

Vigilance behaviour in Alpine ibex (*Capra ibex*) and Alpine chamois (*Rupicapra rupicapra*) kids

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Abstract

In prey species, vigilance is an important behavioural trait with regard to antipredator strategies. It has been studied intensely in animals. However, little is known about vigilance in animal kids. In this study, I investigated the influence of various environmental and social factors on Alpine ibex (*Capra ibex*) and Alpine chamois (*Rupicapra rupicapra*) kid vigilance behaviour. In the Gran Paradiso National Park, Italy, animals were observed from June to August, 2015, using group scan and focal kid observations. Data was analyzed using general additive and general additive mixed models as well as a cross-correlation function. The results revealed that there is no interspecific difference in kid scanning behaviour. A group size effect on kid vigilance is given, however no group size effect could be found for adults. Kid vigilance is strongly affected by the distance to the closest hiking trail, which can be seen as a proxy for human disturbance. This effect does not exist for adults, which suggests a habituation process. Against my expectation, the fear of the group is not reflected in kid scanning behaviour. In general, kids are more vigilant than adults. Animals scan more in rocky terrain than in grassland and more in the morning than in the evening. Kids synchronize their scanning behaviour with that of adults, which suggests a learning effect between generations. The innovative focus of this study on vigilance behaviour in kids reveals that there are still a lot of open questions in this field.

1 Introduction

Throughout evolution, prey species have co-evolved with their predators and developed strategies to avoid predation. Those are mostly complex and can include morphological adaptation, adapted life history traits or behavioural characteristics [Caro, 2005]. To avoid being detected by predators, prey species adapt their behaviour by using antipredator strategies such as spatial adaptation or shifting activity peaks [Christianson and Creel, 2010, Iribarren and Kotler, 2012a]. Besides, prey species can also increase their survival probability by early predator detection. Interrupting an actual activity to scan the surroundings for possible threats can enhance predator detection. This behaviour is generally known as vigilance. In mammals, it is assumed to be expressed by a head-up position, indicating concentrated scanning of the environment [Alados, 1985, Frid, 1997, Wolff and Horn, 2003].

Although vigilance behaviour generally increases survival probability, it can also cause costs such as a decrease in feeding ability [Boving and Post, 1997, Childress and Lung, 2003]. Thus, the individual should aim to find an optimum between safety and the fulfillment of other needs. One strategy to come closer to this optimum is to gather in groups. Grouping can provide several advantages for prey species. In many gregarious species, a so called group size effect has been observed [Beauchamp, 2008]. It describes a negative correlation between group size and individual scanning effort [Shi et al., 2010]. Among the main theories to explain this negative correlation are the 'many eyes' or 'detection effect' and the 'safety in numbers' or 'dilution effect' [Pulliam, 1973, Cresswell, 1994, Li and Jiang, 2008, Shi et al., 2010]. The first theory assumes that the probability to detect predators increases with group size, so that the individual can reduce personal vigilance [Lima, 1995, Shi et al., 2010]. The latter hypothesizes that the probability to be killed is lower in a group [Dehn, 1990]. Thus, an animal perceiving a lower predation risk can afford to decrease time spent vigilant.

Hence, if a lower perception of predation risk allows the animal to be more relaxed, why can vigilance behaviour be observed in predator-free areas, too? On the one hand, this can be explained by the fact that vigilance does not exclusively serve as antipredator behaviour [Cameron and Du Toit, 2005]. Attentive observation of conspecifics can provide advantages such as recognition of competitors [Beauchamp, 2015]. Lung and Childress [2007] classify this kind of vigilance as social monitoring vigilance. On the other hand, it could be shown that antipredator behaviour (and the ability to recognize predators) in some species persists even though predators have long

been extinct or moved to other habitats [Goldthwaite et al., 1990, Boving and Post, 1997, Shi et al., 2010]. For some species, it should also be considered that even though natural predators might long be extinct, humans have taken over the predator's position. Even in nowadays unhunted populations, they might still be perceived as a threat [Grignolio et al., 2007a]. Hence, describing the intensity of risk only by the presence or absence of predation pressure would be too simple. Various other factors influence predation risk additionally. These can for example be age or body condition of the individual. In general, it is newborn animals that are especially vulnerable to predation [Toïgo et al., 1999, Rieucan and Martin, 2008, Dalmau et al., 2010]. This is mainly due to their small body size and their low level of life experience [Pratt and Anderson, 1979, Hunter and Skinner, 1998, Caro, 2005]. Despite of their low level of experience, neonates often show an innate ability of recognizing predators [Owings and Coss, 1977, Hirsch and Bolles, 1980]. Besides this innate predator recognition, parts of antipredator behaviour have to be learned [Hanson and Coss, 1997, Griffin et al., 2001, Griffin and Evans, 2003]. According to their high vulnerability, one might assume that kids should be especially attentive with regard to predators [Caro, 2005]. However, only very few studies could show a higher vigilance in kids than in adults (see for example [Holmes, 1984] for marmots, [Burger and Gochfeld, 1994] for impalas). Much more frequently, adults were observed to be more vigilant than kids (see for example [Alados, 1985, Risenhoover and Bailey, 1985, Burger and Gochfeld, 1994, Lashley et al., 2014]).

The literature concerning kid behaviour in mammals, especially in ungulates, is rather scarce. Papers dealing with kid behaviour often focus on domestic or captive animals [Byers, 1977, 1980, Lickliter, 1987]. Moreover, many studies of ungulate kids have focused specifically on the mother-kid relationship [Langman, 1977, Guinness et al., 1979, Alados and Escos, 1988, Braza and San José, 1988]. Only a few studies have investigated kid behaviour in free ranging ungulates in a broader context. Here, Autenrieth and Fichter [1975] and Riley and Dood [1984] can be mentioned, who studied pronghorn fawns and mule deer fawns, respectively. As far as the context of antipredator behaviour and kids is concerned, the focus of most papers has been set on on the vigilance behaviour of mothers, instead [Toïgo et al., 1999, Kohlmann et al., 1996, White and Berger, 2001]. Many of them found mothers to be more vigilant compared to females without offspring [Burger and Gochfeld, 1994, Kohlmann et al., 1996, Toïgo et al., 1999, Hunter and Skinner, 1998]. This can be explained by the mother's aim to guarantee kid survival and thereby enhance lifetime reproductive success [Toïgo et al., 1999].

Concerning the lack of available information on antipredator behaviour in kids, I set the focus of this thesis on antipredator behaviour of neonates in Alpine ibex (*Capra Ibex*) and Alpine chamois (*Rupicapra Rupicapra*). Both species are gregarious mountain ungulates sharing a lot of characteristics [Mustoni et al., 2002]. They provide an interesting opportunity for studying and comparing antipredator behaviour. For that purpose, the hypotheses stated below were constructed. For clarity, the questions and the corresponding analysis and results are from here on structured in parts A, B and C.

In the context of interspecific differences, it was assumed that (part A)

- *there is a difference between chamois and ibex kid vigilance behaviour, and if so, that*
- *chamois show higher vigilance because they are in more open terrain, or that*
- *ibex show higher vigilance because they tend to be in smaller groups.*

Concerning the gregarious characteristics of both species, it was assumed that (part A)

- *there is a group size effect on kids*
- *kids reflect the fear of the group in their own behaviour*
- *kids increase vigilance with an increasing number of kids in the group due to curiosity.*

Regarding the low level of experience in kids, it was assumed that

- *vigilance in kids is lower than in adults (part B)*
- *there is a learning effect with regard to scanning (part C).*

2 Methods

2.1 Study area

The study area was located in Levionaz Valley, Gran Paradiso National Park (GPNP), Italy. The valley is located above the treeline and ranges from 2000 - 3300 meters above sea level. Besides the main basin, three tributary valleys of Levionaz valley belong to the study area: Loson valley, Inferno valley and Timorion valley (see map 2.1). The study area is mainly characterized by rocky cliffs, screes and alpine meadows (mainly *Festuca spp*, *Carex spp*) [Grignolio et al., 2007b, Brambilla et al., 2013]. The climate is temperate continental, characterized by a long snow period from October/November to April/May [Palmegiani et al., 2013, Brivio et al., 2015]. The warm summer period is usually from June to September [Brivio et al., 2015]. During the study period from June 17th until August 25th, 2015, the average temperature was 13.3°C with a minimum of 2.4°C and a maximum of 25.9°C (weather station of the Regione Autonoma Valle d'Aosta, Pont). According to park staff, the summer of 2015 has been the warmest ever recorded for Aosta valley (Favre, personal communication 2015).

Levionaz valley can only be reached by foot or helicopter. The latter is used only seldomly for transporting goods. A net of hiking trails covers the study area (see figure 2.1). Those trails are generally used by hikers, trailrunners and, occasionally, mountainbikers. It is not allowed to bring dogs to the area. Managed alpine huts do not exist in the study area. Two small cabins are located at the entrance of the valley, only accessible to park staff and researchers. Rearing of livestock only occurs in the adjacent Cogne valley, but not in the study area.

Two mountain ungulate species occur in the study area: Alpine Ibex (*Capra Ibex*) and Alpine Chamois (*Rupicapra Rupicapra*). In 2015, also roe deer (*Capreolus capreolus*) occurred occasionally in the main basin of Levionaz valley.

The area has been free of relevant terrestrial predators of both ungulate species for about one century [Brivio et al., 2015]. However, in 2006 a reproductive wolf (*Canis lupus*) pack returned to Valsavaranche, ranging from 2 to 6 individuals [Palmegiani et al., 2013]. The wolves were present in the valley until 2013, thereafter no signs could be found any more [Brivio et al., 2015]. In summer 2015, the presence of wolves was confirmed in the adjacent Cogne valley (Favre, personal communication 2015). Red foxes (*Vulpes vulpes*) are regularly present in the study area. Predation of ibex by red fox is not confirmed [Grignolio et al., 2007a], however Cagnacci et al. [2003] could show that Alpine ibex are part of fox diet. The part of fox diet covered by chamois is

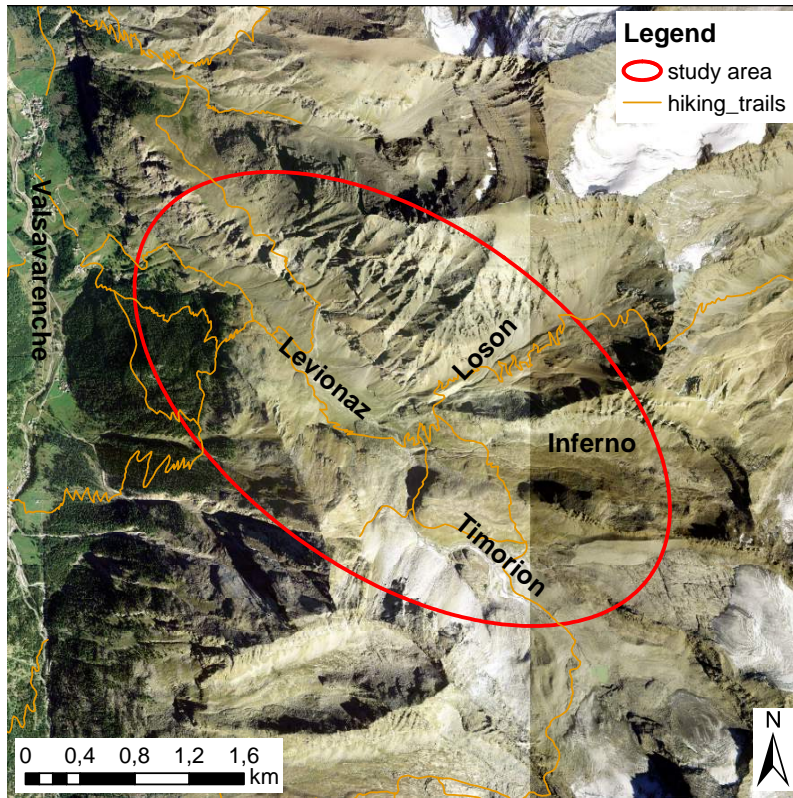


Figure 2.1: Study area: Levionaz valley with tributary valleys.

considerably larger and seasonally ranges up to nearly 50%, which Cagnacci et al. [2003] suggest is due to the consumption of carcasses. Concerning avian predators, the Golden Eagle (*Aquila chrysaetos*) is most relevant [Brivio et al., 2015]. Their focus of predation on ungulates is set on young animals [Pérez-Barbería and Nores, 1994, Iribarren and Kotler, 2012b]. Bearded vulture (*Gypaetus barbatus*) is present in the study area, too, however it is not confirmed whether they actively prey upon ibex and chamois. For Nubian Ibex, bearded vulture is considered to be a predator of neonates [Tadesse and Kotler, 2012]. Hunting is prohibited in GPNP and the adjacent Parc National de la Vanoise in France [Jacobson et al., 2004].

2.2 Study populations

2.2.1 Chamois

The population of chamois in Levionaz valley has not been subject to prior studies. Its general condition, however, is monitored by GPNP park wardens on their regular patrols. Moreover, chamois are, such as ibex, subject of a regular census conducted twice a year by GPNP. In September 2015, 75 males, 95 females, 42 yearlings and 53 kids were counted (GPNP, unpublished data). Except for the rut in winter, females generally live in groups with other females and their offspring [Mustoni et al., 2002]. In spring, females give birth to one or, seldomly, two kids [Mustoni



Figure 2.2: Chamois mother and kid resting (August 2015, picture by S. La Gala).

et al., 2002]. Figure 2.2.1 shows a resting chamois mother with kid. In 2015, the first kids of the population in Levionaz were born in the first days of May (Favre, personal communication 2015).

2.2.2 Ibex

Due to heavy over-exploitation by humans, the species of Alpine Ibex almost went extinct in the 19th century [Stüwe and Nievergelt, 1991]. The only population to survive was the one living in the royal hunting reserve in the Gran Paradiso area, which was transformed into today's GPNP in 1922 [Corlatti et al., 2012]. Thus, the population here is the only existing autochthonous Alpine ibex population [Grignolio et al., 2007a]. The ibex population in Levionaz is subject to the same regular monitoring and census as the chamois population. Moreover, it has been subject of intense research since 1999 [Brivio et al., 2015] (see for example [Bassano et al., 2003, Von Hardenberg et al., 2007, Apollonio et al., 2013]). Many individuals have been marked with ear tags or collars in the context of research projects [Brambilla and Canedoli, 2014]. Besides the focus on male ibex, the research has addressed a few questions concerning females and kids (see for example [Grignolio et al.,



Figure 2.3: Ibex kid with mother (August 2015, picture by S. La Gala).

2004, 2007b)). Despite during the mating season, females usually live in mother kid groups [Mustoni et al., 2002]. Figure 2.2.2 shows a female ibex with kid in Levionaz. The census in 2015 gave a result of 74 males, 67 females, 22 yearlings and 29 kids in June and 73 males, 83 females, 27 yearlings and 36 kids in September (GPNP, unpublished data). The first ibex kids of 2015 were born in the last days of May (Favre, personal communication 2015).

2.3 Data collection

2.3.1 Observational data

Data was collected from June, 17th until August 25th, 2015. Observations were carried out early in the morning or in the evening. This is due to the fact that most ungulates show peaks in feeding activity at those times of the day [Aublet et al., 2009, Hochman and Kotler, 2006, Alemayehu et al., 2011]. Animals were detected in the terrain either by eyesight or with the help of binoculars (Swarovski Habicht 8x56, Swarovski Habicht 7x42). The animals were observed from various, non-fixed locations. Those were chosen each according to factors such as precipitation, visibility and disturbance events such as for example hiking groups. The animals were, depending on the observer's location, observed with binoculars or with a spotting scope (Swarovski 65 ATX). The observer's exact position was marked with a GPS device (Garmin 62s, Garmin GPSmap 60CSx). The distance to the animals was measured with a rangefinder (TruePulse 200). Besides, the angle to the focal animal was taken with a compass (Suunto Tandem Compass). When observing groups, a focal animal was chosen in the center of the group, its position representing the position of the group. Subsequently, the position of the animal was saved in the GPS device. Due to the characteristics of the mountainous terrain, it was not always possible to use this method. Alternatively, a map of the park was used. This map was covered with a grid (250x250m), which was divided into four subgrids, each containing an individual code which was recorded.

For the behavioural observation, two methods were chosen: observation of groups and observation of focal kids. For both observation types, activities were classified as following:

Feeding: An animal was assumed to be feeding when it was clipping vegetation. Moving to the next patch of food with the head kept down was also registered as feeding [Frid, 1997, Hochman and Kotler, 2006]. Drinking water from puddles, streams and rivers as well as licking minerals from stones was considered feeding, too.

Moving: The animal is moving with the head held up [Alados, 1986]. For both adults and kids, but more importantly for the latter, it should be considered that moving can be the beginning of a social interaction. However, the intention of the animal cannot be observed in advance. Thus, moving was registered until a social interaction such as playing could be clearly identified by the observer.

Grooming: The animal is grooming its own body using teeth, claws or rubbing against shrubs, stones or ground. Grooming of other individuals was registered as social behaviour.

Suckling: The kid is suckling milk. However, this category also includes unsuccessful suckling events. Sometimes the mother was hindering the kid from drinking by moving on or edging the kid aside. In such cases it was not possible for the observer to see if the kid was only trying to drink or really drinking. Thus, a kid in contact with the mother's udder was considered suckling.

Social behaviour: Interactions between individuals of all sex and age classes or species were considered social behaviour. This includes direct confrontations, grooming of others as well as playing.

Scanning: An animal standing still with the head raised above shoulder height was considered scanning [Alados, 1985, Frid, 1997, Dalmau et al., 2010]. Movements of the ears often additionally indicate the animals attentive status. If an animal interrupted a feeding session and was thus still chewing when looking up, it was registered as scanning.

Resting: Any animal lying down was considered resting. It was assumed that a resting animal is not active. Observations of focal individuals were stopped as soon as an animal started resting.

Observation of groups

A group was defined as any accumulation of animals containing females and kids. Thus, a single mother with kid was also considered a group. Animals not further than 50m away from the next animal were considered part of the group [Pérez-Barbería and Nores, 1994, Frid, 1997, Grignolio et al., 2007a, Dalmau et al., 2010]. If additional animals occurred during the observation and stayed within the group, they were considered group members, too. If other animals occurred during the observation which were clearly just passing by, they were not considered part of the group. Although it happened occasionally that both study species were using exactly the same spot, mixed groups were not considered as such. The observation was conducted using the group scan method [Martin and Bateson, 2011]. Therefore, the activity of each animal was registered within a fixed interval (1 minute), which was repeated 13 to 15 times. Animals were categorized in two age classes: neonates were referred to as 'kids' whereas all other individuals, thus 1 year and older, were referred to as 'adults'. Animals that were resting were included in the group scan, too. The observation was recorded with a voice recorder (SanDisk SDMX18-008G-E46K). Each group was observed only once during one session.

Observation of kids

To observe the activities of kids the focal sampling method was used [Altmann, 1974, Toïgo et al., 1999, Dalmau et al., 2010, Martin and Bateson, 2011]. An individual kid in the group was observed for up to 15 minutes. Observations shorter than three minutes were omitted [Childress and Lung, 2003]. The observations began and ended only when a natural break in behaviour occurred and always ended when the animal started to rest or disappeared [Ciuti et al., 2012]. The behaviour was recorded with a tablet (ASUS Fonepad 8 FE320) using the app Xebi (© 2015 by Philipp Jund).

Every observation was saved as a .txt file containing an individual kid ID, a time stamp for start and end of the total observation as well as for each activity interval. Additionally, the output contained the total time of each activity. Observing the same individual twice was avoided by considering individual characteristics such as size, colour, contact with a marked mother, type of activity and location.

2.3.2 Environmental data

Besides the observation data of kids, several environmental factors were included in the analysis. Table 2.4.1 gives a full overview over all variables used in data analysis.

Several GIS layers were provided by GPNP. Orthophotos of the park were mainly to get a visual impression of the distribution of observed groups and individuals. A map including land use types was used to characterize the habitat type in which the observed animals were located. A digital elevation model (10x10m) served as a basis to compute slope and ruggedness in ArcGIS. A map of hiking trails was provided, too. Wind and weather data came from the meteorological station in Pont, property of the Regione Autonoma Valle d'Aosta.

Concerning the focus of this work on antipredator behaviour, it was assumed that the role of refuge areas might be important for the analysis. Both species use steep cliffs and slopes $\geq 45^\circ$ as refuge areas [Fox et al., 1992, Pérez-Barbería and Nores, 1994, Kohlmann et al., 1996, Ruckstuhl and Neuhaus, 2001, Dalmau et al., 2010]. Thus, a layer containing refuge areas was created by intersecting areas with the land use types 'rocks' and 'scree' with a slope $\geq 45^\circ$.

2.4 Statistical analysis

All statistical analysis was conducted with the program R, version 3.2.1.

2.4.1 Data preparation

The coordinates of all observed kids and groups were projected to WGS1984 UTM32N. For those individuals and groups whose positions could not be recorded directly in the field, coordinates were calculated based on known grid centre coordinates. I decided to extract the environmental data for the average position between start and end point. In ArcGIS, the data corresponding to this position was extracted from several layers using the tools "Join" and "Extract". This provided the variables elevation, slope, ruggedness, distance to refuge area, habitat type and distance to the next hiking trail (for detailed information see table 2.4.1). For computing the aspect of the animal's position, the start position was chosen. This was due to the fact that I considered it unlikely that an animal could have changed its position for example from a northern to an eastern slope while still being visible. Thus, by using the starting position's aspect, it is assumed that this factor did not change during an observation.

The habitat types used by observed animals were mainly the following: Grassland, Meadows, Rocks and Scree. Only one animal used the habitat type Riverbanks. To avoid a high influence of

this data point, it was reclassified to the next habitat type, which was "Meadows" in 12m distance. Subsequently, the types "Grasslands" and "Meadows" and "Rocks" and "Scree" were merged to "Grass" and, respectively, "Rocks".

Each individual and group observation was supplemented by wind speed and temperature. For both variables, the values registered at the time closest to the start of the observation were selected.

For all variables that were considered to be included in further models, histograms were checked to visualize the data distribution. Boxplots and dotcharts were used to visualize outliers, which could all be explained from an ecological point of view [Zuur et al., 2010]. The time a focal individual spent scanning during one observation and the scanning frequency were meant to be used as response variable in part A of the analysis. Due to skewness, those variables were transformed using the function `boxcox` (package `MASS`). The same was done for the response variable of part B, percentage of adults or kids scanning during one observation. Besides, the variables were checked for collinearity using `pairs.panel` (package `psych`) for numeric and `hetcor` (package `polycor`) for categorical variables, respectively.

2.4.2 Analysis

In part A, it was tested whether there is a difference in chamois and ibex kids vigilance behaviour and how various environmental and social factors influence this behaviour. For this part of the analysis, the data collected with focal kid observation was used, supplemented by group scan level and group vigilance (see table 2.4.1=, which were extracted from the group scan data. To gain an overview over the general importance of the variables used in further models to explain the vigilance behaviour of kids, a random forest model was used. All variables considered to be used in further models were included in the random forest model, regardless of correlations.

To investigate the influence of social and environmental factors on scanning behaviour of kids, a general additive model (GAM) was used. This model type is basically an extension of a generalized linear model (GLM), which allows to visualize non-parametric relationships between response and predictor variables [Zuur et al., 2009, Crawley, 2013]. Thus, flexibility of the model fit is greater. Having several predictor variables (a, b, c, d), it is possible to assume a parametric relationship for some of them (c) while using smoothers (s) for others (a, b). Additionally, random effects can be included in the model (d). The random effect is indicated by `bs="re"`. The form of such a model can exemplarily be described by formula 2.1:

$$y \sim s(a) + s(b) + c + I(c)^2 + s(d, bs = "re") \quad (2.1)$$

The factors slope, ruggedness and distance to refuge area; species, distance to refuge area and slope as well as group vigilance and group scan level were correlated ($p \geq 0.7$). To avoid using them in the same model, six models were run for each response variable, namely for scanning percentage and scanning frequency. The decision for the best fitting model was based on the

Table 2.1: Variables used for statistical analysis.

VARIABLE	DETAILS
Variables used in part A and B	
Species	chamois or ibex
day	Julian date (1 January = day 1)
ddcode	time of the day (dawn or dusk)
temPont	temperature [°C], recorded every 60 minutes, 24hrs/day in Pont
wind_speed_start	wind speed [m/s] recorded every 10 minute, 24hrs/day in Pont
type_av	habitat type grass or rocks at the average position of the individual or group
dem_av	elevation [meters above sea level] at the average position of the individual or group
slope_av	slope [°] at the average position of the individual or group
rugged_av	terrain ruggedness index at the average position of the individual or group
cosasp	aspect at the starting position, cosine transformed
dist_next_hiking_av	distance [m] to the next hiking trail at the average position of the individual or group
dist_ref45_av	distance [m] to the next refuge area at the average position of the individual or group
Variables used in part A and C	
kids_max	maximum number of kids in the group
adult_max	maximum number of adults in the group
Variables used only in part A	
gsl	group scan level, average percentage of adults scanning during one group observation [Childress and Lung, 2003]
group_vigi	group vigilance, percentage of intervals with at least one adult scanning [Childress and Lung, 2003, Ciuti et al., 2012]
social.perc	percentage of total observation time a focal kid spent with social behaviour
scanper_boxcox	percentage of total observation time a focal individual spent scanning, boxcox transformed ($\lambda = 0.3$)
scanfr_boxcox	scanning frequency as the number of scanning bouts per minute, boxcox transformed ($\lambda = 0.5$)
Variables used only in part B	
class	adult or kid
max	maximum number of individuals during one group observation
sociper	average percentage of adults or kids showing social behaviour during one observation
scanper_boxcox	average percentage of adults or kids scanning during one observation, boxcox transformed ($\lambda = 0.4$)
Variables used only in part C	
kids_scan	number of kids scanning per minute
ad_during	number of adults scanning at the same time

Aikake Information Criterion (AIC), which measures the goodness of fit and model complexity [Zuur et al., 2009]. The lower the AIC, the better the fitted model [Zuur et al., 2009].

To avoid an overfitting effect by the GAM, the factors ruggedness, group scan level and group vigilance were included in the model as linear and quadratic terms. Due to a high number of possible predictor variables, some of them were excluded from the model a priori. Supported by the output of the random forest models, the factors habitat type and time of the day were not included in the initial models. After identifying the best fitting full model for each response variable, a manual step AIC selection was performed to find the optimal model (see tables A.1 and A.2). Therefore, the model identified as the best of six was run as many times as variables were included in it, each time omitting one variable. The model with the lowest AIC was then chosen as a starting model for the next selection round, in which again each factor was removed from the model once. This backward selection procedure was repeated until the AIC value could no longer be improved (see tables A.1 and A.2). This led to a final model for each response variable. The final model using scanning percentage as a response is from here on referred to as model 1, that for scanning frequency as model 2.

In part B of the analysis, I aimed to find out whether kids are scanning less than adults. Here, group scan data was used. For scanning and social behaviour, the average percentage of adults or kids showing this activity during one observation was computed (the former variable group scan level used in part A was computed in the same way for scanning adults). I decided to use scanning percent - of both adults and kids, categorized by class - as response variable. Alternatively, one could have used percentage of intervals during which at least one adult or kid was scanning (which was calculated for adults before and used as group vigilance in the first part of analysis). However, concerning the fact that group size varied between observations and could be as low as 2, the latter would have been less representative. The environmental predictors used were equivalent to those in part A. Again, a random forest model was used for data screening. In the dataset used for part B, the number of predictors was considerably lower. No predictors had to be excluded. A first GAM model revealed heterogeneity of data. Therefore, a fixed variance structure was included, which allows for larger residual spread when the variable increases (Zuur 2009). Using the fixed variance required switching to the structure of a generalized additive mixed model (GAMM). The variance structure was fixed using the distance to the next hiking trail and specified as a weights argument. Due to collinearity, six initial GAMM were run. Again, the best model according to the lowest AIC was chosen. As for part A, a manual step AIC was used for final model selection (see table A.3).

For part C, thus to figure out whether kids are scanning after adults, the cross-correlation function `ccf` (package `stats`) was used. In general, this function serves to describe the relationship between two time series. Here, it was used with the number of kids scanning and the number of adults scanning in the same observation interval. By rescaling those numbers to binomial values and in relation to group size (maximum group size or maximum number of kids and maximum

number of adults), I checked for possible variations.

3 Results

From June 17th to August 25th, 2015, 165 groups and 327 individuals were observed in Levionaz valley (see figure 3.1). As far as the species is concerned, 83 chamois groups and 156 inherent focal kids and 82 ibex groups and 171 focal kids were observed. This resulted in two different datasets - focal kid observation data and group scan data. Focal kid observation data was used for part A of the analysis, slightly supplemented with group observation data. Parts B and C of the analysis were entirely based on group scan data. Environmental data was used equally for the complete analysis (for overview see table 2.4.1).

The response variables used in the models of part A and B were all transformed using a box-cox transformation. To better understand especially the visualized results, figure 3.2 and figure

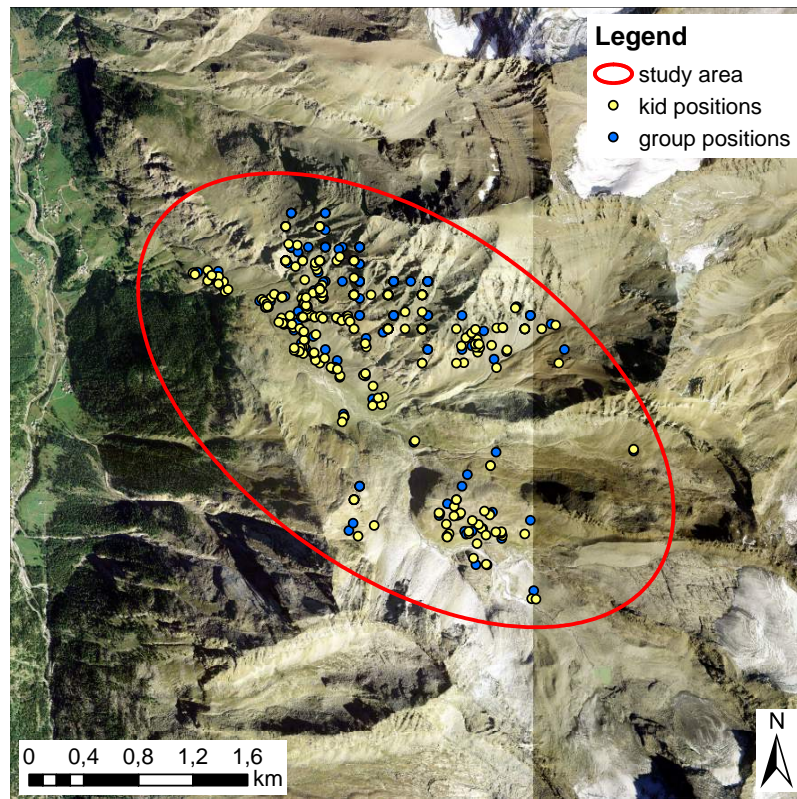
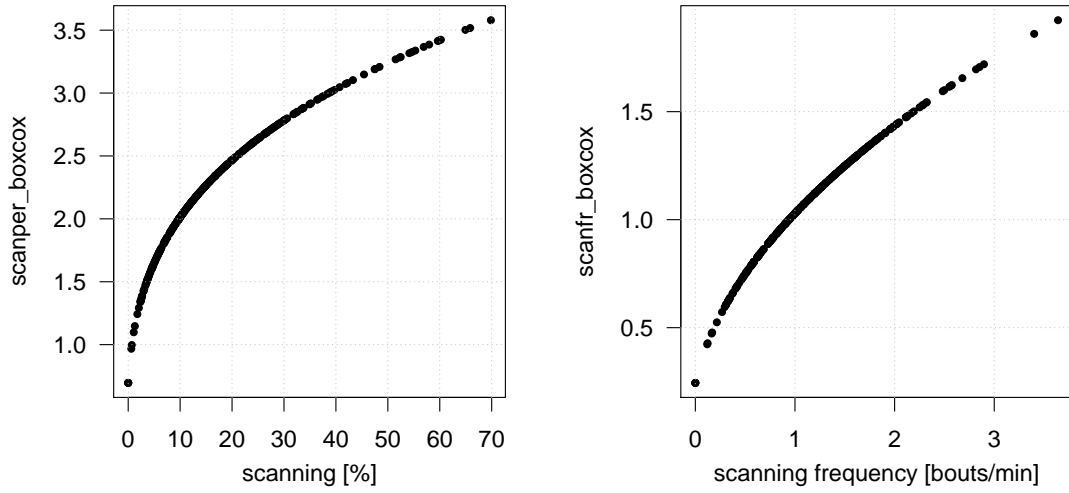


Figure 3.1: Observations of groups and focal kids.



(a) Boxcox transformed variable scanper_boxcox vs. percentage of time focal kids spent scanning. (b) Boxcox transformed variable scanfr_boxcox vs. scanning frequency of focal kids.

Figure 3.2: Transformed response variables used in part A plotted against original values.

3.3 shows the true values of the variables plotted against their transformed version.

To understand the importance of the variables which were considered to be used in the models for part A, a random forest model was run for each response variable (see figure A.1(a) and A.1(b)). The variable importance plots show strong similarities, especially in the lower and upper parts. The selection process which lead to the final models is documented in table A.1 and table A.2 in Appendix A.

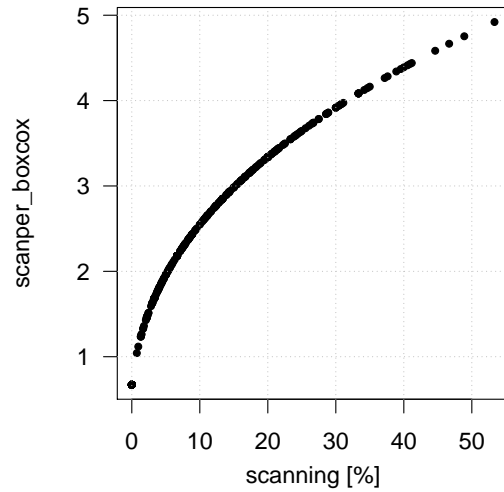
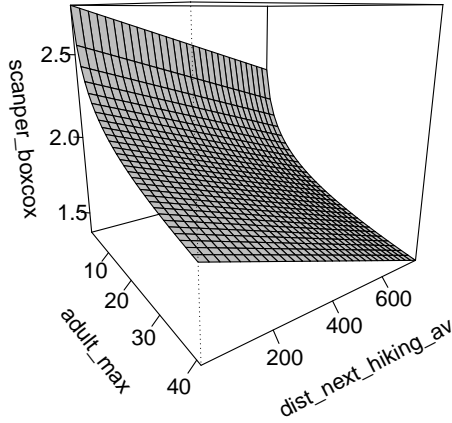
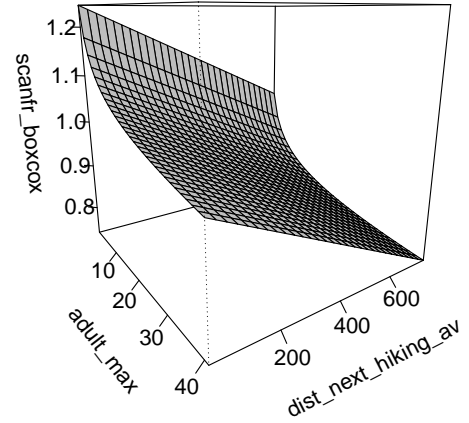


Figure 3.3: Boxcox transformed response variable scanper_boxcox (used in part B) vs. average percentage of animals scanning during one observation.

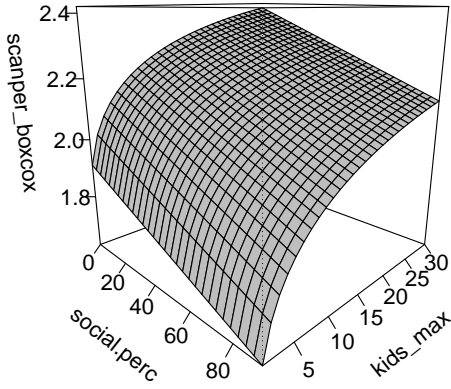
Part A of the analysis led to the following results: An interspecific difference of ibex and chamois kid vigilance behaviour could not be detected. The variable species was rejected very early in the model selection process and is not included in the final models (see tables A.1 and A.2). Thus, the two consecutive questions concerning interspecific differences in kid vigilance were omitted. Against my expectation, kids of both species do not reflect the fear of the group. Both group scan level and group vigilance were omitted during the model selection



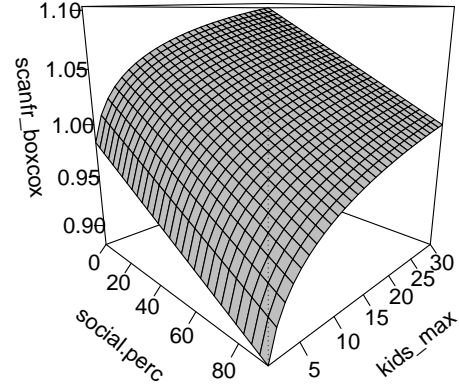
(a) Effect of group size and distance to the next hiking trail on scanning percent.



(b) Effect of group size and distance to the next hiking trail on scanning frequency.



(c) Effect of social behaviour and maximum number of kids on scanning percent.



(d) Effect of social behaviour and number of kids on scanning frequency.

Figure 3.4: Effect of various variables on kid scanning behaviour.

process due to minor importance. By contrast, a group size effect on kids does exist. Both final GAM show a negative correlation between kids' scanning behaviour and group size (see figure 3.4). To figure out whether a part of the displayed vigilance behaviour in kids is due to curiosity, the maximum number of kids was included in both models. In the model using scanning percent as response variable, the maximum number of kids had a significant effect ($p\text{-value}=0.0251$). Considering parts of vigilance behaviour as potential social monitoring vigilance, social behaviour was included in both models, too. Despite a negative trend between social behaviour and vigilance behaviour, no significant effect could be shown (see figure 3.4).

In general, the most relevant factors influencing kids' scanning behaviour are distance to the

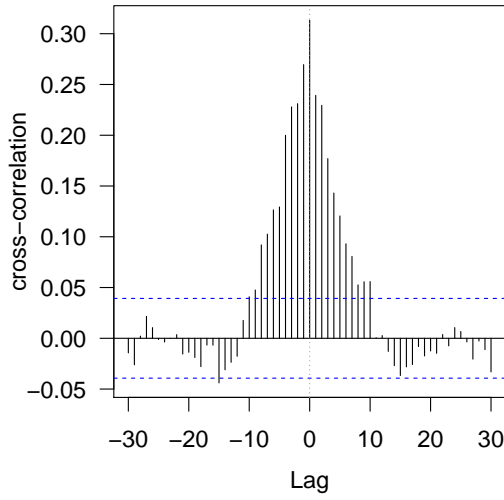
next hiking trail (model 1: p-value=0.0026, model 2: p-value=0.0066) and group size (model 1: p-value <0.0001, model 2: p-value=0.0255)(see figure 3.4). With increasing distance and group size, kids spend less time scanning.

For part B, a random forest model was used as well (see figure A.1(c)). The variable importance plot shows a pattern similar to those in part A (figure A.1(a) and (b)). In part B, no further decisions were made based on this model, as all predictors could be included in the following model. It should be considered that a random forest is not a mixed model. Thus, indications can be misleading if used to decide which variables should be included in a mixed model. This becomes obvious when considering the fact that some of the predictors of - according to the random forest - 'low importance' turned out to be most influential in the final model (see table A.3). The final model reveals that kids do not scan less than adults, on the contrary: kids scan significantly more than adults (see table 3). Besides, animals scan more in the rocks than in the grass (see table 3). There is also a significant difference between dawn and dusk, animals are scanning less in the evening (see table 3). Due to the rather non-intuitive character of plotted predictions of a model containing only categorical variables, raw data was plotted in figure A.4 in appendix A to visualize the results of part B.

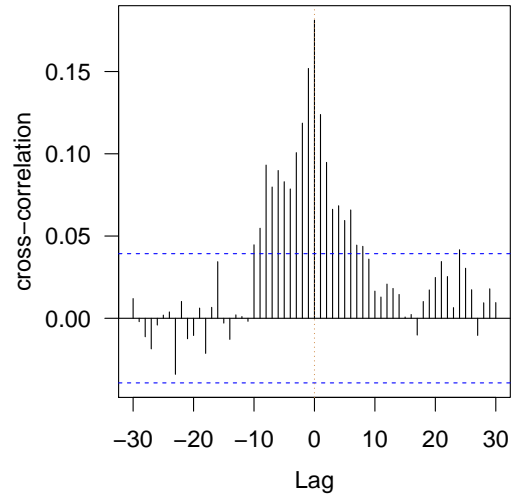
Table 3.1: Summary of the final model in part B.

	ESTIMATE	STD. ERROR	T VALUE	P-VALUE
(Intercept)	2.32119	0.12401	18.718	< 2e-16 * * *
type_ avrocks	0.30976	0.12609	2.457	0.0147 *
ddcodedusk	-0.27186	0.12646	-2.150	0.0325 *
classkid	0.42995	0.05683	7.566	6.73e-13 * * *

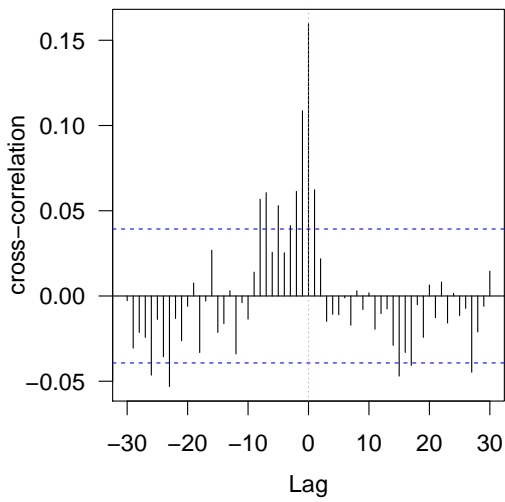
The cross-correlation function used for part C of the analysis reveals that scanning behaviour of kids is synchronized with that of the adults (see figure 3.5). The scanning at time lag 0 has the most significant cross-correlation. Taking the maximum number of animals or the maximum number of kids and adults into account does not change this result (see figure 3.5). On all scales, time lag -1 shows the second strongest correlation, indicating that kids, if they do not synchronize their scanning behaviour, scan rather after the adults than before them. Concerning this combination of strongest and second strongest correlation, one can state that there is a learning effect in kid vigilance behaviour.



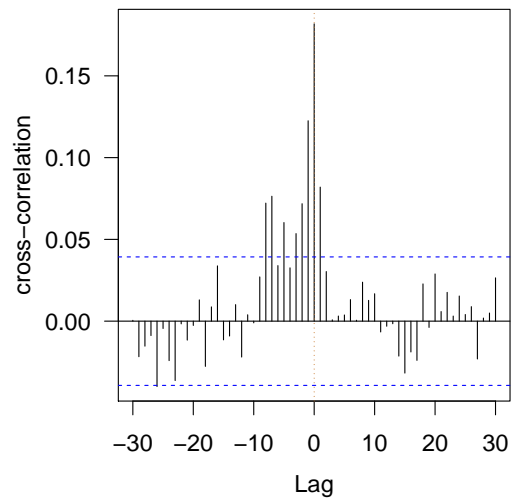
(a) total number of kids vs. total number of adults



(b) kids scanning vs. adults scanning, binomial



(c) total number of kids scanning/max vs. total number of adults scanning/max



(d) total number of kids scanning/kids_max vs. total number of adults scanning/adult_max

Figure 3.5: Cross-correlation function with different scales, all showing the synchronization of kid scanning behaviour with that of adults.

4 Discussion

The first part of the analysis (part A) revealed that there is no interspecific difference in the vigilance behaviour of ibex and chamois kids. A reason for this can be seen in the high similarities of both species. Not only do they use similar habitats, which are - at least in this study area - almost free of predators, but they also show accordances in aspects like body size, general behaviour - like for example gregariousness - and annual life cycle [Mustoni et al., 2002]. Concerning the vigilance behaviour of kids, I assume the predation aspect mentioned above to be the only one in which a change might occur and consequently lead to an interspecific difference in kids' vigilance behaviour. Although wolves were present in the area until about two years ago, the neonates of 2015 never experienced a predation event by wolves. This does not mean that the overall vigilance behaviour of both populations might not still be characterized by the former presence of wolves. However, as there is no literature available that would allow a comparison of the vigilance behaviour before, during and after the presence of the wolf pack, no further conclusions can be drawn here. Concerning the other predators present, their importance seems to be negligible. During 165 group observations and 327 observations of focal kids, not a single sighting of aerial predators such as Golden Eagle occurred. Once a single fox was observed crossing the bottom of the valley, not causing any considerable reactions in the chamois group that used higher elevations of the same slope. If predation risk varied within the study area, this might lead to an interspecific difference in kids vigilance behaviour. In case that the wolves should return to Valsavarenche, it would be interesting to investigate their influence and compare the results with those of the present study.

The summaries of both GAM used in part A show a highly significant effect of day, thus of the course of the season, on kid scanning behaviour (model 1: p -value=0.0028, model 2: p -value=0.0030). A closer look at the model plots reveals that despite the low p -value, there is neither a clear trend nor a repetitive pattern (see figure A.2). The seemingly significant influence results from high environmental noise. Due to the random character of this confounding factor, it was not presented in the results section. Another interesting pattern occurs in the temperature plot, which is characterized by lower scanning in the intermediate temperature range (see figure A.3). Although this does not concern one of the questions set up initially, I checked for a possible explanation of this pattern. A GAM including the percent of time focal individuals spent feeding and `temPont` revealed that kids feed more at intermediate temperatures. Thus, the

pattern of the temperature plot can be explained by the fact that kids do not feel urged to feed at extreme temperatures and therefore spend more time scanning.

Kids' scanning behaviour has shown to be highly affected by the distance to hiking trails (model 1: p -value=0.0026, model 2: p -value=0.0066). Hikers and other people who visit Levionaz usually stick to the hiking trails. Thus, those can be seen as a proxy for human disturbance. Whether kids perceive humans just as 'something new' and therefore show increasing curiosity or whether they categorize them as a source of danger can only be speculated. Interestingly, this effect seems to vanish with age - it could not be detected for scanning behaviour of adults in part B. This indicates a habituation of adult animals to antropogenic disturbances. Habituation of ungulates to human disturbances has been observed in a number of species, among those also ibex [Ruckstuhl and Neuhaus, 2001, Tadesse and Kotler, 2012] and chamois [Hamr, 1988, Bruno and Lovari, 1989]. However, being habituated to human disturbances does by far not mean staying unaffected by them. Several studies could show that human disturbances cause further reactions in habituated populations, too [Tadesse and Kotler, 2012]. Although adults of the ibex population studied here seem to be, according to my results, habituated to human presence, they seem to be well aware of human disturbances: Grignolio et al. [2007a] could show that females with kids are use areas close to hiking trails less frequently than females without kids.

Besides the influences of different environmental aspects on kids' scanning behaviour, it could be shown that kids decrease scanning with increasing group size (see figure 3.4). Thus, the suggested group size effect is confirmed by the data for both scanning percent and scanning frequency. The more individuals there are in the group, the higher the dilution and thus the lower the probability of being killed for the individuum [Dehn, 1990]. Regarding my results and the theory of the dilution effect, one could state that a kid in a large group experiences lower predation probability and is therefore less vigilant. However, one fact going beyond the dilution effect should be considered here: Ungulate mothers are known to protect and defend their kids actively in case of an attack [Berger, 1978, Mustoni et al., 2002, Bertolino, 2003, Hamel and Côté, 2009]. This might enhance the feeling of safety in large groups for vulnerable kids. The hypothesis that kids perceive the group as a relatively safe surrounding is also supported by the finding that kids do not reflect the fear of the group. Thus, even if adults increase their level of vigilance, kids do not adopt their behaviour, maybe because they feel well protected in the group. Adults however do not have a comparable requirement for protection. Although grouping is an essential element of their behaviour, no group size effect could be found on adults' vigilance behaviour in part B of the analysis. This is in accordance with the findings for Nubian ibex and Pyrenean chamois [Tadesse and Kotler, 2012, Dalmau et al., 2010]. Tadesse and Kotler [2012], who investigated Nubian ibex in a national park, suggest low predation pressure as a reason for the non existing group size effect. Alados [1985] differentiated between weak and active watching and could find a group size effect only for active watching in Spanish ibex. Xu et al. [2010] investigated Asiatic ibex, for which he could find a group size effect concerning the group scan level. Contradictory

to my results, Xu et al. [2010] could not find a group size effect on scanning frequency. It should be considered here that terms such as 'group scan level' are no fixed terms, but can be defined in different ways. Xu et al. [2010] for example defined the 'group scan frequency' as the percentage of intervals during which at least one ibex was scanning, whereas I used a very similar definition for the 'group vigilance', corresponding to Childress and Lung [2003].

At the first glance, the finding that kid scanning behaviour decreases with an increasing number of adults but increases with an increasing number of kids seems rather contradictory. It can be assumed that in a group with more adult females also more mothers occur and thus more kids. However, this seemingly contradictory effect might reflect the different functions of vigilance. The decreasing vigilance of kids in a large group can be explained by a 'feeling of safety' and thus stresses the importance of vigilance as antipredator behaviour in kids. The effect of the group size (model 1: $p\text{-value} < 0.0001$, model 2: $p\text{-value} = 0.0255$) is much stronger than the effect of the maximum number of kids in the group (model 1: $p\text{-value} = 0.0251$, model 2: $p\text{-value} = 0.3083$). Still, the fact that vigilance increases with a higher number of kids indicates that especially for kids, vigilance seems to serve as an important social behaviour. The more kids there are, the more coordination with even-aged conspecifics is required. Scanning the surroundings is not only important for detecting potential threats, but rather for orientation and identification of possible playmates. Byers [1980] stressed the important role of playing for the development of Siberian ibex kids. He found male kids to play much more among themselves than with female kids, indicating a possible training effect for later hierarchical fights. Even small ibex kids can be observed using the same postures in play that adults use in agonistic behaviour [Byers, 1980]. Hence, scanning to identify possible playmates is more than just 'harmless distraction', but can support a process which later on leads to an improvement of social position and can enhance lifetime reproductive success. Note that the focus of this study was not set specifically on different functions of vigilance, but rather on vigilance behaviour in general. To investigate vigilance more in detail, further research with an adapted study design would be necessary. To address the coordination with playmates specifically, it could be useful to redefine the category of social behaviour into several social behaviour types.

According to the heretofore discussed results, vigilance in kids is not only important as antipredator behaviour, but it also serves a social function. Part B of the analysis could show that kids are more vigilant than adults, which seems to be in accordance with the first results. In some literature, it is stated that a higher vigilance in kids could be assumed due to their high vulnerability and thereby increased predation risk [Caro, 2005, Lung and Childress, 2007]. Burger and Gochfeld [1994] stress the additional risk of being separated from the mother, which can lead to starvation or predation. However, a higher vigilance in young animals could only be found in few papers, such as by Holmes [1984] for hoary marmots. There are more papers that did not find a higher vigilance in kids (for overview see [Arenz and Leger, 2000, Beauchamp, 2015]). Regarding this, it should be considered that many studies did not set their focus on vigilance behaviour in

newborns, but rather on adults compared to young in general. I think it possible that the vigilance behaviour of newborns compared to that of yearlings varies significantly. Yearlings have more experience, another social status, generally not a tight bond to the mother any longer etc. In further studies, the sex and age classes should probably be considered in more detail. Here, I only differentiated roughly between newborn kids and adults, taking neither age nor sex into account in more detail, a concept which could obviously be refined.

Besides showing a higher vigilance in kids, the final model in part B gave two further results. With regard to habitat types, animals scan more in the rocks than in the grass. Initially, I assumed that animals might scan more in grassland areas. Those are usually more open, which makes it easier for predators to attack their prey. The fact that predators cannot follow them is the reason why both species use especially steep, rocky terrain as escape areas [Kohlmann et al., 1996, Ruckstuhl and Neuhaus, 2001, Dalmau et al., 2010]. In open areas, it is not only easier for predators to detect their prey, but also the other way round. Hence, more scanning might enhance the probability of detecting a predator. However, instead of scanning a lot in grassland and feeling safe in rocky areas, animals show higher vigilance in the rocks. How can this be explained? One reason might be the low predation pressure already mentioned above. Besides, it should be kept in mind that for this study, groups consisting of mainly females and kids were observed. Despite the fact that both species are highly adapted to their alpine habitat [Mustoni et al., 2002], it can be challenging to move along rocks and cliffs, especially for the kids. On the one hand, they do not have much life experience yet. On the other hand they are considerably smaller than adults and thus not able to run as fast and jump as far. Kids face a higher risk of getting injured by falling [Byers, 1977]. Thus, the enhanced vigilance in the rocks can be explained as follows: both age classes, kids and adults, show a higher need to coordinate with the rest of the group. Mothers and kids make sure more often that they are keeping up with each other. Besides, additional time is probably spent being vigilant due to the other purposes described earlier in this discussion, too.

Interestingly, there is also a difference in scanning behaviour between dawn and dusk. This matches with the findings of Alados [1985] for Spanish ibex. Despite his finding, Alados does not suggest an explanation for higher vigilance in the morning. Conversely, Matson et al. [2005] found that impalas show higher vigilance at dusk and suggest this may be due to an increase in nervousity towards the evening, which is the time of day where most predation occurs. However, a similar explanation is not reasonable in the context of my study due to the lack of predators. It is possible that the difference between dawn and dusk which was observed here is due to some factor or an interaction of factors that were not included in the study. Such factors could for example be affected by wind, precipitation or food availability, which have all been found to affect vigilance in previous studies [Beauchamp, 2015].

To figure out if kids learn to be vigilant by copying the behaviour of their mothers and other adults in the group, scanning data was analyzed with a cross-correlation function in part C of

the analysis. This showed that kids mainly synchronize their scanning behaviour with that of adults (see figure 3.5). The second strongest correlation occurred at a time lag of minus one, indicating that kids scan mainly simultaneously with adults or one minute after them. This result seems inconsistent with the finding that kids do not reflect the fear of the group. If they synchronize their scanning behaviour with adults, this should clearly be the case. The results of the cross-correlation function are based on the group observation data. The group observations were conducted in one minute intervals over a approximately 15 minutes. It might be that the results of this part are misleading, considering that quite a lot of activity might be going on in the time between two 'snapshots'. To investigate a possible learning effect in more detail and to come to more meaningful results, I suggest using shorter intervals or video recording. Initially, shorter intervals were planned for this study, but implementation in the field was complicated, especially for large groups. Thus, intervals were prolonged. Video recording would avoid such problems, as posterior analysis is possible. A number of authors have used this method in studies of vigilance behaviour successfully (see for example [Pays et al., 2007, 2010, 2012, Blanchard et al., 2008]).

5 Conclusion

The present study aimed to investigate the effects of several environmental and social factors on Alpine ibex and Alpine chamois kid vigilance behaviour. It was found that a group size effect on kid vigilance behaviour exists. No group size effect was found when I looked at both adult and kid scanning behaviour. Kid vigilance behaviour is highly affected by the distance to hiking trails and thus human disturbance. This effect does not exist for the adults of the group. Concerning the fear of the group, kids do not reflect it in their own behaviour, but slightly increase their vigilance when the number of kids in the group increases, probably due to curiosity. In general, kids scan more than adults. It was also found that animals increase their vigilance in rocky terrain and early in the morning. Kids synchronize their scanning behaviour with that of adults, which indicates a learning effect. However, this aspect could be reinvestigated using a refined methodological approach. Although vigilance behaviour in free-ranging animals has been studied quite intensely in the last decades, vigilance behaviour of kids has not been well investigated by scientific research yet. The focus of this study on vigilance behaviour of free-ranging ungulate kids is innovative. To understand better which factors affect animal kids' vigilance behaviour and to what extent, further research would be necessary. Besides focusing on the influencing factors, the various functions of vigilance should be investigated in more detail, too. Although vigilance is generally believed to be mainly antipredator behaviour, this might be different for kids. The results of my study indicate that there might be a higher proportion of social monitoring vigilance in kids than in adults. In this context, social relationships could be taken into account in further studies as well. Enhancing the knowledge about kid behaviour would probably allow predictions about their development. This could be an interesting additive aspect for example in life history research. Thus, the field of kid behaviour offers a range of open questions for further research.

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A Appendix

Table A.1: Model selection process for model 1, part A.

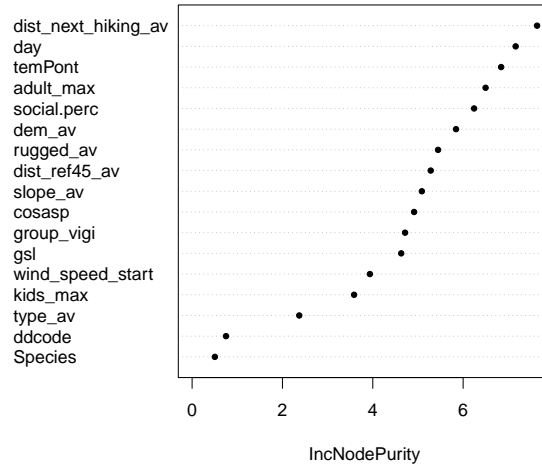
	MODEL FORMULA	AIC
1	gam0.3 <- gam(scanper_boxcox ~ s(dist_next_hiking_av) + s(temPont) + s(day) + s(social.perc) + s(log(adult_max)) + s(dem_av) + s(dist_ref45_av) + s(cosasp) + group_vigi + I(group_vigi2) + s(wind_speed_start) + s(log(kids_max)) + s(Group.ID, bs="re"), data=kids, weights = total.time.sec)	473.8228
2	gam1.8 <- gam(scanper_boxcox ~ s(dist_next_hiking_av) + s(temPont) + s(day) + s(social.perc) + s(log(adult_max)) + s(dem_av) + s(dist_ref45_av) + group_vigi + I(group_vigi2) + s(wind_speed_start) + s(log(kids_max)) + s(Group.ID, bs="re"), data=kids, weights = total.time.sec)	472.0354
3	gam2.6 <- gam(scanper_boxcox ~ s(dist_next_hiking_av) + s(temPont) + s(day) + s(social.perc) + s(log(adult_max)) + s(dist_ref45_av) + group_vigi + I(group_vigi2) + s(wind_speed_start) + s(log(kids_max)) + s(Group.ID, bs="re"), data=kids, weights = total.time.sec)	469.7168
4	gam3.7 <- gam(scanper_boxcox ~ s(dist_next_hiking_av) + s(temPont) + s(day) + s(social.perc) + s(log(adult_max)) + s(dist_ref45_av) + group_vigi + s(wind_speed_start) + s(log(kids_max)) + s(Group.ID, bs="re"), data=kids, weights = total.time.sec)	469.6828
	final model (referred to as 'model 1')	
5	gam4.7 <- gam(scanper_boxcox ~ s(dist_next_hiking_av) + s(temPont) + s(day) + s(social.perc) + s(log(adult_max)) + s(dist_ref45_av) + s(wind_speed_start) + s(log(kids_max)) + s(Group.ID, bs="re"), data=kids, weights = total.time.sec)	469.1724

Table A.2: Model selection process for model 2, part A.

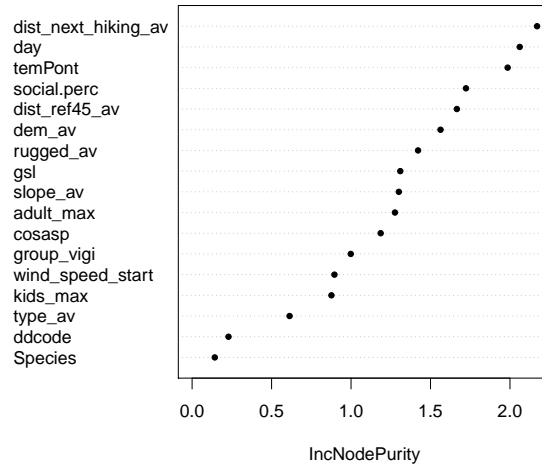
	MODEL FORMULA	AIC
1	gam0.10 <- gam(scanfr_boxcox ~ s(dist_next_hiking_av) + s(temPont) + s(day) + s(social.perc) + s(log(adult_max)) + s(dem_av) + s(slope_av) + s(cosasp) + gsl + I(gsl2) + s(wind_speed_start) + s(log(kids_max)) + s(Group.ID, bs="re"), data=kids, weights = total.time.sec)	26.29586
2	gam1.8 <- gam(scanfr_boxcox ~ s(dist_next_hiking_av) + s(temPont) + s(day) + s(social.perc) + s(log(adult_max)) + s(dem_av) + s(slope_av) + gsl + I(gsl2) + s(wind_speed_start) + s(log(kids_max)) + s(Group.ID, bs="re"), data=kids, weights = total.time.sec)	24.74907
3	gam2.6 <- gam(scanfr_boxcox ~ s(dist_next_hiking_av) + s(temPont) + s(day) + s(social.perc) + s(log(adult_max)) + s(slope_av) + gsl + I(gsl2) + s(wind_speed_start) + s(log(kids_max)) + s(Group.ID, bs="re"), data=kids, weights = total.time.sec)	23.55720
4	gam3.7 <- gam(scanfr_boxcox ~ s(dist_next_hiking_av) + s(temPont) + s(day) + s(social.perc) + s(log(adult_max)) + s(slope_av) + gsl + s(wind_speed_start) + s(log(kids_max)) + s(Group.ID, bs="re"), data=kids, weights = total.time.sec)	22.63305
	final model (referred to as 'model 2')	
5	gam4.7 <- gam(scanfr_boxcox ~ s(dist_next_hiking_av) + s(temPont) + s(day) + s(social.perc) + s(log(adult_max)) + s(slope_av) + s(wind_speed_start) + s(log(kids_max)) + s(Group.ID, bs="re"), data=kids, weights = total.time.sec)	21.45856

Table A.3: Model selection process in part B.

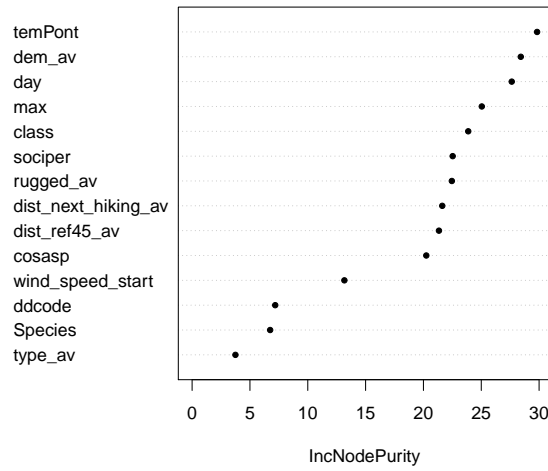
	MODEL FORMULA	AIC
1	m0.1 <- gamm(scanper_boxcox ~ type_av + s(dist_next_hiking_av) + s(dist_ref45_av) + ddcode + class + s(wind_speed_start) + s(sociper) + s(day) + s(cosasp) + s(temPont) + s(max) + s(groupid, bs="re"), data = groupnew, weights=mystructure)	975.5019
2	m1.10 <- gamm(scanper_boxcox ~ type_av + s(dist_next_hiking_av) + s(dist_ref45_av) + ddcode + class + s(wind_speed_start) + s(sociper) + s(day) + s(cosasp) + s(max) + s(groupid, bs="re"), data = groupnew, weights=mystructure)	971.5183
3	m2.6 <- gamm(scanper_boxcox ~ type_av + s(dist_next_hiking_av) + s(dist_ref45_av) + ddcode + class + s(sociper) + s(day) + s(cosasp) + s(max) + s(groupid, bs="re"), data = groupnew, weights=mystructure)	968.1944
4	m3.3 <- gamm(scanper_boxcox ~ type_av + s(dist_next_hiking_av) + ddcode + class + s(sociper) + s(day) + s(cosasp) + s(max) + s(groupid, bs="re"), data = groupnew, weights=mystructure)	964.8262
5	m4.7 <- gamm(scanper_boxcox ~ type_av + s(dist_next_hiking_av) + ddcode + class + s(sociper) + s(day) + s(max) + s(groupid, bs="re"), data = groupnew, weights=mystructure)	961.6442
6	m5.5 <- gamm(scanper_boxcox ~ type_av + s(dist_next_hiking_av) + ddcode + class + s(day) + s(max) + s(groupid, bs="re"), data = groupnew, weights=mystructure)	958.2866
7	m6.5 <- gamm(scanper_boxcox ~ type_av + s(dist_next_hiking_av) + ddcode + class + s(max) + s(groupid, bs="re"), data = groupnew, weights=mystructure)	956.1528
8	m7.2 <- gamm(scanper_boxcox ~ type_av + ddcode + class + s(max) + s(groupid, bs="re"), data = groupnew, weights=mystructure)	955.1828
final model		
9	m8.4 <- gamm(scanper_boxcox ~ type_av + ddcode + class + s(groupid, bs="re"), data = groupnew, weights=mystructure)	954.7175



(a) Variable importance plot for model 1, part A.

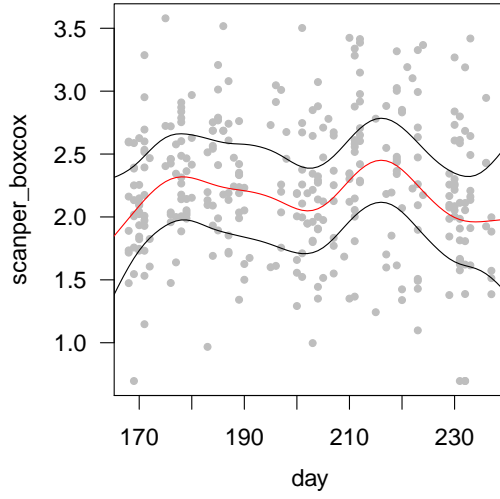


(b) Variable importance plot for model 2, part A.

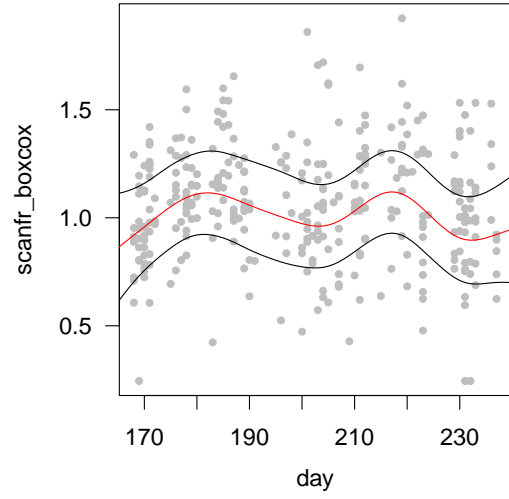


(c) Random forest variable importance plot for part B.

Figure A.1: Random forest variable importance plots for the models used in part A and B.

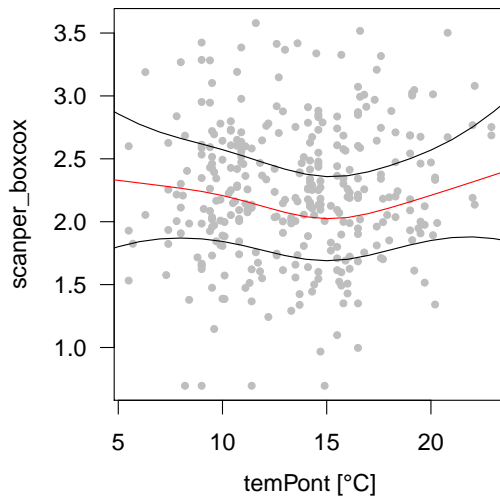


(a) Prediction plot for day in model 1, part A.

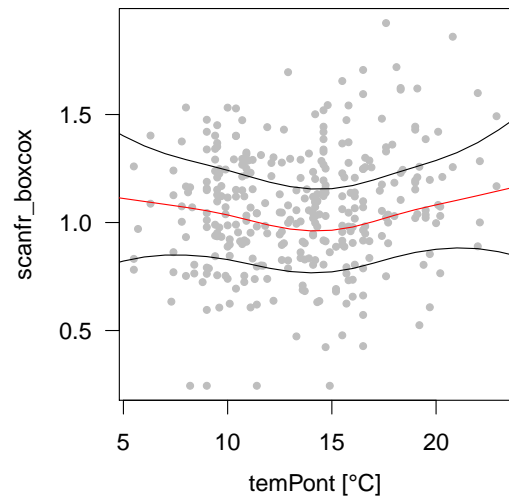


(b) Prediction plot for day in model 2, part A.

Figure A.2: Effect of the course of the season on kid scanning behaviour in part A.

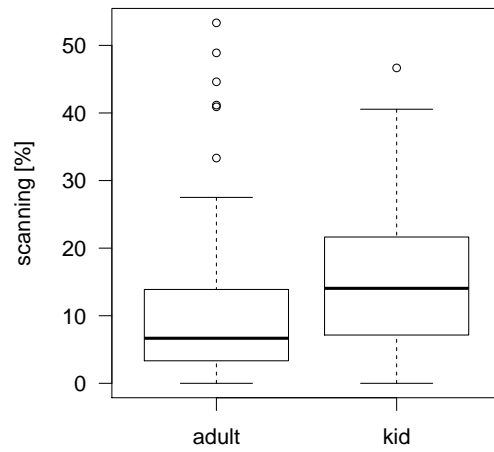


(a) Prediction plot for temperature in model 1, part A.

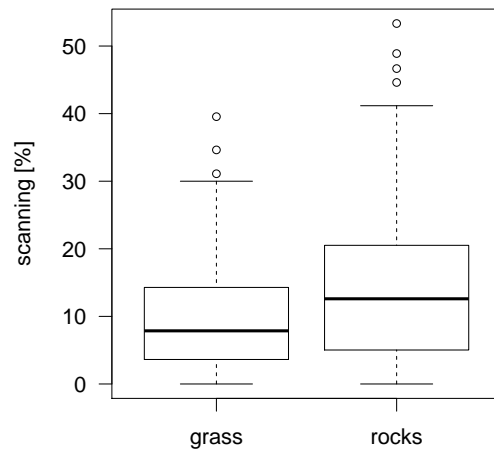


(b) Prediction plot for temperature in model 2, part A.

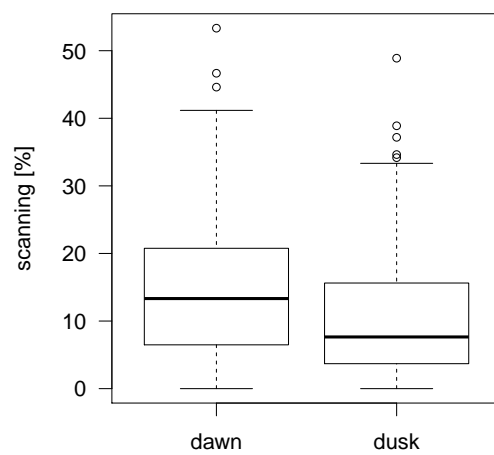
Figure A.3: Effect of temperature on kid scanning behaviour in part A.



(a) Percentage of animals scanning vs. age class.



(b) Percentage of animals scanning vs. habitat types.



(c) Percentage of animals scanning vs. time of the day.

Figure A.4: Significant variables plotted against average percentage of animals scanning using raw data.

Declaration of Authorship

I hereby declare that I have composed this thesis unassistedly and that I only used the sources and devices I declared. Passages taken verbatim or in meaning from other sources are identified as such and the sources are acknowledged and cited. Furthermore, I declare that neither this thesis nor any part of it have been subject to a previous examination procedure.

Freiburg, December 10th, 2015