





## **Acknowledgements**

This master thesis was written at the Department of Ecology and Natural Resource Management and completes my master`s program at Norwegian University of Life Sciences (NMBU).

First I would like to thank my supervisor Leif Egil Loe (NMBU) for all guidance the last year and for giving me the opportunity to write this master thesis. A special thank you to PhD-student Karen Lone for a memorable fieldwork, helping me with the statistic analyzes, answering my many questions and of course the trip to the Nordic Oikos meeting. Thank you to Erling Meisingset at Bioforsk for letting me use the GPS data from the “Hjortemerke” project and making all practical arrangements during the fieldwork. Øystein and Marius at Bioforsk also deserve a thank you for helping with the fieldwork. Also thank you to Atle Mysterud at UiO for economic support during the field work.

To my friends at the study hall, a great thank you for the company and conversations, you have made the two years her at Ås a memory for life. Synnøve, Runar, Jenny and Astrid, thank you for keeping my spirit up! Last but not least thank you to my roommates Ragnhild and Zuba, for always being positive and enthusiastic.

Ås 13.05.2014

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## **Abstract**

The purpose of this study was to test if red deer (*Cervus elaphus*) habitat use affects their risk of being shot by hunters. I compared habitat use of 20 GPS-marked red deer that survived the hunting season with 20 individuals that were shot. I predicted that shot red deer used open areas within forested habitats with a better visibility for hunters than surviving red deer. I also predicted that the use of less risky habitat is costly in terms of foraging opportunity, with shot animals using better foraging habitat than the surviving animals. In the variables we measured I also predicted that there would be sex differences.

I measured small-scale habitat variables (cover and forage availability) in field. Large-scale habitat variables (elevation, slope, distance to roads and pastures) were extracted from geographic information system (ArcGIS). The dataset was analyzed by using mixed models in R.

I did not find support for our hypothesis as there were no differences between surviving and shot red deer regarding use of fine-scale habitat. In the large-scale variables I did see that the different groups followed the same pattern in the four variables. I speculate if the large-scale habitat use, such as seasonal migration and individual differences in behavioral response to hunters (vigilance) may affect the probability of being shot.

My conclusion is that the similar use of habitat by shot and surviving deer may suggest that differential habitat use might not be a suitable strategy to avoid hunters. This may be due to the overall high hunting pressure in the whole terrain, the probability of being shot is high regardless of what parts of the habitat the animals use.

## Sammendrag

Formålet med studien var å undersøke om hjortens (*Cervus elaphus*) bruk av habitatet påvirker dens sjans for å bli skutt av jegere. Jeg kombinerte den individuelle bruken av habitat til 40 GPS-merkede hjort med overlevelsen gjennom jaktseasonen. Studien tok utgangspunkt i at skutte hjort ville bruke åpne områder innenfor skogshabitater med bedre synlighet for jegere enn overlevende hjort. Jeg predikterte også at bruken av lav risiko områder ville være kostnadskrevenende i forhold til kvaliteten på fôr, ved at skutte dyr ville bruke bedre fôrhabitat enn de overlevende dyra. I tillegg predikterte jeg at det ville være forskjeller mellom kjønnene. Jeg målte småskala habitat variabler i felt. Storskala habitat variabler ble hentet fra geografiske informasjonssystemer. Datasettet ble analysert ved å bruke mixed models i R.

Jeg fant ingen støtte for prediksjonene våre, da det ikke var noen forskjeller mellom skutt og overlevd hjort tilknyttet småskala habitatbruk. I storskala habitat bruk så jeg at gruppene fulgte samme mønster i alle de fire variablene. Storskala habitat bruk, slik som sesongavhengig migrasjonsmønster og individuelle forskjeller i adferd ovenfor jegere (årvåkenhet) kan påvirke sjansen for å bli skutt.

Jeg konkluderer med at den lignende bruken av habitatet for skutt og overlevende hjort kan antyde at ulik bruk av habitat ikke er en passende strategi for å unngå jegere. Dette skyldes trolig det høye jaktpresset i området, som gjør at sjansen for å bli skutt er høy uansett hvilken del av habitatet dyra bruker.



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## **1. Introduction**

The habitat selection is an important part of red deer ecology. When the animals select habitat they consider different variables, forage quality and availability, degree of cover and potential predators (Godvik et al. 2009). Other factors that also affect the habitat selection is the animals` sex, age and daily activity (Myrsterud & Østby 1999). Since not all habitat types necessarily contain a sufficient mixture of all the variables, the animals have to do trade-offs between cost and benefits when selecting the right habitat (Lima and Dill 1990; Orians and Wittenberger 1991; Myrsterud and Ims 1998). Often the animals have to choose between open habitats with good foraging where they are visible to predators and habitats that provide more cover from weather and potential dangers. (Sih 1980; Werner et al. 1983; Demarchi & Bunnell 1995; Myrsterud & Østbye 1999; Godvik et al. 2009). These trade-offs vary between seasons, time of day and weather conditions. Optimal foraging theory predicts that animals should select forage locations in a way that maximizes their energetic benefits (MacArthur & Pianka 1966; Charnov 1976), but that also takes into consideration the risk of predation (Lima & Dill 1990; Brown & Kotler 2004). The red deer often prefer habitats with more cover when bedding than foraging (Myrsterud & Ims 1998). The duration of bedding also have an effect, the longer bedding time the more cover the animal wish. The deer often chooses more open habitat with good forage quality in the night, while they prefer habitats with more cover and often poorer food quality during daytime (Beier and McCullough 1990; Godvik et al. 2009; Bjørneraas et al. 2011).

Individuals tackle the trade-off between food and predation risk differently (Wilson et al. 1993), and this may be an expression of differences in personality. In many species individuals differ in the degree of activity, reaction to unexpected incidents and sociability. Animal personality can be defined as behavior tendencies that affect behavior in different contexts, vary across individuals in a given population and are consistent within individuals across time (Sih et al. 2004). These personality traits characterize behavioral trait and explain the concept of “shy” and “bold” individuals, also known as the shy-bold continuum. The shy-bold continuum derived from such metrics can characterize generally how an individual responds to risk-taking and novelty (Rèale et al. 2000; Brick & Jakobsson 2002). Especially the term boldness has been measured among different species of birds, mammals and fish (Biro & Stamps. 2008). Individuals with a shy personality react to unexpected situations by running or hiding. Bold individuals do not change their behavior or become exploratory when



confronted to the same situations (Wilson et al. 1993). Traits such as boldness and activity are often related to mortality risks (Biro & Stamps 2008).

One of the animals' behavioral responses to reduce predation risk is to change the habitat use (Creel et al. 2005). A study by Acebes et al (2013) found that guanaco (*Lama guanaco*) occupied areas offering the minimum productivity capable of meeting their energy requirements to reduce predation risk. Several studies have shown that elk respond to the risk of predation by wolves by increasing vigilance levels (Laundre et al. 2001) or shifting to safer habitat use temporally (Creel et al. 2005; Blumstein & Daniel 2002).

The environment and natural selection changes and shape the phenotypic traits of populations and among these humans is a dominant evolutionary force (Palumbi 2001). Studies have shown that humans might influence on the phenotypes and cause more rapid changes in populations and ecological dynamics (Yoshida et al. 2003; Fussmann et al. 2007; Hendry et al. 2008). Humans can generate these changes faster by harvesting different age- and size-classes than natural predators (Law 2000; Fenberg & Roy 2008), and in this way change both morphological and life-history traits in harvested populations. In a Canadian study researchers tested if elk (*Cervus elaphus*) shot by hunters had less favorable behaviors than the surviving elk (Ciuti et al. 2012). They predicted that the elk, depending on individual personality traits could adopt anti-predator behavioral strategies in response to human hunters. The results showed that harvested individuals had a more bold behavior with a more frequent use of open terrain than the surviving elk (Ciuti et al. 2012). It is not clear if individual variation in selection of cover will have a similarly strong effect in populations with very high harvest rates and hunting in all terrain types.

In polygynous ungulates males are generally more risk prone than females (Langvatn & Loison 1999). To achieve a high fitness they must obtain a high body mass in order to outcompete other males (Clutton-Brock et al. 1982). Males may therefore be expected to choose food-rich areas despite that they may have a higher risk of mortality to a larger degree than females, where successful breeding is less dependent of size. This might give females more room for individual variation in habitat selection along a risk-prone to shy continuum, than males who all need to take risk to obtain maximum size (Clutton-Brock et al. 1982). On the other hand, males are also the sex most intensively harvested and where superior contestants are to a highest degree removed by hunters (Langvatn & Loison 1999). Shy individuals with initially lower body growth might find themselves on the top of the rank

hierarchy if they manage to survive longer than risk prone competitors. Sex-dependent selection of risk-prone versus shy personalities is therefore predicted to be strongly context dependent, in particular shaped by the intensity and spatial variation in hunting pressure.

Norwegian red deer is intensively harvested and is the major source of mortality (Langvatn & Loison, 1999). The number of shot red deer has increased substantially the last years. In 2013 the number of shot red deer was 36 141 (Statistics Norway, 2014). About nine out of ten red deer will eventually die from a bullet (Meisingset, 2009). The hunting success of hunters is likely highest in open areas with a good view of the landscape. This means that open habitats such as pastures and young clearcuts are landscape types the red deer have the highest probability of getting shot. A study shows that 49 % of the red deer harvested in the county was shot on pastures and arable land. The rest of the animals (51 %) are harvested in other terrain types, such as forest, moorland and mountain areas (Andestad, 2004). Males have a higher probability of getting shot compared to females (Langvatn and Loison, 1999). A study by Langvatn and Loison (1999) found that males had less than a 10 % chance of reaching 4.5 years of age, no such trend was detected for females.

Here I investigate using GPS-data on 40 red deer if we can discriminate the habitat use of individuals surviving the hunting season ( $n = 20$ ) and individuals that were shot ( $n = 20$ ). I test the following hypotheses:

1. Differences between the individuals use of cover habitat affects the probability of being shot during the hunting season. Under this hypothesis I predict that surviving animals have a higher use of cover habitats than shot animals.
2. The surviving animals use less good foraging habitat during the hunting season than the shot animals. The use of less risky habitat is costly in terms of foraging opportunity. I predict that if there is a risk reduction the use of good foraging habitat is greater among the shot animals than the surviving.
3. There are differences between the sexes. I predict that males will use less dense cover habitat than females.

## 2. Material and methods

### 2.1 Study area

The fieldwork of this study was carried out in 7 municipalities in Møre og Romsdal and Sør-Trøndelag counties (decimal degrees = N 62.15-63.59; E 6.82-10.69). Study area included the following municipalities: Tingvoll, Halså, Aure, Sunndal, Surnadal, Rindal, Orkdal (Figure 1). The total study area is 5879 km<sup>2</sup> and covered areas from coast to inland. The topography is diverse, with high mountains, valleys and fjords. Areas with agriculture are situated in the flat areas in the bottom of the valleys, mostly as pastures and meadows for grass production. Natural forest was dominated by deciduous (Common species: *Betula spp*, *Salix caprea*, *Alnus* and *Sorbus aucuparia*) and pine forest (*Pinus sylvestris*). Dense plantations of Norway spruce (*Picea abies*), occur scattered across the whole study area. Yearly precipitation is 1000-2000 mm. July and August are the warmest summer months, with a mean temperature of 14°C in both Møre- og Romsdal and Sør-Trøndelag (Dannevig, 2009a; Dannevig, 2009b). Precipitation and temperature decrease from coast to inland areas (Mysterud et al. 2000).



**Figure 1:** Study area, black circles are the field points.

## 2.2 Study species

Red deer is the most common ungulate on the west-coast of Norway (Hjeljord, 2008). The red deer population in this area is a partially migrating population. About 58 % of the marked red deer in Møre- og Romsdal and Sør-Trøndelag migrate between summer and winter habitat (Meisingset et al. 2011). Most of these migrate from winter habitat close to the sea to the summer habitat in the mountains at higher elevations. The seasonal migration is food driven and linked to the delay in plant phenology, with increasing elevation (Bischof et al. 2012). The summer diet it seem that grass is the most important, while heather (*Calluna vulgaris*) and juniper (*Juniperus communis*), shot growth from rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), sallow (*Salix caprea*) (the RAW species) and spruce (*Picea abies*) is important in the diet in autumn and winter (Solberg et al. 2011). The highest activity level is in the night and in the hours of dusk. Last week of April or first week of May is usually the weeks the animals start the migration to the summer areas. The animals use about 10 days on the distance. Most of the animals start the migration back to the winter habitat close to the fjords around the middle of September. The animals use somewhat shorter time on this distance, about seven days (Meisingset et al. 2011). Because of the low populations of large predators in west- and middle Norway, the red deer's main predator is humans (Loison and Langvatn, 1999).

## 2.3 Hunting regime

In Norway the red deer is utilized as game specie and the management is directed towards meat hunting (Milner et al. 2006). The red deer populations have been managed through the use of population plans. The population plans are suppose to contain a goal for the yearly harvest, with a description of the number and proportion of each sex and age category of animals proposed to be harvested during the period of the plan (Olaussen and Mysterud, 2012). The quotas are age and sex specific. Hunting season starts on 1<sup>st</sup> of September and last until 23 December (Klima- og miljødepartementet, 2012). Hunting is performed in all parts of the red deers habitat and since the animals often use pastures for grazing in night time, many of animals are shot here. Hunting on these types of habitats is preferred by the hunters because it's a more predictable and safer way to perform hunting (Andestad, 2004). The animals are calmer and it's possible for the hunters to build hunting towers and measure the shooting distance and in this way reduce the risk of shots that miss or wound the animal (Andestad 2004). One common hunting method is sit-and wait hunting close to meadows, pastures and known migrating tracks. This form of hunting is mostly performed in the hours of dusk in late afternoon – evening, in early morning or during night (in moonlight). Drive

hunting (with and without dog), stalking and call hunting are also common in use. Often a combination of these methods is used (Meisingset, 2009). Drive hunting is mostly used in the weekends, and when hunters have time off work. Stalking and sit-and-wait hunting is more often used when hunters go out alone and in the week time (Mon-Friday). What type of hunt is also determined of the topography of the landscape and weather conditions.

## **2.4 Study design**

This study was based on data from 2007-2012 from 40 GPS-marked red deer with a known fate after at least one hunting season. Ten surviving and ten shot deer of each sex were selected within the same geographical area to have equal sample sizes. The animals were darted and marked with ear tags and GPS collars at feeding sites spread across the municipalities in the counties Møre- og Romsdal and Sør-Trøndelag (Meisingset et al. 2011). This marking was done as a part of the red deer marking project started by Bioforsk Tingvoll. The collars were of the type Tellus T5H GPS basic with a GSM from Followit AB ([www.followit.se/wildlife](http://www.followit.se/wildlife)), and were programmed to record positions with given time intervals.

For each of the 40 individuals we did field registrations at 10-12 different GPS-points, obtained in the same autumn as the animal either was shot or survived. I selected two positions per animal per day. One shortly after sunrise and one shortly before sunset (the closest in time within the time interval: 0.5 hrs before/after and 3.5 hrs after/before). At this time I expected animals to be active, and the light levels sufficient for exposure to hunting. Field plot locations were selected for two time periods, before hunt (last Monday-Wednesday before hunt starts) and 1<sup>st</sup> week (first Monday-Wednesday after first hunting weekend) into the hunting season. Positions in pastures were excluded in order to look only at within-forest variation in habitat selection. Hunting season started on 10<sup>th</sup> September 2007-2011, and on the 1<sup>st</sup> of September in 2012 (one individual from 2012).

The individuals in this study were classified as stationary or migratory based on the Net squared displacement (NSD) pattern. NSD combines characteristics from animal movement trajectories, and is used to estimate the temporal pattern of movements from a site of origin. The NSD measures the straight line distance between the starting location and the following locations for the movement path of a given individual (Bunnefeld et al. 2011). At the winter sites it's expected that the NSD of a given migratory animal is stable, and that the NSD will increase when the spring migration starts. When the animal reach the summer ranges, the

NSD will stabilize, and decrease and reach low levels as the animal migrate and reach the winter ranges (Bunnefeld et al. 2011). For details on the application of the method to the red deer GPS data, see Mysterud et al. 2011.

## **2.5 Methods in field**

Field registrations were done between 18 June and 20 August 2013. To be able to find the GPS-points, I used a GPS (Garmin 62s). On each site I did the following measurements.

**Cover board:** By using a cover board I measured the horizontal visual cover. The cover board was 30 cm wide and 80 cm tall, with four height segments, corresponding to the deer in the terrain (L1: body lying down, L2: head lying down, H1: body standing upright and H2: head standing upright) (Mysterud, 1996). The cover board was placed in the GPS-point and at a distance of ten meters we counted how many squares out of 20 were visible in each height segment. Further the distance for the cover board to disappear completely was determined. This was done in all cardinal directions.

**Relascope:** I used a relascope to find the basal area of trees ( $\text{m}^2$  per hectare). The relascope consist of a 50 cm long chain with a 1 cm wide gap in the end. All trees that fills the gap in chest height (1.3 m) for each of the categories pine, spruce, RAW (rowan, aspen and sallow), and other were registered in each of the four cardinal points. Each tree that fills the gap represents a basal area at least  $1\text{m}^2$  per hectare. All registrations were done in the GPS-point. (Fitje 1989)

**Densiometer:** Canopy closure is the proportion of the sky hemisphere obscured by vegetation when viewed from a single point. To measure this I use a densiometer with a concave mirror that is divided into 24 squares. Each of these squares was divided into four, which gives 96 measuring squares (Lemmon 1956, Lemmon 1957). In each of the four cardinal points the number of open small squares was counted. The densiometer was held horizontal at chest height, the number of open small squares was counted.

**Cutting class:** The forest observations were classified in different types and different cutting classes as according to the standard national forest evaluation of Norway: 1: clear cuts, 2: young plantations, 3: pole size stands, 4: medium-aged stands, 5: older mature stands.

**Ground cover:** The percent cover of dead material, ericoides, ferns, horsetails, mosses, lichens, grass and herbs, was registered so it ended in 100 % all together. These registrations were estimated in three 2x2 m squares, one centered in the GPS-point, one 10 m to the north

and 10 m to the south of the point. In the same squares we registered the number of RAW with green leaves under 150 cm height.

Habitat types: The dominating habitat was classified into seven classes; coniferous forest, deciduous forest, mixed forest, mountain birch forest, alpine, swamp, fields and other.

Distance from pastures was extracted from GIS maps of land use classes (AR50). Distance from roads, slope and elevation was extracted from GIS maps of roads and a digital elevation model.

## **2.6 Statistical analyses**

I ran all analyses using the statistical software R (R Development Core Team 2012). To investigate differences in habitat use between shot and surviving deer I fitted a linear mixed-effects model using the function `lme` in the `nlme`-package (Pinheiro and Bates 2000).

Different continuous habitat and terrain variables were fitted as response variables in separate analyses. Response variables were: Horizontal visibility, coverboard sighting distance, canopy measures, elevation, slope, distance to pastures and roads, proportion of spruce and pine, total basal area, total basal area of RAW, percent cover of herbs, blueberry, ericoides and grass (representing important food resources). Fate (survived and shot), sex and their interaction were fitted as fixed effects in all models. Each individual was always included as a random intercept to account for non-independence between locations from the same animal.

I tested for variation among individuals by using likelihood ratio tests between models with and without individual as a random factor. This test was done for all the response variable. To test for connection between migration status and fate (survived and shot) I used a Chi square test with Yates continuity correction for small samples.

### 3. Results

There were individual variations in use of habitat between the individuals with respect to all habitat- and terrain measures because the log likelihood ratio tests supported inclusion of individual as a random effect in all models (Table 1), suggesting that mixed models is the right way to analyze the dataset.

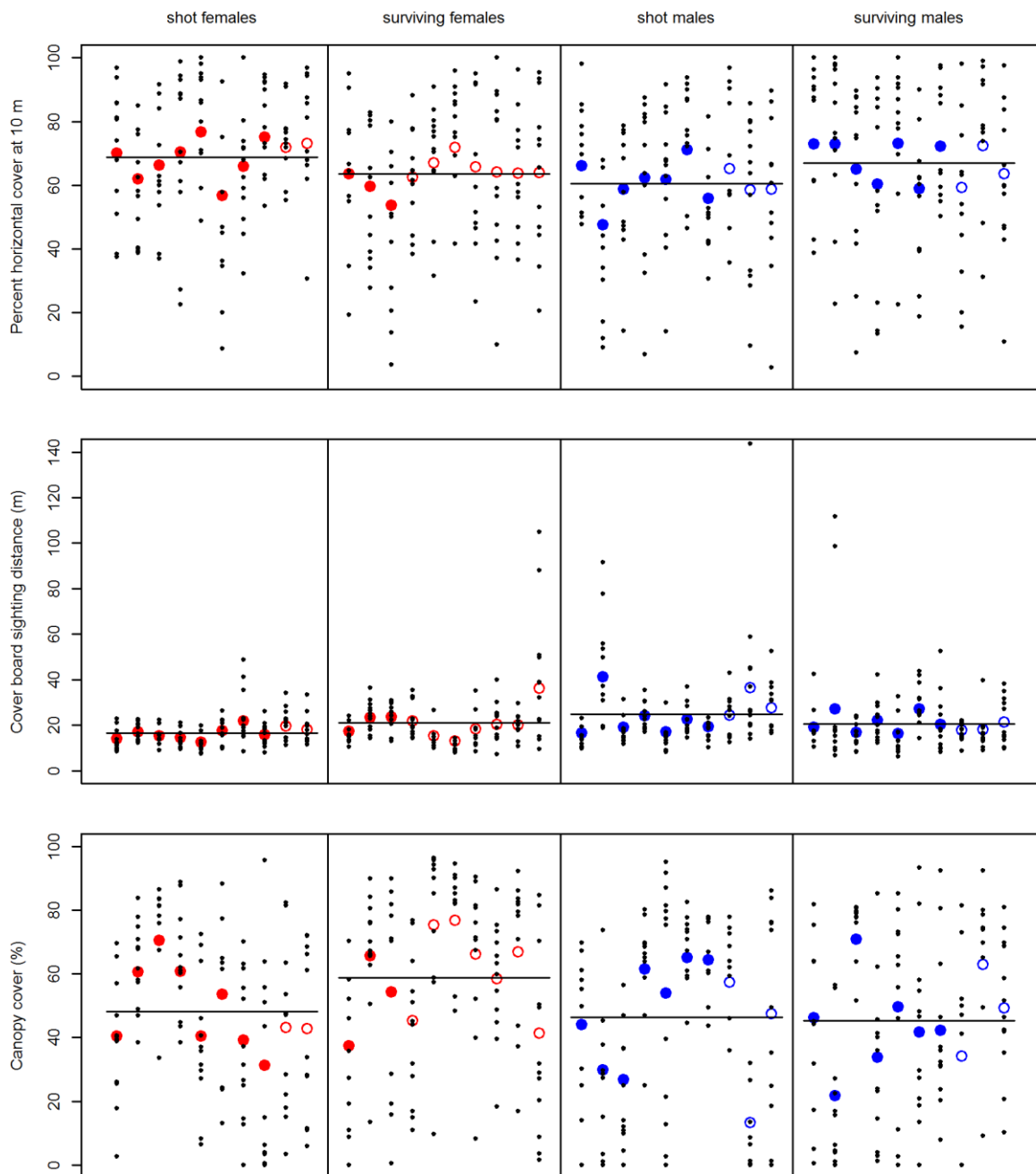
**Table 1.** Log-likelihood test, for testing the inclusion of individual as a random effect (comparing mixed models with a corresponding linear model without random effect).

<b>lme</b>	<b>L.Ratio</b>	<b>p-value</b>
Horizontal coverboard	16.362	<.0001
Cover board sighting distance	52.348	<.0001
Canopy	93.899	<.0001
Percent spruce	127.248	<.0001
Percent Pine	203.393	<.0001
Total basal areal	113.681	<.0001
Basal area RAW	51.959	<.0001
Percent herbs	109.599	<.0001
Percent blueberry	83.368	<.0001
Percent ericoides	129.724	<.0001
Percent grass	50.036	<.0001
Elevation	565.0	<.0001
Slope	319.701	<.0001
Distance pastures	265.057	<.0001
Distance roads	433.454	<.0001

There were no significant differences in the use of cover between harvested and surviving deer of either sex (Table 2), contrary to prediction 1. From the percent horizontal cover figure (Figure 2) measures I can see that surviving males on average used 10 % higher horizontal cover than the shot males. Surviving females used 5 % lower horizontal cover than the shot. When comparing the estimated mean of the groups (the four combinations of shot/surviving and sex) the in the cover board sighting distance were close to the same (Figure 2). For all the four groups the distance for the cover board to be completely hidden was between 18-24 meters. I did find a tendency for a difference between the sexes in both the horizontal cover and the coverboard sighting distance ( $p = 0.071$  and  $p = 0.079$ ). Surviving females had the highest mean value of canopy cover with 60 %, for the other three groups the mean value was

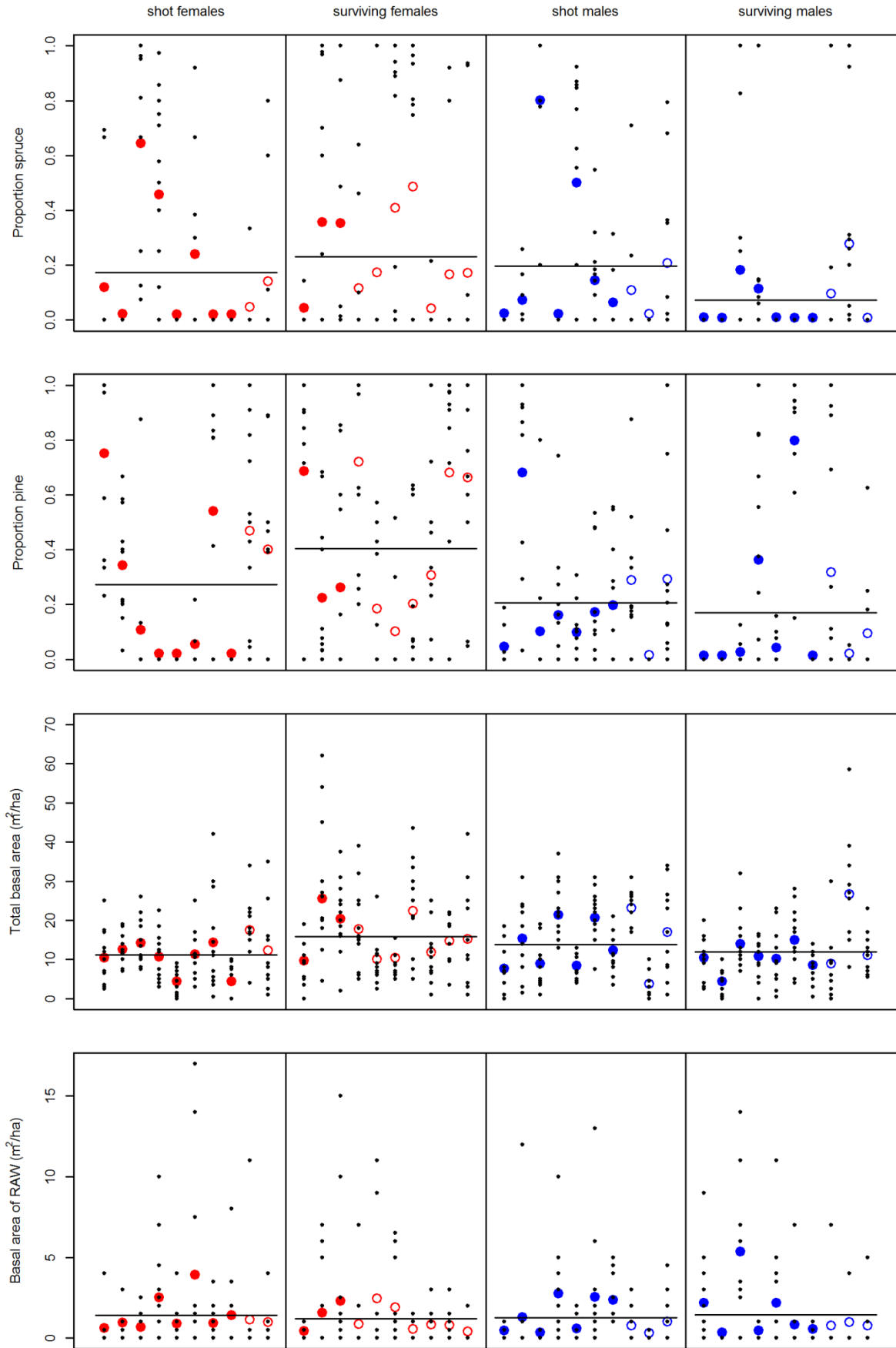


50 % (Figure 2). The mean differences between the groups for all habitat variables was small compared to the individual variation within each group (Figure 2)



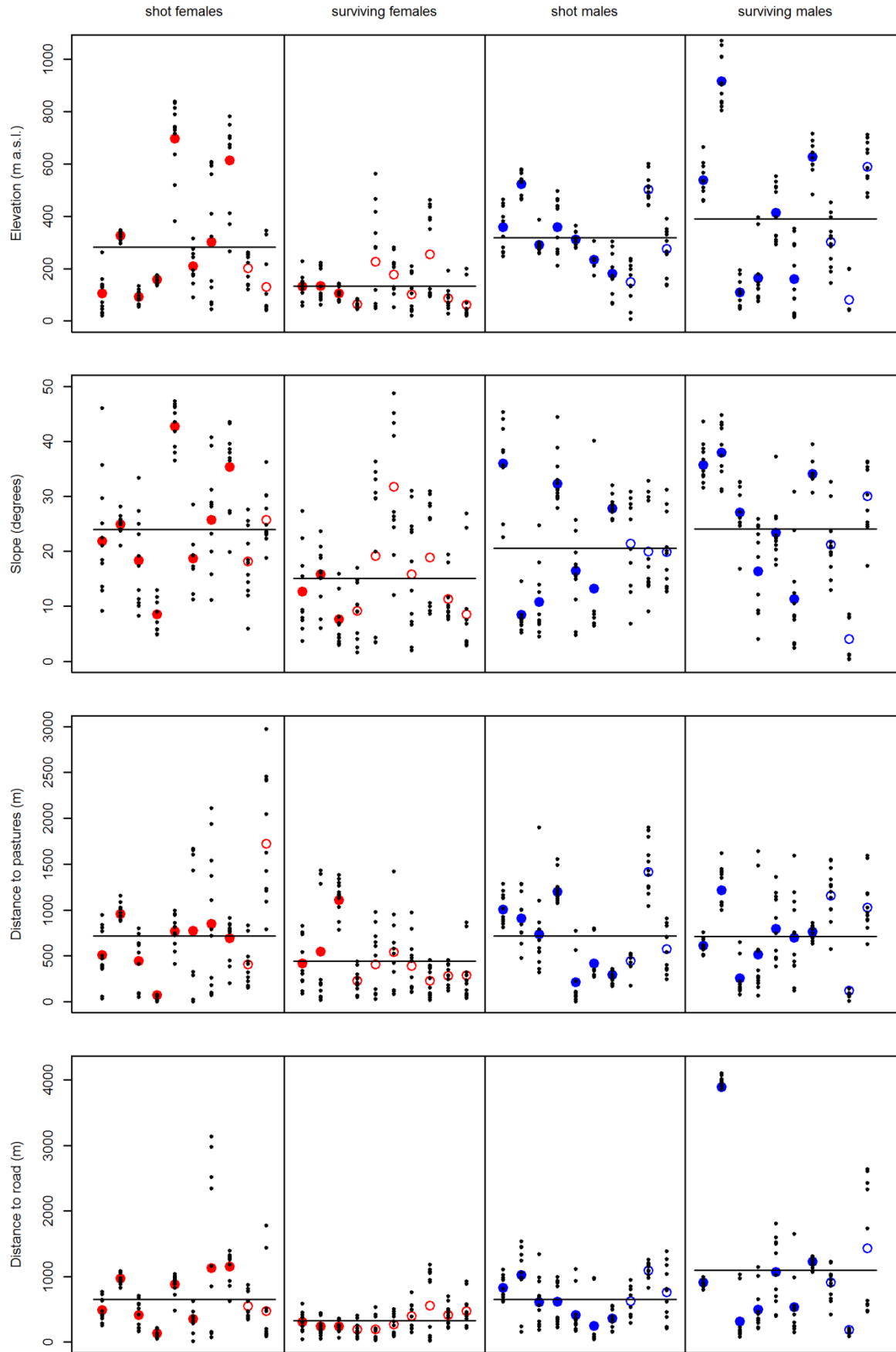
**Figure 2.** Raw data and fitted estimates of horizontal and vertical cover for shot and surviving males and females. Black lines is the estimated mean value of each group, red/blue dots are the estimated tendency for each individual, where hollow symbols are stationary animal and solid symbols are migratory animals. Black dots are the raw data from each individual.

The relascope measure provides measures of density of each tree species, and is thus a complementary measure on to the animal's use of cover (Figure 3). The measures of total basal area and total basal area of RAW were not significantly different between shot and surviving deer, ( $p= 0.128$  and  $p=0.672$ ) contrary to prediction 1. Herbs, blueberry, grass and leafs from the RAW species are the red deer preferred forage in the summer months. There is no large variation between the groups in the forage measures and contrary to prediction 2 harvested animals do not use better foraging habitat than the shot animals (all  $p$  for food related measures  $>0.05$ ; Table 2).



**Figure 3.** Raw data and fitted estimates of proportion of spruce and pine and total basal area and basal area of RAW for shot and surviving males and females. Black lines is the estimated mean value of each group, red/blue dots are the estimated tendency for each individual, where hollow symbols are stationary animal and solid symbols are migratory animals. Black dots are the raw data from each individual.

Surviving males were located marginally higher above sea level than the shot males, while the reverse was true for females (Figure 4). Due to the different direction is the small difference in the interaction between survival category and sex approached significance (Table 2). There was much higher individual variation among shot females than surviving females. I found the same in the measured degree of the slope in the habitat (Figure 4). The figure of distance to pastures show that the chances for females to get shot increases when the distance to pastures increases. For males I did not see the same (Figure 4). There were also larger individual differences among the shot females then the other categories. Test results show that for the females there is a weak non-significant pattern that risk of getting shot increases when the distance to roads increases. For males the chances of surviving with respect to distance to roads is close to significantly in contrast that of females ( $p = 0.051$ ) with a weak tendency to increases when the distance to roads increases (Figure 4). Figure 4 show that the different groups of animals (the four combinations of shot/surviving and sex) follow the same pattern in the large scale variables (elevation, slope and the distance to roads and pastures). I believe that this might possibly be related to the animals' migration behavior.



**Figure 4.** Raw data and fitted estimates of elevation, slope, distance to pastures and roads for shot and surviving males and females. Black lines is the estimated mean value of each group, red/blue dots are the estimated tendency for each individual, where hollow symbols are stationary animal and solid symbols are migratory animals. Black dots are the raw data from each individual.

**Table 2.** Table of the fitted model with coefficients ( $\beta$ ), standard errors (SE) and p-values of each variable measured in field and extracted from GIS and their interaction.

		$\beta$	SE	p-value
<b>Small scale effects</b>				
coverboard sighting distance	intercept (harvested females)	16.62	2.36	0
	surviving vs harvested	4.32	3.33	0.203
	males vs females	8.14	3.34	0.02
	(surviving vs harvested) : males	-8.54	4.72	0.079
Horizontal visibility at 10 m	intercept (harvested females)	68.18	3.15	0
	surviving vs harvested	-5.25	4.45	0.2469
	males vs females	-8.25	4.47	0.0735
	(surviving vs harvested) : males	11.73	6.31	0.071
Proportion Spruce	intercept (harvested females)	0.17	0.06	0.012
	surviving vs harvested	0.05	0.09	0.554
	males vs females	0.02	0.09	0.809
	(surviving vs harvested) : males	-0.1831	0.13	0.192
Proportion Pine	intercept (harvested females)	0.27	0.08	0.001
	surviving vs harvested	0.13	0.11	0.276
	males vs females	-0.06	0.11	0.570
	(surviving vs harvested) : males	-0.16	0.16	0.327
Total basal area (m <sup>2</sup> /ha)	intercept (harvested females)	11.23	2.06	0
	surviving vs harvested	4.55	2.91	0.127
	males vs females	2.6	2.91	0.377
	(surviving vs harvested) : males	-6.41	4.12	0.128
Total basal area of RAW (m <sup>2</sup> /ha)	intercept (harvested females)	1.4	0.45	0.002
	surviving vs harvested	-0.19	0.64	0.765
	males vs females	-0.15	0.64	0.807
	(surviving vs harvested) : males	0.39	0.91	0.672
Percent cover of herbs	intercept (harvested females)	17.15	2.78	0
	surviving vs harvested	-3.02	3.93	0.447
	males vs females	-0.85	3.94	0.829
	(surviving vs harvested) : males	7.21	5.56	0.203
Percent cover of blueberry	intercept (harvested females)	16.37	3.21	0
	surviving vs harvested	0.38	4.54	0.934
	males vs females	-1.04	4.55	0.819
	(surviving vs harvested) : males	-3.3	6.43	0.610
Percent cover of ericoides	intercept (harvested females)	11.43	3.01	0.000

	surviving vs harvested	-4.39	4.25	0.309
	males vs females	-2.99	4.26	0.487
	(surviving vs harvested) : males	3.23	6.02	0.595
Percent cover of grass	intercept (harvested females)	11.09	1.99	0
	surviving vs harvested	2.2	2.81	0.438
	males vs females	1.74	2.82	0.541
	(surviving vs harvested) : males	-4.93	3.98	0.224
Canopy	intercept (harvested females)	48.257	5.52	0
	surviving vs harvested	10.462	7.811	0.189
	males vs females	-1.882	7.822	0.811
	(surviving vs harvested) : males	-11.591	11.0504	0.301
<b>Large scale effects</b>				
Slope (degree)	intercept (harvested females)	23.97	3.09	0
	surviving vs harvested	-8.92	4.37	0.049
	males vs females	-3.38	4.37	0.445
	(surviving vs harvested) : males	12.41	6.19	0.052
Elevation (m.a.s.l)	intercept (harvested females)	283.01	60.32	0
	surviving vs harvested	-149.34	85.29	0.089
	males vs females	34.31	85.31	0.690
	(surviving vs harvested) : males	221.11	120.63	0.075
Distance to pastures (m)	intercept (harvested females)	716.92	125.11	0
	surviving vs harvested	-275.75	176.88	0.128
	males vs females	0.88	176.97	1.00
	(surviving vs harvested) : males	271.5	250.17	0.29
Distance to roads (m)	intercept (harvested females)	649.96	189.58	0
	surviving vs harvested	-325.99	268.06	0.232
	males vs females	3.65	268.14	0.989
	(surviving vs harvested) : males	766.14	379.13	0.051

A larger percentage of the shot females were migratory (Table 3), but a chi squared test with Yates correction does not rule out that this could have occurred by chance under the null hypothesis ( $\chi^2 = 3.2323$ ,  $df = 1$ ,  $p = 0.0722$ ). For the males the ratio of shot to surviving was the same for both migratory and non-migratory (Table 3).

**Table 3.** Table with the sample size of red deer females and males, split according to individual movement strategy (migratory or stationary/other) and individual fate during hunting season ( $n = 40$ ).

<b>Female</b>	shot	survived	Combined
Migratory	8	3	11
Other/not migr	2	7	9
Subtotal	10	10	20
<b>Male</b>	shot	survived	Combined
Migratory	7	7	14
Other/not migr	3	3	6
Subtotal	10	10	20
Grand total	20	20	40



## 4. Discussion

Hunting performed by humans can potentially affect and change species and populations (Coltman et al. 2003). In our study area I did not find any evidence that shot and surviving deer of any sex used the habitat differently. This is contrary to recent evidence in Canadian elk showing that risk prone individuals, using more open food rich areas, have a higher probability of getting shot than more shy deer (Ciuti et al. 2012). My study may suggest that behavioral strategies to avoid hunting is too costly in term of reduced food intake or that hunters are more effective in presumably safe habitat than previously thought in intensively harvested populations.

### 4.1 Cover

Cover might possibly benefit ungulates by lowering the risk of predation. It can reduce visibility to predators and reduce the chances of being attacked (Mysterud & Østbye 1999). It's established that ungulates can use cover as a protection against predation, to conserve energy, and avoid wetting of pelage, animals shelter from precipitation by using habitat with more cover during rainy weather. Cimino and Lovari (2003) found that roe deer (*Capreolus capreolus*) using woodlands during daytime was probably a consequence of the avoidance of human disturbance as a part of an anti predator strategy. They found a tendency for increased use of woodlands during hunting season. Said et al. (2012) found that wild boar preferred using dense vegetative cover during resting periods, in hunting season this selection decreased. The value of using forested areas as anti predator strategy during hunting season has been reported in mule deer (Swenson 1982; Yarmoloy et al. 1988). The lack of a difference in the use of cover habitat between our study animals is therefore surprising, but can be linked to potential trade-offs against other resources. Due to a large red deer population, it is not unlikely that the animals have to use also the open parts where they are more visible to hunters in order to utilize good quality foraging habitat. But contrasting patterns, where the animals vigilance was higher in forested areas compared to the open landscape have been observed in springbok (*Antidorcas maursupialis*) (Burger et al. 2000) and white-tailed deer (*Odocoileus virginianus*) (Lagory 1998). These observations was seen when populations were a subject to natural predation. My results are in contrast to Ciuti et al. (2012) who found that both males and females who survived the hunting season avoided open areas and also had a lower movement rate close to roads, during weekends and in flat terrain. My results do not indicate that there is any difference between shot and surviving animals in our study area. Ciuti (2012) determined that the differences between the harvested and

surviving individuals were linked to the animals' personality as the inter-individual differences in the movement rate were already preset before the start of the hunting season, as the harvested animals choose a bold running strategy and the surviving a shyer hiding strategy. These personality traits do not clearly occur in my study animals. If the animals are to engage in antipredator behavior they have to determine if the payoff is high enough. As the hunting in our study area is performed in all the landscape types, from pastures, woodlands and mountain areas the chances of getting shot is high in the entire habitat of the red deer. The hunting season is also long and hunting is performed all the hours of the day. Different hunting strategies are also used. One of the most common hunting strategies in my study area is drive hunting. When using this strategy some hunters are posted along the outskirts of the hunting area, and other hunters move through the area pushing the deer ahead and to the sides (Meisingset, 2009). When using this method there is a great chance that deer that originally have tried to hide in dens habitat will get scared and try to seek out of the hunting area, thus getting shot by the hunters on posts. Thus it might be difficult for the animals to find an area who provides cover from the predation risk as the hunters might appear almost anywhere in the habitat. The low predictability of the hunters might reduce the possibility for successful antipredator strategies. Because of the overall hunting pressure the antipredator strategies are probably not effective or do not pay off for the animals in this area which might be the case if there are strong constraints in resource selection. Since the red deer population is large, the animals use habitat close to human settlements through the whole year. In the winter season the snow cover at higher elevations often force the animals to utilize habitat closer to the fjords, hence they get well used to roads, human noises and disturbance. Most of the migrating animals return to the winter habitats before November, and stay there until the beginning of May. This means that for the whole population the period close to human settlements is long. The hunting season last for about 16 weeks, with the highest hunting pressure the first weeks (Andestad, 2004). This means that the animals spend much time close to humans without seeing humans as a threat. The lack of differences between the shot and surviving animals in our study might be caused by the animals being well habituated with human disturbance. If the animals don't find it necessary being vigilant in relation to humans, they might not avoid open habitats even if hunting pressure is high.

## 4.2 No detectable forage-risk trade off

I predicted that the trade-off between using better forage areas and cost of reduced time in cover habitat would reveal differences between the study animals, which have been observed in similar studies. Morgantini and Hudson (1985) concluded that winter hunting on wapiti (*Cervus elaphus*) caused a major shift in the animals' diet selection and that the shift resulted in a lower diet digestibility. After hunting season the wapiti returned to their earlier preferred diet, showing that the time spent between antipredator behavior and time spent on foraging indeed is an important trade-off in wild ungulates. Supporting this, Fortin and colleges (2004) reported that vigilance among elk (*Cervus canadensis*) and bison (*Bison bison*) caused by anti predator strategies induced foraging costs, but that these costs were less important than traditionally assumed. In accordance with this Hernandez and Laundrè (2005), found that elk shifted to safer habitat with poor forage quality in response to wolf predation. Studies of Benhaimen et al. (2008) reported that the selection of feeding sites was altered by hunting, as the roe deer (*Capreolus capreolus*) did not select feeding sites on the basis of food quality and that vigilance levels were higher during the hunting season compared to closed season. Mysterud et al. (1999) found evidence that roe deer responded to the trade-off between maximizing foraging benefits and minimizing hunting risk by favoring neither food nor safety when they selected feeding sites during hunting season. In addition they found that there was a trade-off between food availability and distance to human settlements. The roe deer selected feeding sites closer to human settlements at night, when they probably assumed the risk to be lower. My results were contrary to this prevailing pattern, and this is probably linked to hunters appearing in all parts of the habitat. In my study area the animals will eventually have use more open areas during the hunting season because these often provides better foraging opportunities' than more dens habitats will (Mysterud & Østbye 1999). Especially in the beginning of fall, the animals often have to spend time in pastures or open areas with herbs and grass in order to maintain good physical condition. This means that the animals sooner or later will have to do a trade-off between safe and risky habitats. Due to the high hunting pressure with many hunters in the terrain at the same period, the probability of getting shot is high. Therefore it might be accidental witch of our study animals who ended in the shot or surviving categories. It`s very likely that the surviving study animals will get shot in one of the following hunting seasons.

### **4.3 Migration**

Migration can possibly enhance the fitness of ungulates by reducing predation risk, increasing access to sources of nutrition and reducing social interactions (Fryxell and Sinclair 1988; Albon and Langvatn 1992). In my study the different categories of sex and fate follow the same pattern in slope, elevation, distance pastures and roads. In all these large scale variables the pattern between female and male are weakly opposite. Because surviving females tended to use areas on lower elevations, closer to pastures and roads this might be the results of the animal's migration status. It's possible that local hunters recognize the animals who use habitat close to their homes, and in hunting season they save the females simply because they think it's interesting to follow the animals through the year. Even though the migrating females use habitat further from human settlements, they migrate through areas where hunters do not know them thus they get shot. In general the hunting pressure on males is higher than for the females in all municipalities in my study area and this might explain why migrating and stationary males may be shot to the same extent.

A source of error in the small scale variables in cover and forage could be the GPS estimates, who possibly could be near to 20 meters incorrect relative to the animals originally location. This could result in inaccurate cover and forage measures. Still I do not believe that this has affected the results, as others before me have found contrasting habitat use when using the same method (Lone et al. 2014). The relatively small differences in mean values, combined with large individual differences between the animals indicate that a larger sample size not would have affected the results.

### **4.4 Potential future effects**

Harvesting is often selective against certain individuals according to one or more phenotypic traits, and different types of selective harvesting might possibly generate different adaptive responses (Jennings, Greenstreet, & Reynolds 1999; Law 2000). These kinds of directional selection effects are documented in both fish and ungulates (Jørgensen et al. 2007; Coltman et al. 2003). Ciuti et al. (2012) found that the cautious behavior of surviving elk in most certainly was the end result of an extreme individual plasticity, resulting in the ability to adapt behavior to peoples more frequent use of the area in weekends. I did not detect any differences in the habitat choice in our study animals and there was no evidence that hunters are producing neither a shy red deer population nor a bold. The lack of evidence for shy or bold personality might be explained by the animals having adjusted to human disturbance. I did detect some individual differences, but the question is if these were linked to the animals'

personality and therefore repeatable or if they could have been a result of a recent experience. Even if hunters do create a landscape of fear in the study area, the number of hunters is so high that the animals eventually will get shot.

My results suggest that red deer in central-Norway might not engage in antipredator strategies by using denser habitat to avoid hunters. This is a surprising result and is novel compared to what other researchers have found (Blumstein & Daniel 2002; Creel et al. 2005; Ciuti et al. 2012). I conclude that the similar use of habitat is probably due to an overall high hunting pressure in the study area. The probability of getting shot by hunters is high regardless of what parts of the habitat the animals use.

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## **Appendices**

Appendix 1 – forage measures.

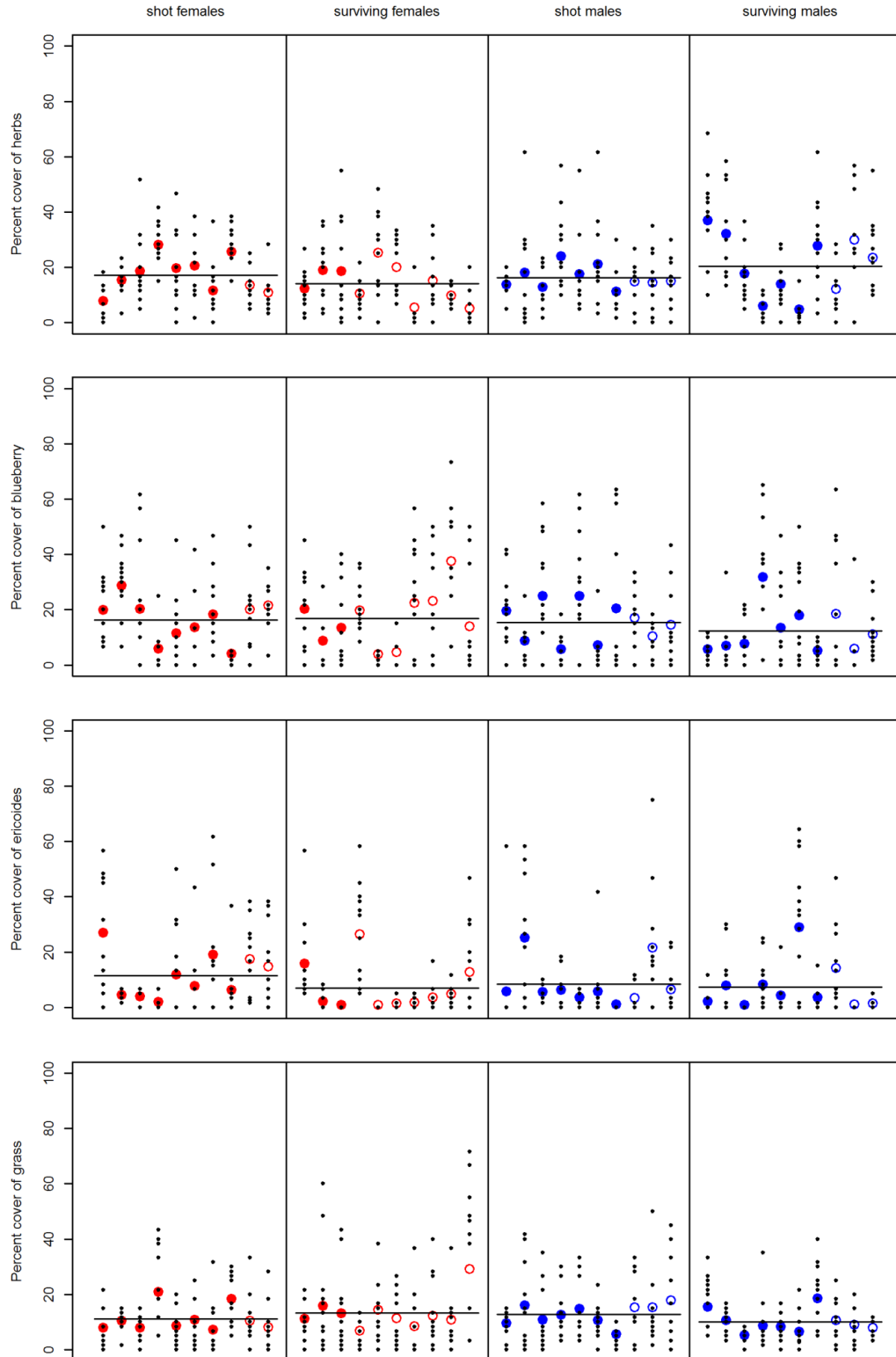


Figure A. Raw data and fitted estimates of the degree of cover of herbs, blueberry, ericoides and grass for shot and surviving males and females. Black lines is the estimated mean value of each group, red/blue dots are the estimated tendency for each individual, where hollow symbols are stationary animal and solid symbols are migratory animals. Black dots are the raw data from each individual.

Appendix 2. Registration form used during fieldwork.

FIELD REGISTRATION FORM - HJORT, SKJUL og SKJEBNE 2013																	
Plot ID				Date		Name											
<b>Vegetation cover 1</b>		<b>Vegetation cover 2</b>		<b>Vegetation cover 3</b>		<b>Relascope factor</b>		<b>Species count</b>									
% Dead		% Dead		% Dead		<input type="checkbox"/> 0,5 <input type="checkbox"/> 1 <input type="checkbox"/> 2		Spruce _____									
% Grass		% Grass		% Grass		<input type="checkbox"/> 0,5 <input type="checkbox"/> 1 <input type="checkbox"/> 2		Pine _____									
% Herbs		% Herbs		% Herbs		<input type="checkbox"/> 0,5 <input type="checkbox"/> 1 <input type="checkbox"/> 2		Birch _____									
% Blueberry		% Blueberry		% Blueberry		<input type="checkbox"/> 0,5 <input type="checkbox"/> 1 <input type="checkbox"/> 2		RAW _____									
% Other ericoids		% Other ericoids		% Other ericoids		<input type="checkbox"/> 0,5 <input type="checkbox"/> 1 <input type="checkbox"/> 2		Other _____									
% Ferns/horsetails		% Ferns/horsetails		% Ferns/horsetails													
% Mosses/lichens		% Mosses/lichens		% Mosses/lichens													
# RAW < 1.5m		# RAW < 1.5m		# RAW < 1.5m		<b>Slope</b>		<b>Aspect</b>									
<b>Edge Habitat?</b>		<b>Dominating habitat</b>				<b>Dominating development class</b>											
<input type="checkbox"/> Yes (<50 m to meadow) <input type="checkbox"/> No		<input type="checkbox"/> Barskog <input type="checkbox"/> Blandingsskog <input type="checkbox"/> Løvskog <input type="checkbox"/> Fjellbjørkeskog		<input type="checkbox"/> Anna _____ <input type="checkbox"/> Høggjells snaumark <input type="checkbox"/> Låglands snaumark <input type="checkbox"/> Myr		<input type="checkbox"/> Ingen <input type="checkbox"/> I (Hogstflate) <input type="checkbox"/> II (Ung) (0-5 år) <input type="checkbox"/> III (Gammal) (5-10 år)		<input type="checkbox"/> III (10-40 år, ung driftsskog) <input type="checkbox"/> IV (40-90 år) <input type="checkbox"/> V (Gammelskog)									
<b>North</b>				<b>East</b>				<b>South</b>				<b>West</b>					
<b>Coverboard</b>		L1	L2	H1	H2	L1	L2	H1	H2	L1	L2	H1	H2	L1	L2	H1	H2
Open squares 20 m _____		_____ meters				_____ meters				_____ meters				_____ meters			
Completely covered at:		<input type="checkbox"/> Veg <input type="checkbox"/> Topo				<input type="checkbox"/> Veg <input type="checkbox"/> Topo				<input type="checkbox"/> Veg <input type="checkbox"/> Topo				<input type="checkbox"/> Veg <input type="checkbox"/> Topo			
<b>Densiometer (open squares)</b>																	
<b>Comments</b>																	





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