09791	0.01113	-8.801	< 0.001
scale(DIST_REFUGEAREA)	0.31892	0.03577	8.915	< 0.001
scale(DIST_REFUGEAREA)^2	-0.25226	0.02557	-9.867	< 0.001
scale(GROUP_DIM)	0.10917	0.03501	3.118	0.002
scale(GROUP_DIM)^2	-0.04693	0.01702	-2.757	0.006
<pre>scale(cos(WIND_DIRECTION))</pre>	-0.00500	0.02018	-0.248	0.804
<pre>scale(cos(WIND_DIRECTION))^2</pre>	-0.00933	0.02739	-0.341	0.733
scale(WIND_SPEED)	0.08627	0.03086	2.796	0.005
scale(WIND_SPEED)^2	-0.03367	0.01185	-2.842	0.004
scale(JULIAN)	0.06703	0.02646	2.533	0.011
scale(JULIAN)^2	-0.00956	0.02931	-0.326	0.744
<pre>scale(log(DIST_HIKINGTRAIL))*scale(GROUP_DIM)</pre>	-0.07937	0.01879	-4.225	< 0.001
<pre>scale(DIST_REFUGEAREA)*scale(GROUP_DIM)</pre>	-0.24021	0.02431	-9.882	< 0.001
scale(MAX_TEMPERATURE)*scale(NDVI)	-0.22239	0.02389	-9.307	< 0.001
<pre>scale(cos(ASPECT))*scale(cos(WIND_DIRECTION))</pre>	0.06486	0.01987	3.264	0.001

<pre>scale(cos(ASPECT))*scale(WIND_SPEED)</pre>	-0.08801	0.02157	-4.080	< 0.001
<pre>scale(cos(WIND_DIRECTION))*scale(WIND_SPEED)</pre>	-0.01507	0.01990	-0.758	0.449
scale(NDVI)*scale(JULIAN)	-0.19628	0.02518	-7.795	< 0.001
<pre>scale(SLOPE)*scale(JULIAN)</pre>	0.14703	0.02746	5.354	< 0.001
<pre>scale(cos(ASPECT))*scale(JULIAN)</pre>	-0.06797	0.01963	-3.463	0.001
<pre>scale(log(DIST_HIKINGTRAIL))*scale(JULIAN)</pre>	-0.06845	0.01932	-3.542	< 0.001
scale(DIST_REFUGEAREA)*scale(JULIAN)	-0.26711	0.02684	-9.953	< 0.001
<pre>scale(cos(ASPECT))*scale(cos(WIND_DIRECTION))</pre>	-0.07099	0.01934	-3.671	< 0.001
*scale(WIND_SPEED)				

Resource selection – Also at the small scale the interaction between NDVI and maximum air temperature was the main driver of resource selection (see Figure 6). According to it, male ibex strongly selected areas with high NDVI values, when the maximum air temperature was appropriately low.

Unlike the large scale, in terms of the maximum air temperature conditions the selection behaviour did not vary depending on the Julian date, exhibiting that male ibex always selected the coolest available locations (see Figure 7).

In case of the NDVI, however, male ibex still showed a clear selection pattern significantly changing in time (see Figure 5). The main difference to the large scale is thereby not shown in the selected values of the vegetation index, but in its importance for the resource selection, exhibiting a greater influence in autumn than in spring.

Also in terms of the distance to the refuge areas, the importance of the parameter as a driver increased again in autumn; however, it still mainly influenced the selection in spring, showing a strong preference of areas far away from the refuge areas (~ 250m) (see Figure 5). The dependency on the group dimension exhibited the same pattern as at the large scale, revealing that bigger groups are more likely to be found close to the refuge areas than further away (see Figure 8).

As a selection pattern regarding the distance to hiking trails, male ibex showed also at the smaller scale a clear preference for locations within a short distance. Its importance as a driver thereby varied only slightly among the different group sizes (see Figure 8) and seasons (see Figure 5).

In contrast to the large scale, a certain selection pattern depending on the Julian date was also visible in case of the aspect, with a minor preference of north-facing areas in spring and a clearer selection of south-faced locations in autumn (see Figure 5). The preference of north-faced aspects in case of strong winds form the south was still also exhibited at the fine scale (see Figure 9).

As favorited slope, they again mainly selected areas of medium steepness, showing a significant selection dependency on the Julian date by moving from rather flat areas ($\sim 20^{\circ}$) in spring to steeper areas ($\sim 40^{\circ}$) in summer and autumn (see Figure 5). Compared to the larger scale, however, the importance of this variable as a driver of the resource selection increased, especially at the end of the season.



Figure 5: Relative selection probability depending on the Julian date for a) aspect, b) slope, c) distance to hiking trails, d) distance to refuge areas and e) NDVI at the small scale considering the respective availability



Figure 6: Relative selection probability of NDVI depending on maximum air temperature conditions at the small scale.



Figure 7: Relative selection probability of the maximum air temperature at the small scale, constant over time.



Figure 8: Relative selection probability for the distance to the hiking trails (left) and the distance to the refuge areas (right) depending on the group size at the small scale



Figure 9: Relative selection probability for the aspect depending on the wind direction in case of low wind speed (left) and high wind speed (right) at the small scale.

4. Discussion

This study revealed that the resource selection of male ibex is over all mainly driven by their trade-off decisions between maximizing the energy intake by selecting high quality food (high NDVI), and reducing the exposure to unfavourable climate conditions (van Beest et al. 2012), which for ibex primarily are high air temperature values. Thereby it could be determined that ibex actually select their habitat rather in expectations of the maximum values than in consideration of the actual conditions. This was shown for both scales where in each case the resource selection model including the maximum air temperature data, performed much better than the one including the hourly data. This means that even in the morning the highest temperature value of the day explained much more of the selection behaviour of the male ibex than the actual temperature. As a consequence it can be assumed that ibex have a certain predictive capability for imminent temperature conditions which might possibly be explained by having a certain perception of air pressure or the like.

Considering the results of the resource selection analyses at both scales in respect to the maximum air temperature conditions, male ibex clearly favoured the coolest available places, especially in summer, which conforms to the results of previous studies (Aublet et al. 2009). But also throughout the rest of the season they strongly avoid areas with higher air temperature values. Only at the large scale did they show a slight selection of warmer places in spring. This behaviour was assumed to mainly be a consequence of favouring good food quality over reduced heat exposure, as even in the selected areas with high food quality the maximum air temperature did not exceed their heat related threshold of 15-20°C (Aublet et al. 2009). At the fine scale this selection pattern was already not detected any more, showing a constant preference of the ibex for the coolest available locations independent of the season. This indicates that also in spring, when ibex select their habitats mainly based on the provided food quality, they still show a certain thermoregulation by selecting the coolest places within the available area.

In respect to the wind, however, they did not exhibit the expected thermoregulation behaviour. In contrast to the expectations, the data revealed a clear avoidance of windy areas. This was especially seen in case of strong winds from the south when they selected north-facing areas sheltered from the wind. Since the wind was found to significantly increase the vigilance behaviour of animals (Carter und Goldizen 2003), the selection pattern shown by the ibex might possibly result from their need to reduce predation risk, as strong winds could inhibit their hearing and leave them unaware of possible predators sneaking up on them. This however is only a suspicion and further analyses are clearly required to explain the selection behaviour of male ibex in relation to the wind. The absence of a corresponding selection pattern in the event of northerly winds is assumed to be caused by the orientation of the valley which opens out to the north-east. Consequently, when the wind came rather from the

north, it was directly diverted into the valley. So actually no specific wind sheltered aspects were available. These circumstances and also the great instability of the wind in terms of both speed and direction might probably be a reason why no clear preference of a certain aspect over time could be detected in the analysis.

For the NDVI, indicating the food quality of the available resource units, however, a distinct selection pattern could be identified over the season. As expected the ibex showed a strong selection of areas with high quality food in spring, when the maximization of the energy intake probably was most important for them to compensate the forage shortage they faced in winter due to limitations by snow (Bon et al. 2001). A reason for why they thereby did not go for the highest available NDVI values might be the fact that vegetation exhibiting a really high productivity index are less attractive for ungulates, as they accumulated structural tissues and show an increased fibre content, which leads to worse digestibility (Pettorelli et al. 2011). Over the season then a clear decrease of the selected NDVI values could be determined. In summer this was probably mainly caused by the air "*temperature constraints, which* [...] force them to [also] forage in sub-optimal patches" (Brivio et al. 2014, S. 1657) providing lower food quality, but probably also reduced quantity when dominated by rocks and screes. In autumn, however, the selection of low quality forage might be a consequence of both the limitations due to the predominant maximum air temperature values and also the general scarcity of good food in this time of the year (Mysterud et al. 2011).

Regardless of the quality, they seemed to always have a strong preference for areas with high food quantity. This was inferred from the predominant selection of locations close to the hiking trails, which was also detected by Grignolio et al. (2007a). As these trails are mainly situated in the meadow, the places in a short distance from them obviously provide a greater quantity of forage than the steep rocky slopes, which are mostly found further away from the trails (Grignolio et al. 2007a, S. 1489). The unexpected great importance of this food driven parameter in summer, when they usually tend to completely stop feeding during daytime and rather retreat to rocky areas at higher elevations due to the prevailing air temperature conditions (Aublet et al. 2009), can be traced back to the fact that the data for this study was mainly selected in the mornings and evenings. According to Brivio et al. (2014) exactly at these times of the day, especially in the mornings, ibex rather intensify their forage activity in summer to compensate the reduced feed intake during the hottest hours of the day and consequently select areas with a high food density. In spring and autumn however when the maximum air temperature values are lower, they probably are able to choose their habitat in respect to the forage quality rather than its quantity, which might be the reason for the slightly decreased importance of this parameter in the beginning and end of the season. Looking at the selected distance to the hiking trails depending on the group size, larger groups of ibex showed a strong selection of the areas a short distance away, where enough food for everyone was provided. Smaller groups were also mostly found close to the hiking trails, however the predictors importance was lower, as they might also find sufficient forage where the quantity is lower.

The group dimension also showed an influence in regard to the chosen distance to refuge areas. However, the results were completely contrary to the expectations, indicating that bigger groups were more likely to be seen close to the safer areas than solitary ibex. A possible explanation for that might be, that the respective distance to the refuge areas was not selected due to its importance in reducing the predation risk, but due to the respective maximum air temperature and NDVI values, which both increase with a growing distance to the refuge areas (see Figure 10). Hence, the preference for locations close to those areas shown by larger groups of ibex would indicate that they mainly go for the cooler places closer to rocks, however, only as a secondary selection pattern as for large groups the distance to the hiking trails is of greater importance for their habitat choice.



Figure 10: Available NDVI and maximum air temperature values within different distances to the refuge areas (seasonal average).

The interpretation of the selected distance to the refuge areas as a consequence of the preferred air temperature and NDVI conditions would also explain the seasonal pattern at both scales. The strong preference for places further away from the refuge areas in spring could therefore be explained by the high food quality (NDVI ~ 0.5) which was mostly found within the selected distance of 200-300m (see Figure 11). As the maximum air temperature increased and the food quality becomes of less importance for the ibex however, they seemed to retreat to higher grounds (see Figure 12) moving closer to most of the refuge areas (see Figure 13) where the air temperature is cooler.

A movement trend to higher elevation in consequence to the chosen trade-off between the food quality and the reduction of heat-stress, would also explain the shown selection pattern of slope at both scales. As expected, in the beginning of the growing season ibex stay in flatter terrain, where according to Grignolio et al. (2007a) the food density is much higher than in the rugged terrain. Over time however, when moving to higher elevations they get closer to steep areas (see Figure 13), which is also shown by the data.



Figure 11: Available NDVI values in different distances to the refuge areas for May.



Figure 12: Model of the used elevation over the course of the season (calculated by means of a GAM).



Figure 13: AVAILABLE slope and distance to refuge areas along the altitudinal gradient.

In the beginning of the growing-season, when the maximization of the energy intake is still important for the male ibex, the seasonal migration to steeper locations closer to refuge areas might not only be caused by increasing air temperature values, but also be an effect of following the emerging vegetation up along the altitudinal gradient as according to Zweifel-Schielly et al. (2009, S. 104) young plants are *"rich in both utilizable energy and protein"*.

Overall, it can be summarized that the seasonal selection patterns shown for the parameters were mostly a consequence of the respective trade-off decisions of the male ibex weighing up their need to maximize their energy intake by foraging high quality food against their exigency to reduce the exposure to heat. And in fact, at both scales the interaction between NDVI and maximum air temperature was the main driver of the resource selection of these animals, showing the strong preference for places providing high quality food when maximum air temperature was low and a clear avoidance of these locations in favour rather rocky areas (= low NDVI), when the maximum air temperature was high.

A reason for the rather low importance of predation risk reduction in the habitat selection of male ibex might be the fact that the data was mostly collected of adult male ibex (\geq 5 year). Therefore, the observed selection patterns were mainly driven by older ibex which do not have to fear predation as much as young individuals and females (Grignolio et al. 2007a). This could also be an explanation for the general low importance of the age as a parameter for this analysis.

Comparing the results among the chosen scales two dissimilarities could be determined. One is obviously that on the fine scale they always prefer to stay in the cooler areas regardless of the Julian date. The other difference is shown in the very different weighting of the parameters over time, especially in autumn. On the large scale the importance as a driver decreased for every predictor at the end of the season, whereas it increased on the fine scale. A possible explanation for this could be that at the large scale the selection of male ibex was mainly driven by a parameter, which was not considered in the

model, and only at the second scale, where another AVAILABILITY was presumed, the selection pattern in regard to the included parameters could emerge more strongly. As the rutting season begins in this time of the year the 'missing' parameter might represent a certain internal factor connected with the rutting behaviour of by male ibex in autumn. However, this is only a suggestion and regarding to it further analyses are clearly required.

Despite those differences among the scales, in summary the results were pretty similar and most of the selection patterns shown within the monthly reachable areas were already exhibited at the large scale. Accordingly, the second scale did not really describe an important decision scale for male ibex in summer (Bowyer und Kie 2006). Further downscaling for small scale analyses, however, was limited due to the large spatial resolution of the NDVI layer (250x250m). As according to Mayor et al. (2009) the spatial decision scales are ultimately linked to the temporal ones (see Figure 14), small scale analyses were additionally restricted by the lack of ibex data collected during midday, so the daily selection behaviour of ibex and their committed trade-off could not be examined on a small scale.



Figure 14: "The link between spatial and temporal scales of habitat selection" as depicted from Mayor et al. (2009) in their publication in terms of habitat selection at multiple scales.

Therefore, further analyses are required, in which the use of telemetry data is recommended to ensure a sufficient temporal resolution of data collection. Giving the results of this analysis it would additionally be necessary to get more precise data about the distribution of high quality food over the study area, as it is evidently an important driver of the resource selection of male ibex, but according to Zweifel-Schielly et al. (2009, S. 103) also shows a strong variation in space, especially in rugged terrain.

In conclusion, the findings of this study clearly showed that the resource selection of male ibex is first of all driven by their seasonal dependent trade-off decisions between reducing their exposure to unfavourable climate conditions, especially to heat, and maximizing their energy input by foraging high quality food. Moreover, it could be shown that in selecting their habitat, these animals react in expectation of the maximum air temperature values rather than in consideration of the current circumstances. Regardless of the food quality and the predominant temperature conditions male ibex additionally exhibited a clear preference for areas providing high food quantity. The exposure to possible predators, however, was not detected to have a great impact on the habitat selection of male ibex. which is consistent to the result of former studies.

5. References

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6. Appendices



1,5 Kilometers

Map A. 1: Transects, which have been walked twice a day for data collection of ibex' location.



Map A. 2: Ibuttons. Spatial distribution of the ibuttons, which were set up for hourly recording the air temperature data in the study area in the years 2010 (ibuttons 1-15) and 2011 (additional ibuttons: 7b, 14b).



Kilometers

Map A. 3: Hydro-geographic sectors. Zones in the study area with certain microclimates.



Map A. 4: Minimum convex polygon (MCP). Large scale for the analysis defined be the home range size of the whole population of observed marked ibex (brown points) in the years 2010 and 2011.

GPS-collar ID	Age of the male		Total number of localizations											
		May 2013	Jun 2013	Jul 2013	Aug 2013	Sep 2013	Oct 2013	Nov 2013	Dec 2013	Jan 2014	Feb 2014	Mar 2014	Apr 2014	Total
12227	8		141	54										195
12228	9	94	111	95	96	100	96	67	83	60	50	68	51	971
12229	13	99	90	91	86	90								456
12230	9		27	154	4									185
12231	9	95	114	87										296
12232	9	110	96	50										256
12233	11		26	294	95	96	78							589
12234	9	131	93	95	4									323
12235	8		134	96	98	99	95	77	81	72	55	81	49	937
12236	11	133	95	101	98	100	99	25						651
Total		662	927	1117	481	485	368	169	164	132	105	149	100	4859

Table A. 1: Total number of locations. Number of locations recorded for each collared male ibex (GPS-collar ID) every month from May 2013 to April 2014. These telemetry data was used to depict ibex movement behavior and thus define availability of fine scale resource selection functions.

	model parameters											
I-button	time shift	у	year	Julian	Julian^2	time	time^2	time^3	Julian*time	Julian*year	adj. R ²	AIC
1.Tignet	no	ibutton (2.)	yes	yes	yes	yes	yes	yes	yes	yes	0.945	24988.8
2.Panett	3 hours	weather station	yes	yes	yes	yes	yes	yes	yes	yes	0.935	23904.9
3.Granzetta	3 hours	weather station	yes	yes	yes	yes	yes	yes	no	yes	0.933	20230.9
4.LevSotto	3 hours	weather station	yes	yes	yes	yes	yes	yes	yes	yes	0.922	25953.9
5.ZigZag	no	ibuttonn (8.)	no	yes	yes	yes	yes	yes	yes	no	0.922	19956.4
6.Lezou	2 hours	weather station	yes	yes	yes	yes	yes	yes	no	no	0.937	18384.8
7.LevMezzo	2 hours	ibutton (6.)	yes	yes	no	yes	yes	yes	yes	yes	0.820	20958.0
8.Bivio	2 hours	weather station	yes	yes	yes	yes	yes	yes	yes	yes	0.910	24352.9
9.LevSopra	no	ibuttion (8.)	yes	yes	yes	no	yes	yes	no	yes	0.947	20161.3
10.Laus2700	no	ibutton (12.)	no	yes	yes	yes	yes	yes	yes	no	0.946	21128.2
11.Timor2500	2 hours	ibutton (6.)	yes	yes	yes	yes	yes	yes	yes	yes	0.950	17380.0
12.Timor2700	2 hours	weather station	yes	yes	yes	yes	yes	no	yes	no	0.900	23733.8
13.Timor2900	no	ibutton (12.)	yes	yes	yes	yes	yes	yes	yes	yes	0.912	24250.5
14.Inferno	no	ibutton (12.)	yes	yes	yes	yes	yes	yes	yes	yes	0.911	20784.8
15. Laus2900	no	ibutton (8.)	yes	yes	yes	yes	yes	yes	no	yes	0.951	18416.5
7b.LevMezNew	no	ibutton (6.)	no	yes	yes	yes	yes	yes	no	no	0.778	15388.8
14b.PianaInferno	1 hour	ibutton (4.)	no	yes	no	yes	yes	yes	no	no	0.929	3612.1

Table A. 2: Summary of the models used for filling the missing values in the I-button datasets.



Generalized Additive Model: large scale

sample size

Generalized Additive Model: small scale

Figure A. 1: Large scale. General Additive Model (GAM) of temperatures' estimates depending on the sample size, showing a stabilization of the parameter's estimates when the number of random available points was 15.



sample size

Figure A. 2: Small scale. General Additive Model (GAM) of temperatures' estimates depending on the sample size, showing a stabilization of the parameter's estimates when the number of random available points was 13.