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Habitat modelling as a predictive tool in human-wildlife conflicts

Brown bear (*Ursus arctos*) and free-ranging cattle in central Sweden

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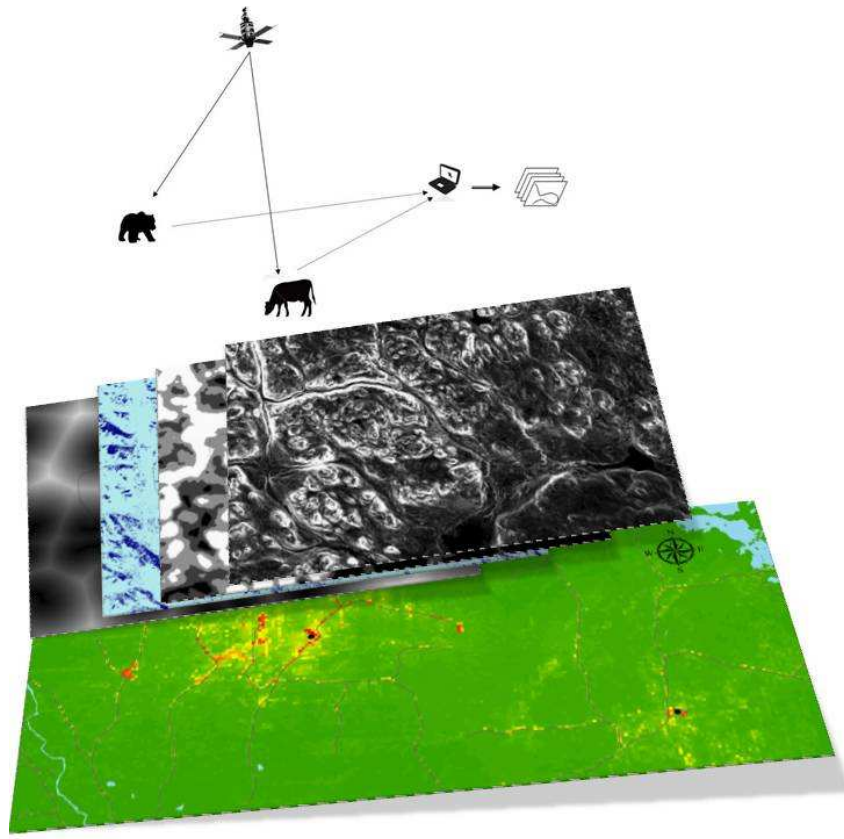

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Habitat modelling as a predictive tool in human-wildlife conflict

Brown bear (*Ursus arctos*) and free-ranging cattle in central Sweden

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Preface

My career as a Wageningen student began in 2000. Driven by a passion for nature and the awareness of its additive value in the quality of life; I enrolled in the 'forest and nature conservation programme' of Wageningen University. This programme offered me the opportunities to experience true wildlife and the outdoors. Tracking wolves and bears in knee deep snow in Slovakia felt like a child's dream come true, and pinpointed my ideas and wishes considering the future. I wanted to work with these impressive flagship and indicator species as large carnivores are, and because of natural curiosity; in a scientific context. After graduating, the lack of proper GIS skills showed to be an obstacle hard to bypass if I wanted to focus on this field. It was during a beautiful beach walk in New Zealand's Marlborough Sounds that I decided to take a second master, in GIS (MGI), again at Wageningen University, which turned out to be a very good decision.

In my search of a wildlife related MGI thesis project, I contacted the Scandinavian Brown Bear Research Project (SBBRP; www.bearproject.info), a world leading bear research project. I could join in a SBBRP and Swedish Wildlife Damage Center (Viltskadecenter; www.viltskadecenter.se) collaborative project on human wildlife conflicts in Sweden, with brown bears and free ranging dairy cattle as case study species. The thesis turned out to be an internship-thesis combination, with a wonderful 4-month fieldwork period at the SBBRP field station in Sweden full of great experiences and people. This report is the end product of this thesis-internship combination, and finalizes my MGI programme. It as well marks the end of my Wageningen student life and residence in the Netherlands.

In the first place, I would like to thank Dr. Ole-Gunnar Støen, and the SBBRP in general, for offering me the thesis- internship opportunity. I would like to thank Dr. Ron van Lammeren for his valuable comments and supervision on the GIS side of this thesis. I thank Dr. Jan Bokdam for his inspiring theoretical and ecological thoughts and teaching, the supervision during this and my former thesis. Anne Doeksen reviewed this document, which I am very grateful for. I thank my parents, family and friends for all the support and opportunities they gave me. Furthermore, the people at the field station all contributed to the great period it was!

Summary

Livestock depredation is a fundamental aspect altering human's perception of large carnivores and in the past has contributed to justify large carnivore eradication programs with local extirpations as a consequence. In central Sweden, brown bears (*Ursus arctos*) coexists with traditional livestock husbandry of dairy cattle, which range freely during daylight hours during the grazing season, from mid May to mid September. Bear-cattle conflicts in Sweden were reported to be amongst the lowest in Europe. We hypothesized that bears in the study area do not actively prey on cattle, and that conflicts occur by chance through coexistence.We analyzed and related resource selection of 7 GPS marked cattle herds, co-existing with 11 GPS marked bears during the grazing season, to define encounter –and potential conflict- risk areas and determinative factors. We found that bears and cattle utilize their resources in a spatiotemporal different way, driven by inverse responses to human activity related variables, vegetation densities and land cover types. Additionally, the type of livestock husbandry prevented nocturnal free-ranging, avoiding the activity peaks of bears, and reducing encounter probabilities. The traditional way of cattle husbandry appeared to be suitable to co-exist with brown bears in Scandinavia. Depredation losses can however not be excluded. Livestock managers should be willing to absorb potential losses or take additional preventive measures such as electric fencing, aversive repellents or guarding animals. The reappearance of wolves (*Canis lupus*) will probably challenge future co-existence between livestock managers and large carnivores. It is therefore stressed that predatory behavior by wolves on livestock should become a primary research need, in order to facilitate future coexistence between humans and large carnivores.

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1 Introduction

The Scandinavian brown bear population is currently expanding in size and distribution (Swenson et al. 1998a, Nellemann et al. 2007). The bear is classified as a carnivore, and its presence is therefore often considered as being in conflict with human interests, i.e. bear depredation on livestock and game, damage to crops, orchards and beehives; and as a threat for human safety (Swenson et al. 1998b, Swenson et al. 1999, Zimmerman et al. 2003). Furthermore, bear habitat –and habitat quality in general- has been gradually degrading in Scandinavia over the years due to human induced habitat fragmentation. The simultaneous occurrence of these two spatially opposing developments is expected to result in an increase in human-wildlife conflicts and challenge future co-existence between humans and brown bears –and other wildlife- in these regions (Nellemann et al. 2007, Zabel and Holm-Muller 2007).

Human-carnivore conflicts can lead to negative human attitudes towards large carnivores, which could result in the adoption of legal and illegal eradication programs (Kaczensky 1999, Linnell et al. 1999, Goldstein et al. 2006). For example, in many states of the USA, wolves (*Canis lupus*) were completely removed as a result of state-sponsored eradication programs (Treves et al. 2004). Solving or minimizing human-carnivore conflicts is essential for the conservation of large carnivores and for biodiversity in general (Rondinini and Boitani 2007, Zabel and Holm-Muller 2007).

Free-ranging livestock husbandry systems –as are common in many parts of Scandinavia- in bear or other large carnivore habitat involve a risk of depredation losses. However, this risk differs across regions. In Norway for instance, bears were estimated to kill an average of about 50 sheep per bear annually (Swenson and Andrén 2005). Most bear species are also known to be able to kill large domestic ungulates such as cattle and horses. The Andean bear (*Tremarctos ornatus*) was reported to sporadically prey on free-ranging, unguarded cattle (Goldstein et al. 2006). Grizzly bears (*Ursus arctos horribilis*) in the USA have been considered as famous cattle killers. Murie (1948) and Knight and Judd (1983) however reported that a large part of these claimed grizzly bear kills in fact concerned scavenging, taking place after cattle had died a natural cause of death due to age, poisoning or disease. In many parts of Europe, brown bears have been reported to prey on cattle. For some regions, cattle but also horses have even been reported to represent the preferred prey item. In the Dinaric Mountains in Croatia and Bosnia for instance, 87% of the bear damage claims concerned cattle, representing 619 cases during one year. Also in Spain, the Cantabrian brown bear tends to prefer cattle (Kaczensky 1999). In contrast, in other European countries, sheep appears to be the preferred domestic prey.

As the study of Murie (1948) and Knight and Judd (1983) already emphasized, bear predation figures should be interpreted with care. Since it is difficult to discern between direct bear related kills and scavenged prey, and since direct depredation events have only rarely been directly observed, bear damage claims are often considered overestimated. Murie (1948) further concluded that 'a bear story ranks with a fish story so far as reliability is concerned', suggesting caution is required when interpreting bear damage claims. For instance, an impressive 81% of the livestock damage claims caused by black (*Ursus americanus*) and brown bears in Alberta concerned cattle. When considering however that this 81% only represented 0.02% of the total cattle population in the area this figure is relatively low, and much lower than for other domestic species such as sheep (for which bear-related damage was estimated at 0.11% of the total population) (Horstman and Gunson 1982).

Besides direct predation effects, such as death or injury, predation can lead to secondary related predation effects. These effects may include lactation problems, higher occurrence of mastitis, calf abortion, and livestock control difficulties (Murie 1948, Zimmerman et al. 2003) but also shifting ungulate grazing routines and habitat use, and even land degradation (Howery and DeLiberto 2004). The economic impacts of these secondary effects are considered by some authors to be potentially even more far-reaching than those associated with direct predation. Secondary predation effects are however, extremely difficult to quantify.

1.1. Livestock depredation preconditions

The conditions that lead to predation are unclear and prove very difficult to predict and vary depending on the eco-region, predator- and prey characteristics, seasonality, food availability, etc

(Murie 1948). The study of Kaczensky (1999) suggests that most depredation events occur at night, during mist or heavy rain, and in the vicinity of forest, with unguarded livestock herds.

With respect to predator characteristics and predation, there seems to be a strong indication that livestock depredation varies between male and female bears and concerns predominantly mature or adult male bears. This is related to the fact that solitary large carnivore species –such as brown bears- are generally sexually dimorph, implying that sexes differ in diet and habitat preferences. Solitary socially organized large male carnivores tend to have larger home ranges, and wider movement patterns; and therefore have an increased potential to encounter livestock. On the other hand, intrinsic individual behaviour could explain this male bias (Horstman and Gunson 1982, Linnell et al. 1999, Goldstein et al. 2006).

Cyclic patterns of recurring depredation was reported to often temporally cease after a particular predator individual was hunted down (Goldstein et al. 2006). This removal of so called 'problem individuals' is rather non-selective because of individual identification difficulties and human attitudes of preventative killing; and can therefore result in unnecessary over-hunting (Murie 1948, Linnell et al. 1999, Goldstein et al. 2006, Rondinini and Boitani 2007).

Depredation rates seem to be related to natural food availability. Higher rates of sheep depredation were reported in Targhee National Forest when bear food failures occurred (Jorgensen 1983). Similarly, damage statistics in Europe reveal higher depredation rates coinciding with years of soft mast, when bears lack a bulk forage item such as acorns and berries (Kaczensky 1999). Following the optimal foraging theory, it appears that bears shift to livestock when natural foods are scarce, and by doing so make a trade-off between food quality and foraging risk (Jorgensen 1983, Knight and Judd 1983).

Domestic livestock generally lack natural anti-predator behaviour and therefore make easy prey. This is especially true for young animals. Murie (1948) for instance, reported an observation in which cattle calves approached a grizzly bear, scavenging on a cattle carcass, indicating calve curiosity and naivety. Furthermore, most damage claims originate from newly colonized predator areas or zones around conservation areas, where domestic animals are not yet habituated to coexist with predators (Murie 1948, Horstman and Gunson 1982, Kaczensky 1999, Linnell et al. 1999).

Most authors conclude that depredation rates are closely related to the system of livestock husbandry (Horstman and Gunson 1982, Knight and Judd 1983, Kaczensky 1999, Linnell et al. 1999, Goldstein et al. 2006). Most damages were reported for free-ranging, unguarded herds and at larger distances from human settlements. To make a comparison: in Norway, free-ranging, unguarded sheep husbandry in predator area is common. The depredation rate was reported to be amongst the highest worldwide. In contrast, in Sweden where sheep are usually fenced or guarded, depredation losses are very low (Kaczensky 1999, Zimmerman et al. 2003). Reports of bears breaking into sheds taking prey are rare, but occur (Horstman and Gunson 1982, Kaczensky 1999).

1.2. Prevention and compensation measures

Livestock damage can be attempted to minimize by a range of prevention measures, of which success depend on the predator species, eco-regions and intensity of use. Electric fencing has shown to be successful at protecting beehives and livestock herds to some extent, but effectiveness varies across predator species. The use of livestock-guarding dogs has shown to be efficient in guarding sheep in many European countries, but has the drawback that it requires training and causes potential danger to people and its use therefore declines. Donkeys and Llames are also used as guarding animals, as they have a natural herding behaviour and aggression towards intruders (Smith et al. 2000b, Rigg 2001). Experiments with deterring collars and projectiles, audio and visuals, and aversive repellents (aversive tasting compounds with which bait and animals may be treated) have shown to be unreliable and little promising at large scales and for longer time periods (Smith et al. 2000a). Lethal measures, i.e. the killing of the culprit, were concluded to be non-selective and only temporarily effective.

In most countries where large carnivores coexist with livestock, state or NGO governed funds are in place to compensate farmers for predator inflicted livestock damages. Depending on the country and region, these compensations have been claimed to be inadequate, fraudulent and cumbersome (Zabel and Holm-Muller 2007). They also described a promising alternative compensation regulation, based on carnivore conservation performance payments rather than post-priori carnivore damage compensation payments. This method was successfully tested in Northern Sweden, where Sami people endure carnivore damage on their semi domestic reindeer (*Rangifer tarandus*). Despite the fact that there are a range of carnivore damage compensation regulations, losses or damages can be of significant importance for individual farmers, and contribute to negative attitudes towards carnivores.

1.3. Project specific: context and setting

In the Dalarna-Gavleborg region in Sweden, a traditional dairy cattle husbandry system coexists with a bear population. The farmers take their cattle to so called cattle summer farms (in Swedish: fäbod) during the grazing season, from around mid May to mid September. The cattle summer farms are traditionally situated in the forest. Cattle is released every morning and range freely during daytime. As –in the study area- it involves dairy cattle, they return to the farm every evening for milking, where they will stay throughout the night. Conflicts between bears and cattle in the study area –as for whole Sweden- were reported to occur only rarely (Støen, personal communication) In 2007, in Sweden, three cows were killed by bears, and in 2008, only one got injured (Viltskadecenter 2008;2009). Total livestock losses (cattle, sheep, goats and horses) by predators (wolves, bear, wolverine (*Gulo gulo*) and lynx) in Sweden were estimated to be the lowest in Europe, with an average annual loss of 0.1 livestock per capita predator (Kaczensky 1999). Secondary depredation effects are however unknown. Despite these low predation rates, knowledge questions regarding bear-cattle coexistence and potential direct and indirect predation effects became imbedded in a proactive long-term livestock-carnivore conflict study conducted by the Swedish Wildlife Center (Viltskadecenter).

Considering the particularly low conflict rate in the Dalarna-Gavleborg region, we hypothesized that bears in this area do not actively predate on cattle and that encounters –which could potentially lead to conflict- between coexisting bears and cattle occur by chance, as a result of habitat use or resource selection by both species. This working hypothesis is supported by a preliminary research conducted in Sweden by the SBBRP. This study found that bear diet depends predominantly on berries, and although ungulates did form a small part of the bear diet, this concerned mostly sheep and carrion of moose (*Alces alces*) (Dahle et al. 1998). This working hypothesis was further on in line with Knight and Judd's (1983) their statement; i.e. that most bears that do encounter livestock do not kill; and with the concluding hypothesis of Linnell et al. (1999), that most individuals of large carnivores species will at least occasionally kill accessible livestock that they encounter.

According to the optimal foraging theory, animals are assumed to optimize habitat use in order to meet all primary life requirements (e.g. food, shelter and mates). The specificity of these needs and therefore habitat usage varies across species: whilst generalist species may exploit a broad range of habitats; specialist species have a much more narrow and specific ecological niche (Townsend et al. 2000a). With regard to bears and cattle, (respectively, a large carnivore[1] and a large free-ranging, domestic, herbivorous ungulate) large differences in primary needs and thus habitat use were assumed between the species: both spatially and temporally. This assumption is based on the following reasoning: Firstly, cows and bears have strongly different dietary requirements. This, in combination with landscape heterogeneity makes differences in habitat usage very likely. Secondly, cattle in the study area range freely during day time only. In contrast, bears in this region tend to be nocturnal and are mainly active in the crepuscular hours (Moe et al. 2007). These behavioural differences reduce the likelihood of an encounter between bears and cows. Finally, differences in spatiotemporal habitat usage patterns have been strengthened by a history of human-animal interactions: Bears in Sweden have a history of being intensively hunted. Swenson (1990) suggested that bears in hunted areas appear to be more wary of humans and that this may have resulted from selective hunting, in which less wary individuals have a higher probability of being selected or hunted. The study of Moe et al. (2007) showed that bears in the study area do in fact tend to avoid human infrastructures (i.e. tourism resorts and settlements). In contrast to bears, domestic species associate humans with safety –anti-predator behaviour- and forage, and may therefore be expected to remain in the vicinity of human infrastructure.

[1] A classification based on craniometry. Bears are however largely vegetarian, and thus a rather omnivorous species.

1.3.1. Main methodology: Resource Selection Functions and Geographical Information Systems

In this study, habitat use by brown bears and free-ranging cattle has been modeled with 'resource selection functions' (RSF). The concept of RSF has its origin in the theory of natural selection, and was applied to characterize resource utilization by animals (Boyce et al. 2002). Resource selection is a fundamental ecological process in which animal species attempt to optimize the utilization of their natural environment, taking into consideration conditional factors such as food availability (Townsend et al. 2000a), predation risk (Ciarniello et al. 2006), terrain characteristics (Walker et al. 2007) and climatic conditions. In this process, life history characteristics, individual preferences and competition play a key role (Kittle et al. 2008). Manly et al. (1993) defined an RSF as "a function of characteristics measured on resource units (e.g. a pixel or an area of land) such that its value for a unit is proportional to the probability of that unit being used". Resource usage was defined by these same authors as "the quantity of resources being used by an animal –or population- in a given period of time". Quantifying this resource use (u), relative but independent to its availability (a), determines whether that resource is being selected (u/a >> 1), avoided (u/a<<1) or neglected (u/a ~ 1) by an individual or a population of animal(s) (Manly et al. 1993, Alldredge and Griswold 2006).

Other than many other –mainly expert-opinion based- habitat suitability indices, RSFs are statistical models, determined with empirical data (Boyce et al. 2002). In animal ecology, data types that suit RSF application/development are usually binary presence/absence data or use/availability data. In presence/absence studies, the complete study area is divided into resource units (pixels) and assigned a 0 or a 1 according to presence or absence of a certain organism. This design is commonly used for non-mobile organisms and often suffers from non-symmetrical errors. This implies that although used units can be determined with some certainty, unused units may be observed as being 'used' when increasing the sampling intensity (Johnson et al. 2006). The use/availability design is more rigid towards this asymmetrical error: it assigns a 1 to each true observation, i.e. an animal print, a direct observation or a telemetry position; and a 0 to a random number of point locations drawn in the study area. In a Geo Information System

(GIS), attribute data of relevant covariates can be derived (Boyce et al. 2002) for each point location and can be used for model building.

Many studies, in different application fields have successfully used RSFs to model species' distribution, density and interactions. In combination with GIS, Boyce et al (2002) and Walker et al. (2007) respectively modeled grizzly bear (*Ursus arctos*) and female Stone sheep (*Ovis dalli Stonei*) distribution in relation to a range of habitat variables. Grizzly bear distribution and densities have been modeled by Ciarniello et al. (2006). Species interactions, like wolf-elk (*Canis lupus*, *Cervus elaphus*) predator-prey relations have been modeled through RSFs by Hebblewhite et al. (2005). Also in fishery sciences, RSFs are a commonly used tool, e.g. in stock distribution and density estimates (Manly et al. 1993).

Since RSFs are highly scale dependent –spatially and temporally- the design of the model setup and sampling plan is of crucial importance for the model outcomes (Alldredge and Griswold 2006, Boyce 2006, Ciarniello et al. 2007). This especially applies when considering species showing high diel and seasonal variation in behavior (Moe et al. 2007). Therefore, an appropriate sampling plan needs to be established in accordance with the proposed objective of the study. Manly et al. (1993) defined three design types for resource selection studies: design I, II and III. Design I suits population related research questions, in which unique identification of individuals is not necessary or possible. In this type of design, samples of used, unused or available resource units can be drawn from the complete study area. The second design, design type II, identifies each individual study animal, but samples the availability over the whole study area. With design type III, all study individuals are identified, and the used, unused or available resource units are sampled for each individual. This design makes it possible to analyze variation in resource selection between individuals according to gender, age classes etc.

Geographical Information Science/Systems as well as and Remote Sensing (RS) have become indispensable in ecological research (Raffaeta et al. 2008). Their application ranges from spatial data infrastructures (SDI's) for ecological data (Cagnacci and Urbano 2008) to RS applications in predicting wildlife habitats (Osborne et al. 2001), as well as general GIS applications to derive relevant spatial data in modeling studies (Clevenger et al. 2002). Some rather fundamental GIS related topics were even covered in the ecological literature (Girard et al. 2002, Hansen and Riggs 2006). Recently, satellite telemetry by Global Positioning Systems (GPS) has become an extremely valuable tool in tracking animals, for a number of purposes (Buerkert and Schlecht 2008). In this study, the main source-data was obtained by tracking both cattle and brown bears with GPS-GSM technology.

1.3.2. Research objective and questions

The working hypothesis of this study states that bear-cattle conflicts arise by chance through coexistence. The objective of this research project is therefore to relate bear and cattle resource selection in order to define and map encounter-risk zones between coexisting brown bears and free-ranging cattle.

In order to meet this research objective, two main research questions were formulated:

I. How does resource selection of co-existing free-ranging cattle and bears relate to each other?
    a. Which variables define resource selection by both species?
    b. What are the responses of both species to these variables?
    c. Is there spatiotemporal variation in these responses?

II. Which variables determine bear-cattle encounter probabilities?

The outline of this report is as follows: chapter 2 covers the research methodologies. Resource selection functions and habitat use are discussed in general, whilst habitat use modeling for bears and cattle is dealt with in more detail. In addition, methodological approaches applied for each research question are elaborated on. Chapter 3 covers the research results. Study results are presented of: resource selection by bears and cattle, relations between bear and cattle habitat use and bear and cattle responses to environmental variables included in the models. The chapter concludes with a presentation of the encounter-risk results. Chapter 4 provides a methodological and ecological discussion of the research results, and includes the general conclusion and some management implications. Appendices present additional study results that were not included in the report. The appendices include: model selection procedures and background, the general working plan that was followed in order to obtain the results, a detailed description of the land-cover classification procedure that was developed for the purpose of this study and a summary of all model coefficients.

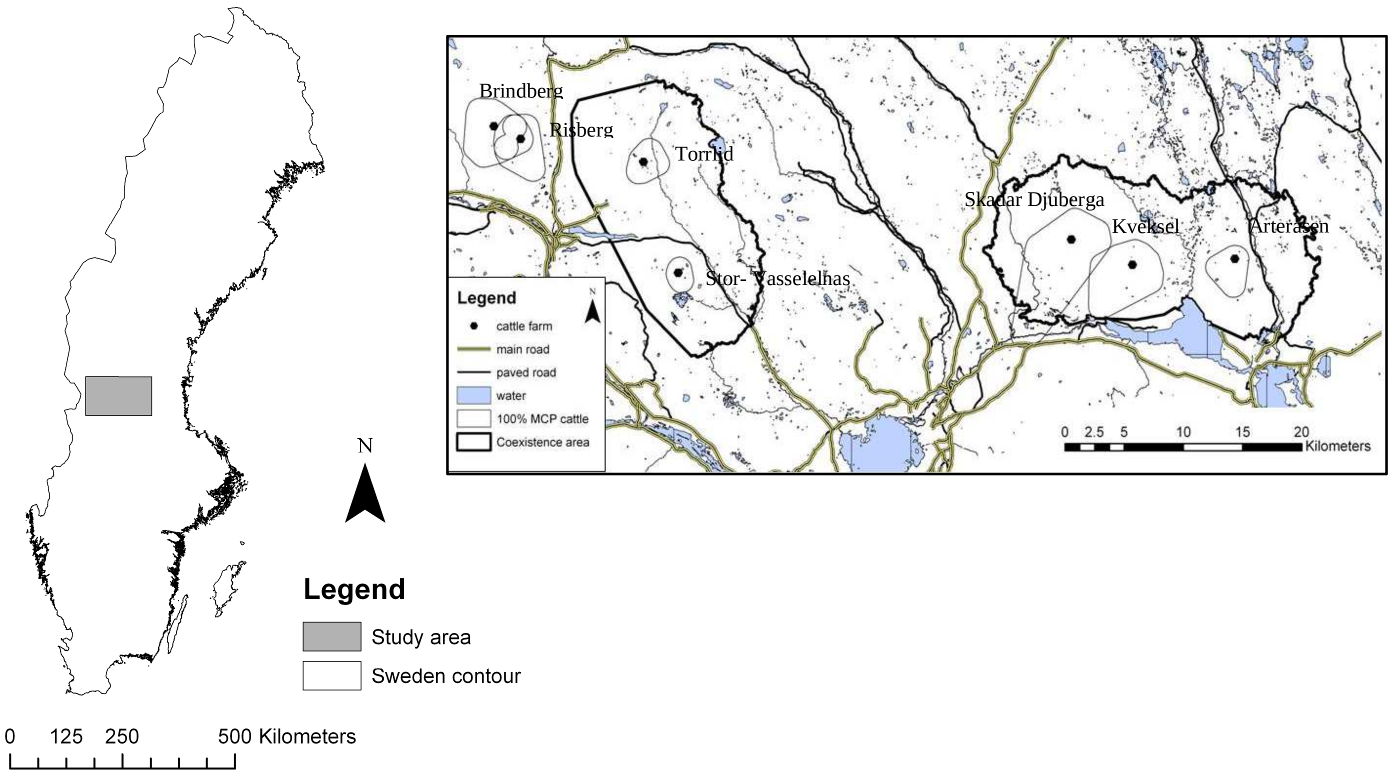
2 Methods

2.1 Study site

The research field station is located in Tackåsen, 61° 32' N and 15° 02' E, in the hilly Dalarna region of Central Sweden. The SBBRP study area encompasses about 13000 km^2 and about 95% is covered with intensively managed boreal forest. Dominant tree species are Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), but deciduous species like Silver birch (*Betula pendula*), mountain birch (*Betula pubescens*), gray alder (*Alnus incana*) and European aspen (*Populus tremula*) are common. Understory vegetation consists mainly of juniper (*Juniperus communis*) or of species of the willow family (*Salix spp.*). The forest floor is covered mainly with lichens, blueberry (*Vaccinium myrtillis*), mountain crowberry (*Empetrum hermaphroditum*), common heather (*Calluna vulgaris*) and cowberry (*Vaccinium-vitis-idaea*). The elevation ranges from about 200 m to 1000 m above sea level. Road density is ca. 0.3 km/km^2 and consists mainly of smaller gravel logging roads. There are 6 towns in the study area, with a population of 3000 to 11000 inhabitants. Two major tourist resorts are situated in the study area, which together account for over 1,000,000 visitor nights annually (Nellemann et al. 2007).

Brown bears in the area have an estimated population density of 0.030/km^2 and are dispersing to the South, West and East sides of the study area (Solberg et al. 2006). There are 7 traditional cattle summer farms in the study area, with cattle free-ranging during daytime from mid May to mid September (Nelleman et al. 2007, Støen, personal communication). Elk (*Alces alces*) is the dominant ungulate species in the study area, roe deer (*Capreolus capreolus*) are common, and red deer (*Cervus elaphus*) occur rarely.

The operational study area around the cattle summer farms was defined as the area in which bears and free-ranging cattle coexist. It was defined after cattle resource selection was modelled. The operational study area included all pixels for which the average cattle resource selection value exceeded 0.5, and thus the relative probability of use higher than 50%. Map 2.1 shows an overview of the operational study area, with the 7 cattle farms and the 100% MCP (Minimum Convex Polygon) home range per cattle herd.



Map 2.1: detail of the study area, and its location in Sweden

2.2 Data acquisition

To create resource selection functions, two types of data are necessary. Firstly, animal positions, (from sign data, radio and satellite telemetry), and secondly, digital GIS layers with environmental variables to relate the animal positions to. The acquisition of this data is dealt with in this section.

2.2.1. Positioning data

2.2.1.1. Cattle location data

From the 14th of June until the 20th of September 2008, 10 Televilt Tellus Domestic GPS-SMS System^{TM} collars were fitted on free-ranging dairy cattle from 7 different cattle summer farms, forming 7 herds. At least 1 collar was provided per herd. Televilt collar performance was very low; the GPS fix rate averaged 38.2%, and ranged between 4.55% and 78.53%. These figures were calculated between 7:00 and 17:00, and for periods when cattle were free-ranging. Additional collar "time outs" frequently occurred, with data loss as a consequence. Because of the poor collar performance, 5 Vectronic Aerospace GmbH GPS PLUS collars with SMS function were additionally fitted on cattle from three herds from mid July until the end of the grazing season. The fix ratio of these collars was excellent, and on average close to 100% (SBBRP, personal communication). The collars were scheduled on 30 minute time-intervals. The SMS function of the collars –both Televilt and Vectronic- made it possible to download real time data from a web service. After the field season, all collars were returned to their company, in order to download positioning data straight from the collar to bypass SMS transmittance failures.

Cattle herds were relatively small and usually comprised of 5-12 adult cows. The herds ranged free from early morning (earliest ~ 6:00) until the evening (latest ~ 21:00), upon which they returned the farm to be milked. A 50m buffer zone –which was assumed to include the complete farm- was drawn around each cattle farm. Positions falling within the buffer were withdrawn from further analysis, in order to prevent contamination from 'on farm' positions in the 'free-ranging' sample. A dilution of precision (DOP) value of 5 was considered as the upper-limit to include positions into the analysis. The data was further harmonized with respect to space and time. This was done by preparing a final dataset, in which only 1 collar per cattle farm at a time was taken into account. One cattle farm was completely taken out for analysis because of the low number of valid positions (N=12, from July 25 to September 15). In total, 3012 cattle locations were selected for further analysis.

The cattle data was pooled and divided into seasons: the pre-berry (before 6 July), intermediate (7 July – 15 July) and berry season (from 16 July onwards) (Dahle et al. 2003), following Manly's design type I (Manly et al. 1993). As it was assumed that diel behavior in cattle was less important than for brown bears, and because of the low data availability, daytime was divided in morning (5:00 - 9:30), midday (10:00 -14:30) and afternoon/evening (15:00 – 20:00), instead of hourly intervals. Table 2.1 summarizes frequency data per cattle farm. Note that the farm of Stor-Vasselnas was excluded out from the data set.

Table 2.1: distribution of point locations per cattle farm per season (Pre-berry, Intermediate and Berry season) and per time of the day (Morn. = mornings, Mid.= midday and Aft.= afternoon/eve).

Cattle farm	***Monitoring period***	***Pre-berry***			***Intermediate***			***Berry***			***Total***
		Morn.	Mid.	Aft.	Morn.	Mid.	Aft.	Morn.	Mid.	Aft.	
Arterasen	14/06 - 13/08	39	35	8	32	51	33	48	59	11	316
Brindberg	19/06 - 20/09	49	45	4	49	49	5	257	429	58	945
Kveksel	14/06 - 02/07	39	10	5	32	14	3	99	63	7	272
	10/07 - 04/08										
Risberg	16/06 - 22/08	73	43	7	152	109	23	170	148	41	766
Skadar Djuberga	19/06 - 19/08	69	47	5	62	40	11	130	185	41	590
Torrlid	25/07 - 09/08	0	0	0	33	26	1	27	29	7	123
Total		269	180	29	360	289	76	731	913	165	**3012**

2.2.1.2. Bear Location data

During the annual bear-marking campaign, bears are located by VHF telemetry and/or snow tracking, and darted and drug-immobilized using an air gun from out of a helicopter. A detailed marking protocol is given in Arnemo (2006). Captured bears were provided with GPS-PLUS collars (VECTRONIC Aerospace GmbH, Berlin, Germany). The collars were scheduled on a 30 minute time-interval. Special effort was made by the capturing team to mark bears in the vicinity of the cattle farms in the study area.

An intersection of the operational study area with all valid bear positions (with a DOP < 5, obtained in the study period (14/06 – 20/09)) resulted in 9347 positions of 11 bears useful for further analysis (Table 2.2). Two of the cattle farms did not overlap with marked bear home ranges and were excluded from the sampling area. Of these 11 bears (6 males and 5 females), 4 bears frequented the study area only sporadically. The bear position data was pooled and divided into three seasons, when coexisting with free-ranging cattle: the pre-berry, intermediate and berry season (as defined in 1.2.1.1.), following Manly's design type I (Manly et al. 1993). During the pre-berry and intermediate season the data was further separated in 6 time frames: 00:00 – 02:30, 03:00 – 04:30, 05:00 – 9:30, 10:00 – 14:30, 15:00 – 20:00 and 20:30 – 23:30; and further referred to as respectively: 'night', 'late night', 'morning', afternoon', 'evening', late evening'. The data availability from the berry season allowed the data to be divided in hourly time-intervals. Data distribution per time step is shown in table 2.3.

Table 2.2: number of valid GPS positions per bear per season.

Bear name	***ID***	***sex***	***age***	***N pre-berry***	***N intermediate***	***N berry***	***Total***
Oda	W0004	f	14	683	242	1999	2924
Bose	W0228	m	10	0	65	678	743
Hirva	W0010	f	9	63	76	245	384
Jamta	W0422	f	5	623	265	1406	2294
Lillen	W0718	m	adult	0	14	9	23
Noen	W0802	m	adult	0	1	0	1
Nacka	W0303	f	6	21	58	6	85
Roudin	W0012	m	17	44	0	0	44
Tjabe	W0827	m	?	96	0	458	554
Tvaska	W0620	f	3	361	132	1039	1532
Vattun	W0805	m	adult	92	94	577	763
Total				1983	947	6417	**9347**

Table 2.3: distribution of pooled bear positions over the seasons and time steps

Timestep	*Pre-berry*	*Intermediate*	*Berry*
1	227	120	816 (256+279+281)
2	248	131	874 (299+290+281)
3	406	159	1068 (271+281+252+254)
4	521	155	1302 (233+227+260+286+296)
5	306	265	1626 (295+276+261+250+289+255)
6	275	117	731 (250+249+232)
Total	1983	947	6417

2.2.2. Spatial data layers

This section elaborates on the acquisition of source data and the derivation of spatial data layers that were assumed necessary for modeling resource selection by brown bears and free-ranging cattle.

2.2.2.1. Source data

The variables to model resource selection of bears and free-ranging cattle were selected based on literature (2.2.2.2.), expert knowledge and field experience. The variables –further on referred to as covariates- were derived from three source layers (satellite imagery, a topographical map and a digital elevation model) that were obtained through the Swedish Land Survey (Lantmateriet) clearinghouse.

I. IRSP6-LISS3 satellite imagery

Two satellite images, obtained through the LISS3 sensor of the IRSP6 satellite, were used to create an up-to-date land-cover classification of the study area, and to derive the Normalized Difference Vegetation Index (NDVI). The images dated from the 2nd and 7th July of 2007. The spatial resolution of the images was 23.5 m. Two image tiles were needed in order to cover the entire study area. A detailed description of the land-cover classification based on these images is given in appendix 3. The images were registered in the Swedish RT90 2.5 gon West reference system.

II. “ Gronkarta” topographical map

A vector based topographical map, referenced in the RT90 2.5 gon West system, was used to derive project source data such as road classes, creeks, lakes and rivers, tracks, villages, settlements and single buildings. Furthermore, the land-use classes “build up”, “agriculture”, “other open land”, “water” and “roads” were derived from the topographical map, converted to raster format and added to the land-cover classification in order to improve its accuracy. Last revision dates from 1997, but the rather static nature of the project source data derived from the topographical map minimizes this shortcoming.

III. DEM – Digital Elevation Model

A 50*50 m raster-based digital elevation model of the area was used as a source to derive terrain ruggedness indices (3 scales), and aspect and slope data. The DEM was generated based on digitizing altitude curves and profile measurements, and was published in 2001. The DEM was referenced in the RT90 2.5 gon West reference system.

The RT90 2.5 gon West reference system is the Swedish standard reference system. This Transverse-Mercator projection has a false easting at 1500000 m. The false northing is 0.0 and is based on Bessels’ earth dimensions. The longitude of the central meridian is 15°48’29.8”, with a scaling factor of 1 (Source: Lantmateriet).

2.2.2.2. Derived data layers

15 covariates were derived from the source data. Because of the nominal nature of two of the variables, i.e. land-cover and aspect, dummy variables for these two classes were created. This resulted in 27 candidate covariates to include in the models (8 dummy variables for aspect and 5 for land-cover) (Table 2.4). This section provides a motivation for each chosen covariate, how the covariates were derived from the source data, and discusses some data characteristics. The derivation of the data layers was performed with ESRI ArcGis 9.2 and/or Leica Geosystems ERDAS IMAGINE 9.1 software packages. Protocols and data action models are included in appendix 1.

Land-cover

An up-to-date land-cover classification is indispensable in resource selection studies. Animals – both species and individuals- use their physical environment in spatiotemporally differential ways, in order to fulfill primary life requirements such as food availability, predation avoidance, microclimate selection, etc (Townsend et al. 2000a). As has already been proven for female brown bear's habitat use in the study area, spatiotemporal variation in land-cover type selection can be large in the short-term (Moe et al. 2007). The following land-cover classes were defined after image classification and integration of topographical map data: bog, young dense forest, young open forest, older forest, road, main road, agriculture, build-up, water and other open land. As this data is nominal, each land-cover type was derived from the land-cover map, and handled as a binary dummy variable in the modeling procedure.

Slope

Steepness has been shown to be determinative in resource selection by female black bears (*Ursus americanus*) in Orogon (Vander Heyden and Meskow 1999), and in grizzly bears (*Ursus arctos*) (Ciarniello et al. 2007). Black bears tend to prefer steeper slopes. The reasons behind this vary from food availability to shelter or predator avoidance, as well as species and individual specific preferences. In this study, slope was derived from the DEM and reclassified in 9 ordinal classes of 5°.

Aspect

The slope aspect is determinative for plant species composition and phenology due to microclimatic variation. Slope aspect therefore alters many ecological processes, including resource selection by animals (Badano et al. 2005). Slope aspect has been included as a variable in modeling habitat use for a range of species, e.g. elk in the Greater Yellowstone ecosystem (Creel et al. 2005), elk, wolf (*Canis lupus*) and black bear in Banff National Park (Clevenger et al. 2002, Hebblewhite et al. 2005). Slope aspect was derived from the DEM, classified in 8 cardinal –and nominal- direction classes (N, NE, E, SE, S, SW, W and NW), and included in the modeling procedure as dummy variables.

Terrain ruggedness (TRI)

Like slope and aspect, terrain ruggedness influences plant species composition, structure and phenology (Nellemann and Thomson 1994). Moreover, Nellemann et al. (2007) have shown that terrain ruggedness affects habitat use by brown bears in the study area. Rugged forested terrain, far from human settlements was used significantly more than expected. This was ascribed to various inherent benefits such as food availability, abundance of denning- and-cover sites and the lower accessibility for humans. In this research, the terrain ruggedness index was calculated based on, but adapted from the index developed by Riley et al. (1999). Rather than taking the sum-change of a central pixel towards its eight neighboring cells of a DEM, the variety of aspect, slope and curvature in a 3*3 kernel was included as well. Curvature was derived from the DEM and classified in 6 classes: from maximum upward concave to maximum upward convex. The terrain ruggedness index was calculated as follows [equation 1]:

$$TRI_r = \frac{\sqrt{(\sigma_r / \sigma_{\max})} \cdot \left[(S_r \cdot C_r \cdot A_r) / (S_r + C_r + A_r) \right]}{TRI_{max}} \qquad \text{[eq. 1]}$$

In which:

- TRI_r = terrain ruggedness index for a given pixel based on the 3*3 sized kernel
- σ_r = variation in elevation in the r-sized kernel
- σ_{max} = maximum observed variation in elevation in the study area
- S_r = relative variety in slope classes for a central pixel and its neighbors (variety of slope classes/ maximum variety of slope classes in a 3*3 kernel in the study area (= 7)).
- C_r = relative variety in curvature classes for a central pixel and its neighbors (variety of curvature classes / maximum variety of curvature classes in a 3*3 kernel in the study area (= 6))
- A_r = relative variety in aspect classes for a central pixel and its neighbors (variety of aspect classes / maximum variety of aspect classes in a 3*3 kernel in the study area (= 9))
- TRI_{max} = maximum observed terrain ruggedness index value in the study area

The resulting TRI values were scaled from 0 to 1, and classified in quartiles. Considering the 50*50 m DEM and a 3*3 kernel, the TRI was thus calculated for a pixel, centering a 150*150 m area. To include terrain ruggedness at larger scales as covariates, the average TRI for each cell over a circular area with a radius of 500 and of 1000 m was calculated, classified into quartiles, and further on referred to as TRI500 and TRI1000.

Normalized Difference Vegetation Index (NDVI)

The NDVI is a spectral vegetation index that strongly correlates with net primary above-ground production. NDVI is being increasingly used as a covariate in ecological studies, with many applications; e.g. monitoring primary production, predicting animal movements and habitat use (Osborne et al. 2001, Pettorelli et al. 2005). The NDVI –and other spectral vegetation indices- is based on contrasting reflectance of vegetation in the red (R) and near infra red (NIR) part of the optical spectrum (Gamon et al. 1995), and calculated according to equation 2.

$$NDVI = \frac{(NIR_r - R_r)}{(NIR_r + R_r)} \qquad \text{[eq. 2]}$$

In which:

- NIR_r = reflectance in the near infrared part of the spectrum
- R_r = reflectance in the red part of the spectrum

The NDVI was calculated based on the IRSP6-LISS3 satellite imagery. Each pixel returned a value ranging from -1 to 1. Negative values indicate pixels free of vegetation cover and high pixel values correspond with dense vegetation cover (Chen and Brutsaert 1998).

Human presence

A number of human presence related variables were derived from a topographical map and included as covariates. For each of these 6 variables (tracks, unpaved roads, roads, cattle farms, single standing buildings and settlements with less than 200 inhabitants), the Euclidean distance from each 20*20 m pixel to the specific feature was calculated. For all of the human presence related covariates, an inverse response between bears and cattle was expected. Bears have been shown to avoid human presence –as is the case in the study area- as a kind of anti-predator behavior (Ciarniello et al. 2006, Moe et al. 2007). For cattle, and domestic livestock, the opposite is most likely true, as human presence can provide shelter, predator protection and forage.

Creeks and open water

Access to water is a primary life requirement for mammals in general. Therefore, as has been done for human-presence proxies, the Euclidean distance from each 20*20 m pixel in the study area to creeks and open water was calculated. These covariates are further referred to as 'Water' and 'Creeks'. All the selected covariates are summarized in table 2.4.

Table 2.4: summary of the selected model covariates. The X's indicate the covariates that were considered to include in respectively bear and cattle resource selection, and encounter risk modeling.

Category	***Covariate***	***Scale***	***Remarks***	***Bear RSF***	***Cattle RSF***	***Risk***
Terrain ruggedness	TRI	Ordinal, quartile classes between 0 and 1	TRI for a center 50*50m cell of a 3*3 kernel.	X	X	X
	TRI500	Ordinal, quartile classes between 0 and 1	Averaged TRI in circle of 500m radius			X
	TRI1000	Ordinal, quartile classes between 0 and 1	Averaged TRI in circle of 1000m radius	X		X
Slope	Slope	Ordinal, 9 classes of 5 degrees	-	X	X	X
Aspect	N	Nominal, 8 classes, all included in the models as dummy variables	-	X	X	X
	NE			X	X	X
	E			X	X	X
	SE			X	X	X
	S			X	X	X
	SW			X	X	X
	W			X	X	X
	NW			X	X	X
Land-cover	Bog	Nominal, 5 classes, all included in the models as dummy variables	Bog and tree rich bogs	X	X	X
	Young dense forest		< 7m trees, > 10000 stems/ha	X	X	X
	Young open forest		< 7m trees, < 10000 stems/ha	X	X	X
	Older forest		> 7 m trees	X	X	X
	Road		Unpaved and paved merged	X	X	X
	Other open land		Forest meadows, settlement land, etc	X	X	X
NDVI	NDVI	Ratio, between -1 and 1	Negative values indicate vegetation absence	X	X	X
Distance to:	Water	Ratio, continuous	Larger lakes and rivers	X		X
	Creeks		Small streams	X	X	X
	Tracks		Inaccessible < 1m hiking track	X	X	X
	Unpaved roads		Usually gravel road	X	X	X
	Paved roads		Concrete roads	X		X
	Cattle farms		-	X	X	X
	Single buildings		Single standing buildings, hunting cabines etc.	X	X	X
	Settlements		Settlements< 200 inhabitants	X	X	X
RSF cattle	-	Interval scale, between 0 and 1	Cattle resource selection function values	X		

2.3. Data analysis

This section gives a general description of the modeling procedure that was applied to create resource selection functions; and the model selection and the model validation process. This section further describes the modeling procedure in specific for cattle and bear resource selection. The cattle and bear RSFs served as a basis for further analysis, to answer the proposed research questions which are elaborated on in sections 2.3.2 and 2.3.3. Figure 2.1 presents a simplified flowchart of the process: from GIS and point location data towards the end results –encounter risk maps-. Bear and cattle resource selection modeling followed the same procedure, with the exception that cattle RSF estimates were included as a covariate in bear RSFs. A more detailed flowchart is presented in appendix 1.

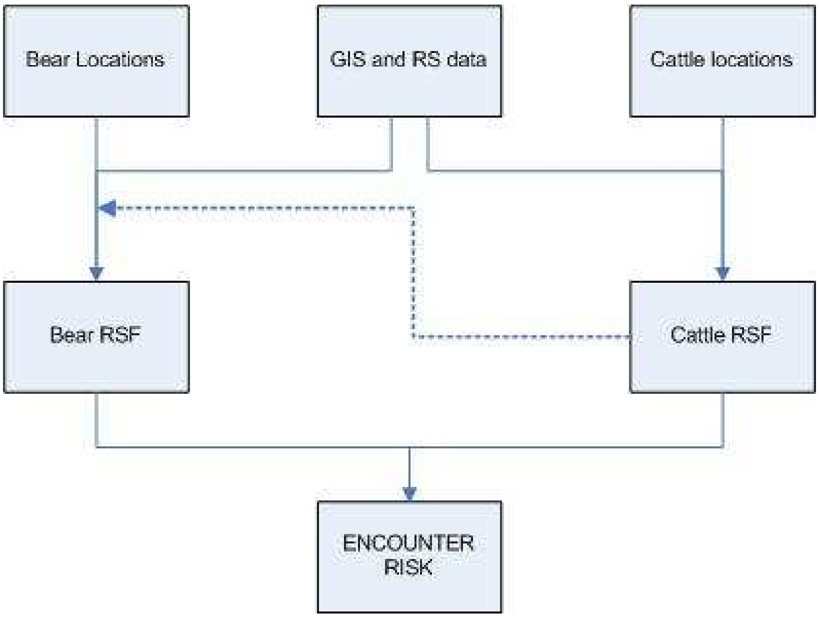


Figure 2.1: simplified flowchart of the modeling procedure.

2.3.1. RSF modeling procedure

Considering the nature of the dependent variable (binomial, 1's and 0's for used/available locations), and the aim of an RSF, i.e. to give a value proportional to the probability of use, logistic regression is an appropriate approach in the modeling process (Manly 2002, Keating and

Cherry 2004). Following Boyce and McDonald (1999), the relation between the relative probability of use of a resource unit ω(x), and a vector of n covariates, $x = x_1, x_2, x_3, \ldots, x_n$ can be estimated by the log-linear form [eq. 3]:

$$\omega(x) = \exp(\beta_0 + \beta_1 \cdot X_1 + \beta_2 \cdot X_2 + \ldots + \beta_n \cdot X_n) \qquad \text{[eq. 3]}$$

The mathematical relation between the Poisson- and the binomial distribution allows for estimating the β coefficients of equation 3 from logistic regression. The estimation function is than estimated by (Manly et al. 1993, Boyce et al. 2002) [eq. 4]:

$$\tau(x) = \frac{\exp(\beta_0 + \beta_1 \cdot X_1 + \beta_2 \cdot X_2 + \ldots + \beta_n \cdot X_n)}{1 + \exp(\beta_0 + \beta_1 \cdot X_1 + \beta_2 \cdot X_2 + \ldots + \beta_n \cdot X_n)} \qquad \text{[eq. 4]}$$

All covariates were first tested for co-linearity with a Spearman Rho correlation test. For pairs of covariates that had a correlation coefficient greater than 0.6, one of the variables from the pair was excluded from the regression. The estimates of the β coefficients could then be implemented in a GIS, in the form of the estimation function τ(x) [equation 4]. As a result, a raster based map with values for each cell proportional to the probability of use of that cell was then created.

Model selection was based on the information theory approach, with Akaike's Information Criteria scores (AIC) as a measure to select the most parsimonious a priori defined candidate model. In brief, the AIC score expresses for each candidate model the amount of information lost, due to the approximation of reality. A mathematical and statistical elaboration of the information theory approach and model selection based on AIC is given in appendix 2.

4 candidate models for modeling resource selection and encounter risk were defined (see section 2.6). These models were defined based on expert knowledge and literature. A land-cover model was defined, assuming that land-cover types were most determinative for bears' and cattle's resource selection. Similarly, a human presence model was defined, with the assumption that anthropogenic 'sources' as roads, settlements etc. were most determinative in resource selection by both bears and cattle. Additionally, an expert model was defined, including only the

covariates that were expected to be most determinative for both species' resource selection. Finally, an all-inclusive model was decided to be included as well.

Each candidate model was cross validated by the default 10-fold cross validation procedure for generalized linear models (GLM's) of the binary family of "R", of the DAAG package. This implies that the dataset was randomly assigned to a number of 'folds' (i.e. a random part of the data set). Each fold was removed once, while the remaining data was used to refit the GLM, and to predict the excluded observations. The procedure returned a cross-validation estimate of accuracy, i.e. a percentage that indicates how well the model predicted on the excluded n-fold data.

When standard errors (SE) of the estimates of covariates (β) showed extreme values (>10 times the value of the SE), the variable was excluded from the analysis, and the model rerun.

The estimates of the covariates were evaluated by plotting them with standard errors or 95% confidence intervals over appropriate time steps, and checking the level of significance for each estimate of the covariate. Significantly positive β-values indicated true preference for a given variable, and vice-versa with negative values. β-coefficients with non-significant p-values (which include 0 in their confidence interval) could not be considered as preferred or avoided. In contrast with the information theory approach (see appendix 2), p-values –were here considered as meaningful and informative, in order to evaluate the importance of the covariates in resource selection.

2.3.1.1. Cattle resource selection modeling

RSFs for cattle were determined according to Manly's sampling design type I. This implies that cattle data was pooled over cattle farms –with each herd still identifiable-, and created RSFs per season and per time step (Manly 2002). All cattle locations were assigned a "1", or a "used position". 100% MCP home ranges were created for each cattle herd. Overlapping home ranges were merged into one. Map 2.1. shows the 100% MCP home range per cattle herd. This 100% MCP dissolved home range area was defined as the "cattle study area". Unused land use classes (open water, build-up and unclassified, agriculture and main road) were masked prior to drawing a random number of points from the cattle study area. The random points had a density of ~ 1/0.5 ha and were assigned a "0". This density of random points was chosen following Ciarniello et al. (2006).

The following covariates were assumed to be relevant for resource selection by cattle:

- TRI
- Slope
- Distance to tracks (Tracks)
- Distance to unpaved roads (Unpaved)
- Distance to cattle farms (Farms)
- Distance to single standing buildings (Buildings)
- Distance to small settlements (Settlements)
- Distance to creeks (Creecks)
- NDVI
- Land-cover (Bog, Young dense forest, Young open forest, Older forest, Road, Other open land)

These covariates were extracted in ArcGis for the cattle point locations and the random points. For each model, a dataset was created, comprising of the appropriate selected cattle locations (e.g. pre-berry - afternoon), and for each cattle location, 4 random points. Aspect was excluded out of the analysis for cattle RSF, as high autocorrelation was expected, considering the farm location, and the point density in relation to distance to the farms.

Using 15 covariates, 4 candidate models were defined:

1. *All-inclusive:* all 15 above mentioned variables
2. *Land-cover:* Bog + Young dense forest + Young open forest + Older forest + Road + Other open land
3. *Human presence:* Tracks + Unpaved + Farms + Buildings + Settlements
4. *Expert:* TRI + Unpaved + Farms + Bog + Young open forest + Older forest + Road + Other open land

2.3.1.2. Bear resource selection modeling

Bear RSFs were modeled following a protocol similar to that used for cattle resource selection modeling. Random locations, representing resource availability in the study area were drawn in a 4/1 ratio in respect of the “used” locations within the coexistence study area. Again, unavailable land use classes or environmental variables not present in this area were withdrawn from the analysis. The following variables were assumed relevant for bear habitat use:

- Terrain ruggedness (TRI, TRI500, TRI1000)
- Slope
- Aspect (N, NE. E, SE, S, SW, W, NW)
- Distance to tracks (Tracks)
- Distance to unpaved roads (Unpaved)
- Distance to paved roads (Car)
- Distance to cattle farms (Farm)
- Distance to single buildings (Building)
- Distance to small settlements (Settlement)
- Distance to creeks (Creek)
- Distance to open water (Water)
- NDVI
- Land-cover (Bog, Young dense forest, Young open forest, Older forest, Road, Other open land)
- Resource selection functions by cattle, for each particular modeling time step (RSF)

Using the 28 covariates, 4 candidate models were predefined and run in “R” for each of the defined time steps:

1. *All-inclusive:* includes all 28 above mentioned variables
2. *Land-cover:* NDVI + Bog + Young dense forest + Young open forest + Older forest
3. *Human presence:* Building + Settlement + Tracks + Unpaved + Car + Farm
4. *Expert:* Building + Settlement + Tracks + Unpaved + Car + NDVI + Bog + Young dense forest + Young open forest + Older forest

2.3.2. Research question I: How does bears' and free-ranging cattle resource selection relates?

The outputs of the resource selection modeling procedures for both cattle and brown bears served as an input to answer this research question. In order to visualize resource selection of both species for each defined time step, the estimates of the covariates were entered into a single map algebra expression in ESRI ArcGIS 9.2 following the logistic regression equation [2]. The first step in assessing this research question was a visual interpretation of resource selection maps.

Encounter risk maps were created by multiplying the resource selection values for each pixel of a given RSF map. The encounter risk maps were visually interpreted to get a better understanding in bear-cattle resource selection relations.

To strengthen further analysis, a more confined area was selected, in which the relative probability for bear-cattle encounters was found to exceed the 5% (further on referred to as the "encounter-risk area"). This threshold was chosen according to traditional statistical testing –as 5 % can still be a significant risk-, and to avoid over-sampling in low co-existence areas.

The relation between cattle and bear resource selection was numerically expressed by correlating resource selection maps of both species for any given time step. Therefore, the encounter risk area was randomly sampled with point density of 0.5 points/ha, resembling 9848 random points. Bear and cattle resource selection values for these 9848 points were extracted from each RSF map. The resulting dataset, a bear-cattle resource selection value paired sample dataset, enabled further statistical testing. As the data was non-parametric, Spearman Rho Correlation tests were performed between each time step for bear and cattle resource selection values. Additionally, Sign tests and Marginal Homogeneity tests were performed for each appropriate time step, to test whether general bear and cattle resource selection was statistically different. These tests were performed in the SPSS 16.0 statistical software package after the dataset was binned into 0.05 probability classes. The use of significance testing was believed to be justified here, as in combination with the correlation coefficients, the p-values have an informative meaning.

Additionally, significance levels of estimated covariates were evaluated, and time-series of estimates of covariates (and standard errors) of both cattle and/or brown bear resource selection were plotted to visualize and evaluate covariate behavior over time. These plots were made in the open source statistical software package of R for every covariate and time step.

2.3.3. Research Question II: Which factors determine encounter risk probabilities?

A GLM of the Poisson family was chosen to derive the determinative covariates for bear-cattle encounter probabilities. The encounter risk values of the encounter risk maps were therefore binned into ordinal 0.05 probability classes, and served as the dependent variable in the regression process.

All covariates defined in section 2.2.2.2 were assumed as independent variables. Both the values of the dependent and independent variables were extracted by a random point sample of 2 points/ha in the encounter risk area (thus again resembling 9848 points).

All models were 10-fold cross validated. Based on AIC scores, the most parsimonious model of 4 a priori defined models was selected for each time step and season. The candidate risk models had the following forms:

1. *All-inclusive:* includes all variables as mentioned in 2.2.2.2.
2. *Human presence:* Building + Settlement + Tracks + Unpaved + Car + Farm + Road + Other open land
3. *Land Use:* Road + Bog + Young dense forest+ Young open forest + Older forest + Other open land
4. *Expert:* Building + Settlement + Unpaved + Water + NDVI + Farm + Road + Young dense forest + Other open land

The significance levels of the estimated coefficients for each covariate were then evaluated and plotted over time in the “R” statistical software package.

3. Results

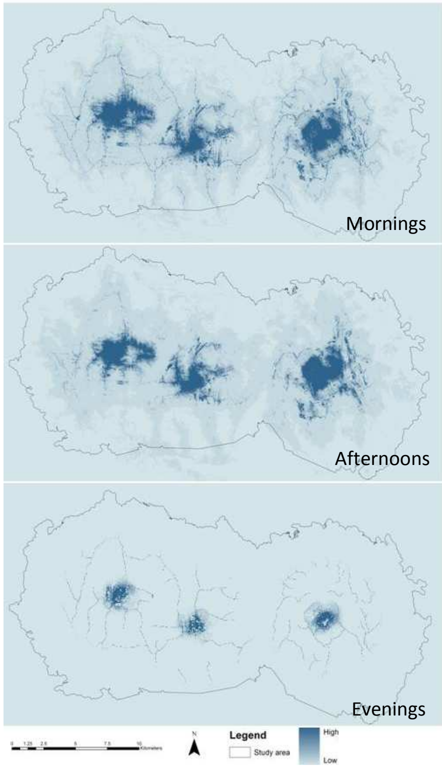
3.1. Model selection

The all-inclusive, a priori defined candidate models generally performed best in predicting resource selection by bears and cattle. For all time steps during the pre-berry and the berry season, the all-inclusive model for bear resource selection was selected. Only once, during the intermediate season in the afternoons, the expert model for bear resource selection had the lowest AIC score and was chosen as the most parsimonious. The expert model was selected twice for cattle resource selection, during the “evening” time step in the pre-berry and berry season. For all selected models, the likelihood or the plausibility of having selected the model with the minimum of information loss relative to reality was 1 (on a scale from 0 to 1, see appendix 2). The probability of having selected the most parsimonious model was in all but one case very close to 1 (0.6527 for cattle in the intermediate season, in the evening period). Sample sizes for bear resource selection models ranged between 565 (intermediate season, from 21:30 to midnight) to 2595 (pre-berry season, from 10:30 to 15:00). Model accuracy ranged from 76.2 to 88.2% after a 10 fold cross validation. Sample size of the cattle resource selection models ranged from a minimum of 145 points (pre-berry season, evening) to 4565 sample points (berry season, afternoon). All selected cattle resource selection models had an estimated accuracy between 86.3 and 92.4% after a 10-fold cross validation.

For the encounter risk models, the all-inclusive candidate model performed best. The human presence model was selected three times, in the evening periods of the pre-berry and intermediate season, and from the 13:00 to 14:00 time-interval during the berry season. Sample size was equal for all models (N = 9848), as this Poisson regression did not depend directly on animal positions, but on a random sample of points within a predefined area. The accuracy, here expressed as the estimation of the prediction error (i.e. the standard error of the prediction) was generally lower than 1. Note that 1 represents one 0.05 binned risk probability class. Details of each model selection procedure are given in appendix 4. The resulting selected RSFs, encounter risk models and their coefficients are given in appendix 5.

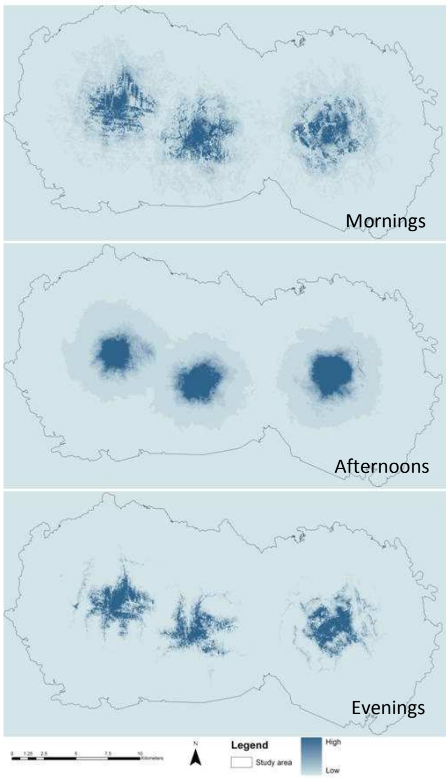
3.2. Cattle resource selection

Implementing the regression coefficients of a selected RSF in a GIS resulted in cattle resource selection maps, in which each pixel represents a probability relative to the use of that pixel by cattle during the particular study period. Cattle resource selection is shown in maps 3.1, 3.2 and 3.3, which represents the eastern part of the bear-cattle coexistence area, for morning, afternoon and evening time steps in the pre-berry, intermediate and berry season.



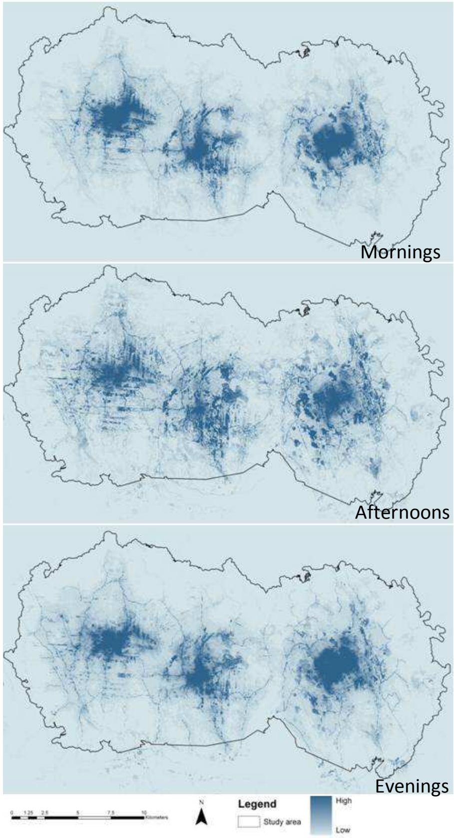
Map 3.1: resource selection of free-ranging cattle in the pre-berry season, during mornings (upper map), afternoons (middle map) and evenings (lower map).

The most obvious pattern that was observed in each map is the somehow concentrically diminishing pattern in resource selection around a central area. These cores are located around the cattle summer farms. The probability that a pixel will be used by cattle seems to be negatively related with the distance to a cattle farm. In all maps, linear patterns can be observed in certain extent. These lines represent unpaved roads or tracks.



Map 3.2: resource selection of free-ranging cattle in the intermediate season, during mornings (upper map), afternoons (middle map) and evenings (lower map).

Not all the cattle maps originated from the all-inclusive candidate model. Cattle pre-berry and intermediate 'evening' maps therefore differed somehow from the others, as NDVI, slope, young dense forest, distance to creeks, buildings, settlements and tracks were not included as covariates in these models. However, these ‘expert’ models were chosen by AIC scores and weights, and were considered the most suitable to describe cattle resource selection at these specific times. The resource selection patterns for cattle during afternoons in the intermediate season deviated from all other models. The land-cover covariates (bog, young dense, young open, etc) were excluded from the model, as the standard error of these estimated covariate coefficients reached extreme values. Without these covariates, the all-inclusive model scored better than the other candidates and was thus selected.



Map 3.3: habitat use of free-ranging cattle in the berry season, during mornings (upper map), afternoons (middle map) and evenings (lower map).

Numerical expression of covariates gives a more profound insight in cattle responses to environmental variables. Table 3.1 shows the response of cattle to each selected covariate. During the pre-berry season, cattle showed a clear negative relation with distance to cattle farms, thus preferring closer distances to these farms. There was a similar relation for distances to single standing buildings, tracks or unpaved roads, in the mornings or afternoons. In the evenings, these preferences were unknown or had no direct influence on cattle resource selection. The habitat classes “road” and “other open land” influenced cattle resource selection in a positive way. It therefore suggests that cattle were attracted by these land-cover types, at least during mornings and afternoons. Slope remarkably affected cattle resource selection in a positive way as well. The other covariates, NDVI, distance to settlements, bogs, older forests, young forests, distance to creeks and TRI did not have a significant influence on cattle resource selection during the pre-berry season.

During the intermediate season, we observed a similar pattern as in the pre-berry season, for distance to farms and unpaved roads, and for the land-cover type ‘other open land’. TRI and creeks as well, were determinative covariates. Cattle avoided creeks during mornings and afternoons, and selected more rugged terrain during afternoons and evenings. Because of the occurrence of many unknown responses to covariates, it was unreliable to evaluate other covariates.

Slope, distance to creeks and settlements, the land-cover types ‘young dense forest’ and ‘older forest’ had no strong influence on cattle resource selection in the berry season. Cattle preferred closer distances to cattle farms, tracks and unpaved roads. Roads and other open land were preferred land-cover type, as well as bogs. Young open forests seemed to be selected during mornings. Areas with a high NDVI were avoided during mornings and afternoons, and rugged terrain was preferred by cattle in the berry season.

In general, over the whole study period, we found that the distance to cattle farms and to unpaved roads, as well as the land-cover types ‘roads’ and ‘other open land’ were determinative for cattle habitat use and resource selection.

Table 3.1: influence of model covariates on cattle habitat use in during mornigs (m), afternoons (a) and evenings (e) in the pre-berry season, the intermediate season and the berry season. - , 0 and + indicate respectively negative, none and positive influence of the covariate with a significance level of 0.05. ‘?’ indicates unknown, as the covariate was not included in the most parsimonious model.

		Pre-berry			***Intermediate***			***Berry***		
	Covariate	**m**	**a**	**e**	**m**	**a**	**e**	**m**	**a**	**e**
Distance to:	**buildings**	-	-	?	-	-	?	0	+	0
	cattle farms	-	-	-	-	0	-	-	-	-
	creeks	0	0	?	+	+	?	0	0	0
	settlements	0	0	?	0	0	?	0	0	0
	tracks	-	-	?	0	+	?	-	-	-
	unpaved roads	-	-	0	-	0	-	-	-	-
Land cover	**Young dense forest**	0	0	?	0	?	0	0	0	0
	Young open forest	0	0	0	0	?	-	+	0	0
	Bog	0	0	?	0	?	?	+	+	+
	Older forest	0	0	0	0	?	-	0	0	0
	Road	+	+	0	0	?	0	+	+	+
	Other open land	+	+	0	+	?	+	+	+	+
Terrain	**Slope**	+	+	?	-	0	?	0	0	0
	NDVI	0	0	?	0	-	?	-	-	0
	TRI	0	0	0	0	+	+	+	+	+

Two determinative covariates, influencing cattle resource selection in a positive way –distance to cattle farms and unpaved road- were plotted for the three seasons, to give an impression of the magnitude of cattle response to these covariates. The responses of bears to these variables were included in the plots as well (fig. 3.1).

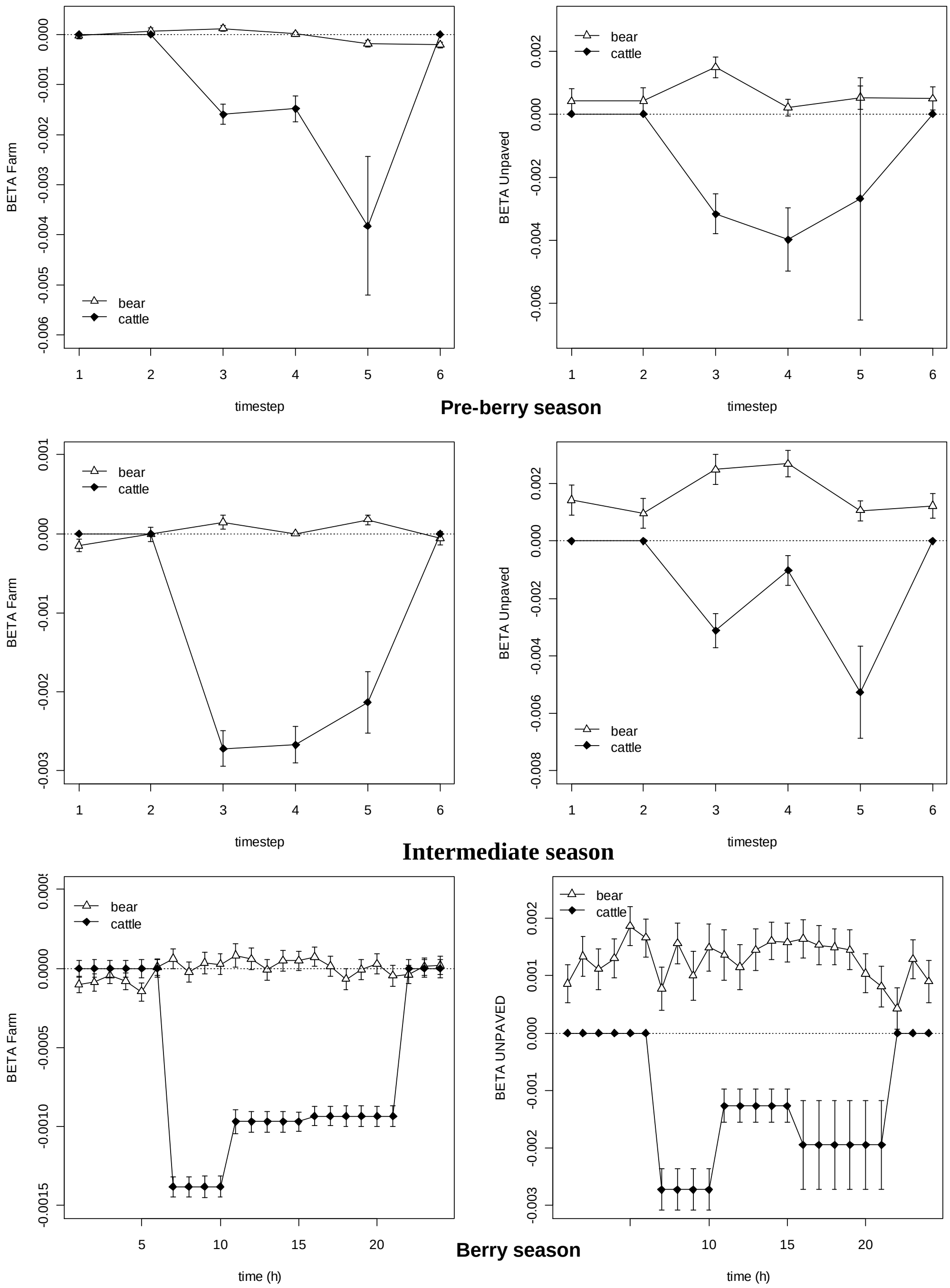


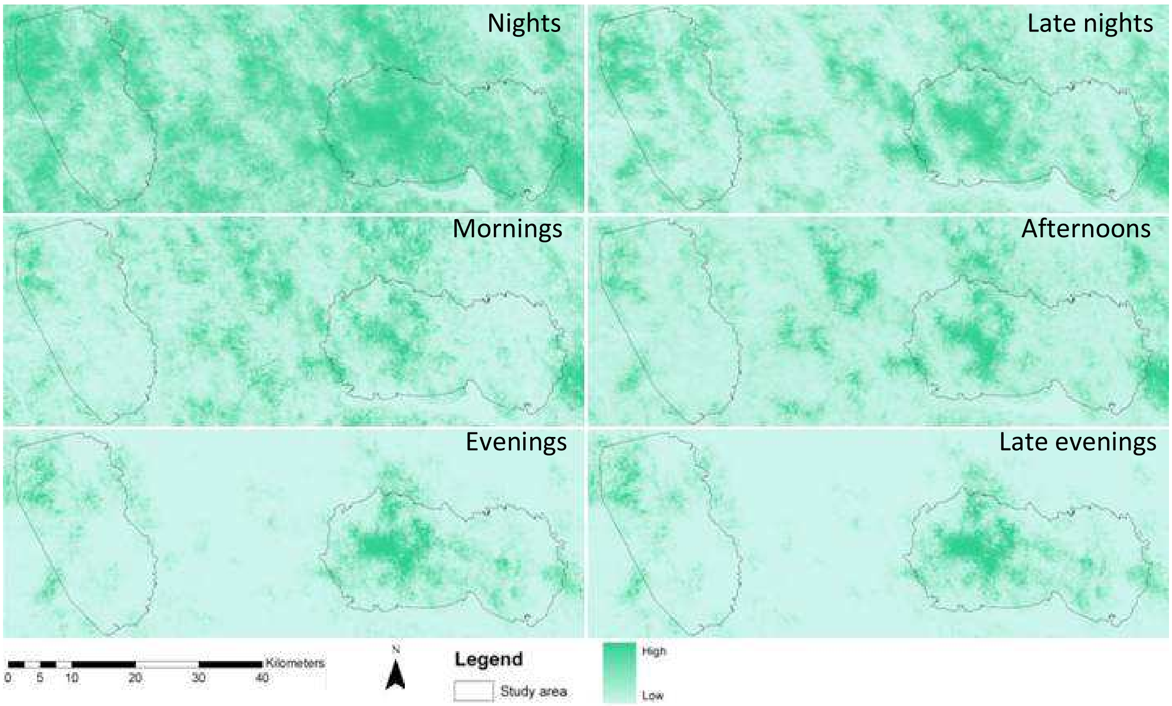
Figure 3.1: cattle –and bear- response to distance to cattle farms (left) and distance to unpaved roads (right) during the pre-berry, intermediate and berry season. Bars indicate standard errors of model coefficient estimates (Beta 'covariate', on the y-axis).

Cattle responses at night, late night and late evening was put 0, as the cattle were inside the farm enclosures and thus not coexisting with bears at these times. During mornings, afternoons and evening, or the hourly intervals during these time steps (during the berry season), all cattle responses to distance to farms and unpaved roads over each season and time step were –if not strongly- negative.

3.3. Bear resource selection

3.3.1. Pre-berry season

Visual interpretation of bear resource selection maps during the berry season showed that the probability that a pixel was used by bears during the pre-berry season was most evenly distributed over the study area at night and gradually decreased –and thus showed more 'clustered' patterns- in the late night and mornings. This implies that bear habitat use became less random over these time steps. The clustered pattern remained during afternoons, evenings and late evenings (map 3.4).



Map 3.4: bear resource selection in the pre-berry season, for each time step of the day.

Two parts of the study areas seemed to be selected more than other areas by bears, i.e. northwest in the western study area and west in the eastern area. These two areas were situated around 2 of the cattle farms included in this study.

Expressing the responses of bears to each covariate included in the RSF numerically (see appendix 4), and summarizing each response into negative, no and positive effect classes (-, 0 and +) according to a $\alpha = 0.05$ significance level gave more insight in bear resource selection (Table 3.2). Open water and paved roads were avoided during each time step. Settlements and single standing buildings were avoided at certain time steps, and otherwise did not affect bear resource selection. Unpaved roads had no effect on bear resource selection, except during the morning time. Tracks seemed to attract bears, except during mornings and afternoons, when tracks did not strongly affect bear's resource selection. Creeks seemed to have a positive effect on bears' habitat selection, but not during nighttime, evenings and late evening. Bears avoided cattle farms during the mornings, but seemed to be attracted to them at nighttime. Distance to cattle farms otherwise did not significantly affect bears' habitat selection.

Young open and young dense forests were selected during night time and the latter during mornings as well. Otherwise young forests did not show any selection influence. Bogs and older forest were avoided during the afternoons. The NDVI showed to be a strong determinative covariate; bears selected pixels with high NDVI values, except during nighttime, when NDVI appeared to have no strong effect on bear habitat selection.

Terrain features as slope, aspect, TRI and TRI1000 were not determinative in bears' resource selection during the pre-berry season.

The response of bears to single standing buildings, settlements, open water and paved roads was plotted and shown in figure 3.2 and 3.3 to give an impression of the magnitude of the response by bears to these covariates. These graphs revealed that bears avoided paved roads and open water strongly during each time step in the pre-berry season.

Table 3.2: influence of model covariates on bear habitat use during the pre-berry season, for 6 time steps. - , 0 and + indicate respectively negative, no and positive influence of the covariate on resource selection with a significance level of 0.05. '?' indicates unknown, as the variable was not included in the most parsimonious model.

	Covariate	*Night*	*Late night*	*Morning*	*Afternoon*	*Evening*	*Late evening*
Distance to:	**buildings**	0	+	0	0	0	0
	cattle farms	0	0	+	?	0	-
	creeks	-	-	-	-	0	0
	open water	+	+	+	+	+	+
	paved roads	+	+	+	+	+	+
	settlements	0	+	0	+	+	+
	tracks	-	0	0	-	-	-
	unpaved roads	0	0	+	0	0	0
Aspect	**N**	0	0	?	0	0	0
	NE	0	0	?	0	0	0
	E	0	0	?	0	0	0
	SE	0	0	?	0	0	0
	S	0	0	?	0	0	0
	SW	0	0	?	0	0	0
	W	0	0	?	0	0	0
	NW	0	0	?	0	-	-
Land cover	**Young dense forest**	+	?	+	0	0	0
	Young open forest	+	?	0	0	0	0
	Bog	0	?	0	-	0	0
	Older forest	0	?	0	-	0	0
	Other open land	?	?	?	?	0	0
Terrain	**Slope**	0	0	0	0	0	0
	NDVI	0	+	+	+	+	+
	Cattle RSF	?	?	+	0	0	?
	TRI	0	0	0	0	0	0
	TRI1000	0	0	0	0	0	0

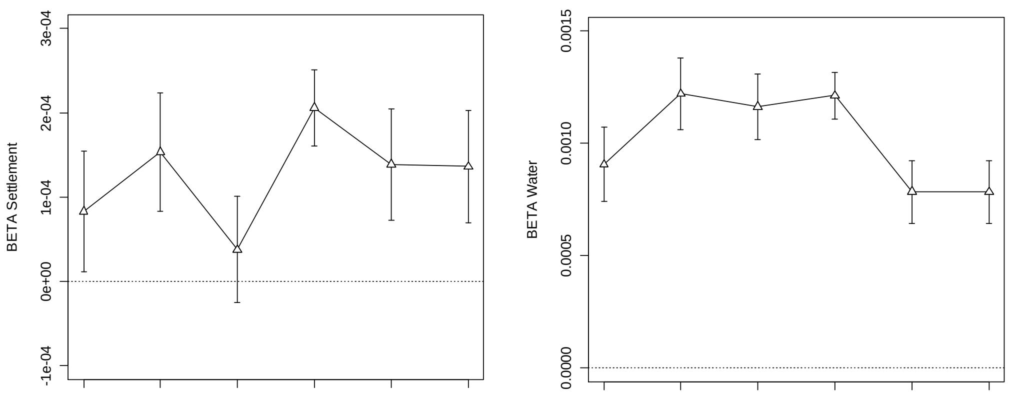


Figure 3.2: bear response to distance to settlements (left) and distance to open water (right) during the berry season. Bars indicate standard errors of model coefficient estimates.

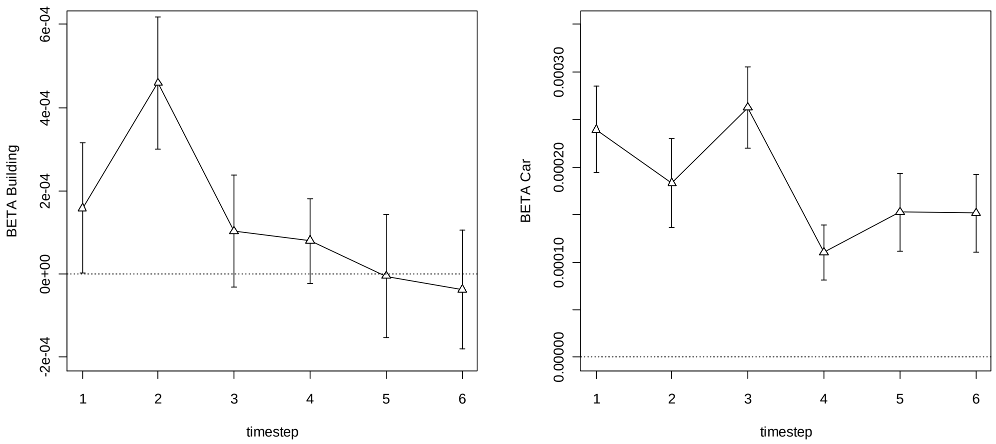
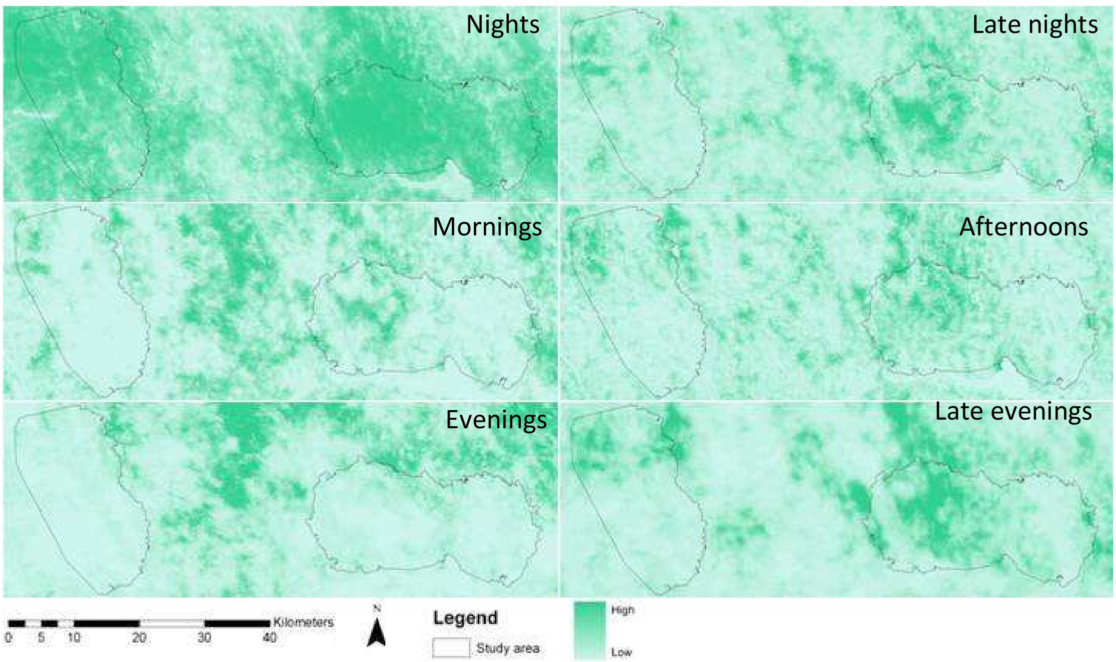


Figure 3.3: bear response to distance single buildings (left) and distance to paved roads (right) during the pre-berry season. Bars indicate standard errors of model coefficient estimates.

3.3.2. Intermediate season



Map 3.5: bear resource selection in the intermediate season, for each time step of the day.

Similar as during the pre-berry season, bears seemed to use the study area most evenly during nighttime, and more clustered patterns in habitat use appeared during the other time steps (map

3.5). The two heavily used areas, as mentioned in 3.3.1. were used again frequently, except during evenings, when bear's habitat use was situated more to the north of the study area.

Land-cover types, as well as slope aspect were often excluded in the models, due to extreme standard errors. Table 3.2 expresses bear responses to the covariates included in the models. Distance to unpaved and paved roads, and to open water were strong determinants for bears' resource selection during the intermediate season. Bears selected areas preferably further away from these covariates.

Table 3.3: influence of model covariates on bear habitat use during the intermediate season, for 6 time steps. - , 0 and + indicate respectively negative, none and positive influence of the covariate with a significance level of 0.05. '?' indicates unknown, as the variable was not included in the most parsimonious model.

	Covariate	***Night***	***Late night***	***Morning***	***Afternoon***	***Evening***	***Late evening***
Distance to:	**buildings**	0	+	0	0	+	0
	cattle farms	-	0	0	?	+	0
	creeks	+	-	-	?	-	-
	open water	+	+	+	?	+	+
	paved roads	+	+	+	+	+	+
	settlements	0	0	+	0	+	+
	tracks	0	0	-	0	-	-
	unpaved roads	+	+	+	+	+	+
Aspect	**N**	0	?	?	?	0	?
	NE	0	?	?	?	0	?
	E	0	?	?	?	0	?
	SE	0	?	?	?	0	?
	S	0	?	?	?	0	?
	SW	0	?	?	?	0	?
	W	0	?	?	?	0	?
	NW	+	?	?	?	0	?
Land cover	**Young dense forest**	?	?	?	?	0	?
	Young open forest	?	?	?	?	0	?
	Bog	?	?	?	?	0	?
	Older forest	?	?	?	?	0	?
	Other open land	?	?	?	?	?	?
Terrain	**Slope**	0	0	-	?	0	0
	NDVI	0	+	+	+	+	0
	Cattle RSF	?	?	0	?	+	?
	TRI	0	0	+	?	+	0
	TRI1000	0	0	0	?	0	-

Bears were attracted by creeks, except during night time, when they avoid them. Settlements were avoided as well, during mornings, evenings and late evenings, and did otherwise not significantly affect bears' resource selection. Similar for single standing building, bears selected areas further away from them during late nights and evenings. NDVI again showed to be a strong determinant for bear habitat use. Figure 3.4. (left) shows the trend of the estimated covariate 'NDVI' during the scope of the day in the intermediate season. Similar as in the pre-berry season, bears preferred areas with high NDVI values, especially during daytime (mornings, afternoons and evenings). As examples, the behavior of distance to paved roads, tracks and buildings as covariates are presented in figure 3.4 and 3.5.

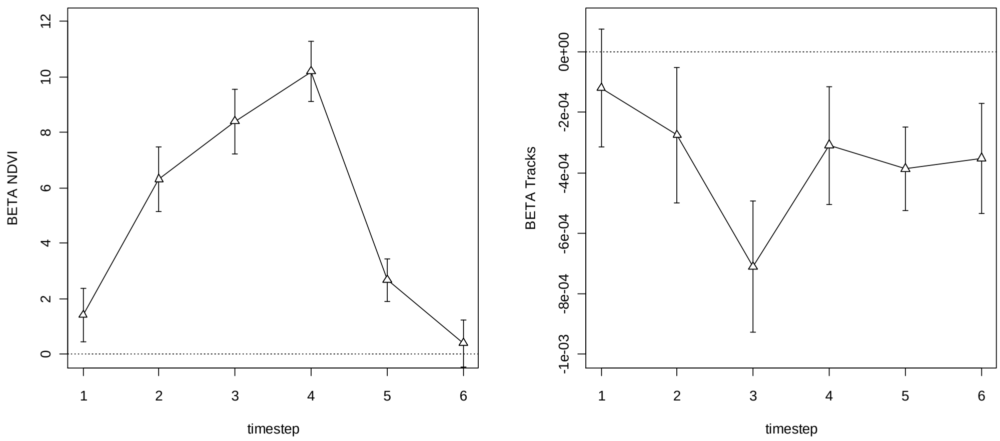


Figure 3.4: influence of model covariates on bear habitat use during the intermediate season, for 6 time steps. - , 0 and + indicate respectively negative, none and positive influence of the

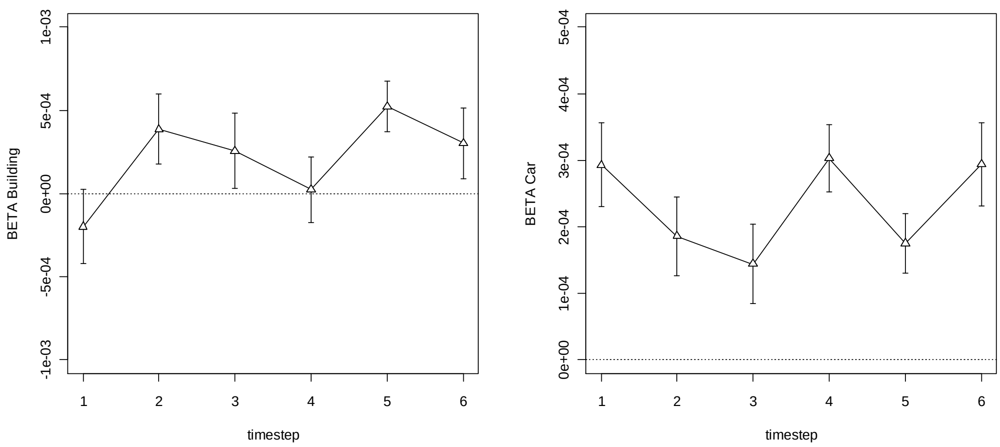
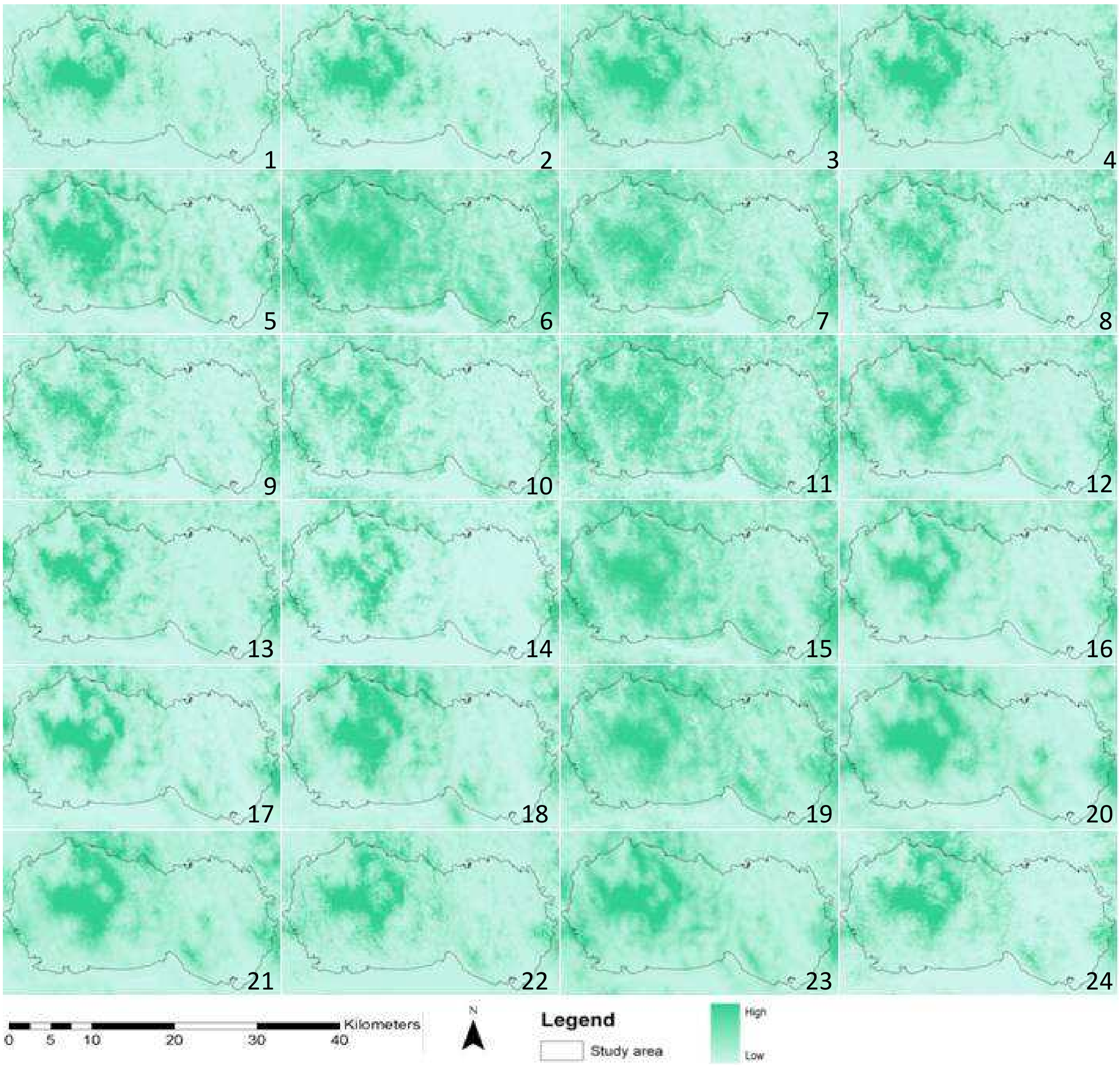


Figure 3.5: bear response to distance settlements (left) and distance to paved roads (right) during the intermediate season. Bars indicate standard errors of model coefficients estimates.

3.3.3. Berry season

Map 3.6 shows bear's resource selection in the berry season for each hourly time-interval during a day, from the eastern part of the study area. In all of the time-intervals, some clear patterns can be observed. Habitat use can be considered clustered and non random. One area is used by bears in higher proportion than other areas (the Western part). This area is situated around the cattle farms of Skadar Djuberga and Kveksel. Numerically expressed responses to covariates gave a better understanding of bear's resource selection (table 3.4).



Map 3.6: bear resource selection in the berry season, from each hour of the day, from midnight (upper left) onwards.

Similar as in the pre-berry and the intermediate season, bears –if not strongly- avoided settlements, paved and unpaved roads, and open water. Single standing buildings did not show a strong influence on bears' resource selection, as well as distance to the cattle farms and tracks. Creeks attracted bears during mornings and early afternoons.

Aspect, slope, TRI and TRI1000 did not strongly affect resource selection by bears in the study area and period. Young forests and older forests appeared to be selected during mornings, from about 7:00 to 10:00. Other land-cover types did not strongly affect bears habitat use. The NDVI again showed to be a relatively strong determinant in bears' resource selection, and influenced bear's resource selection positively, mainly during daytime.

Figures 3.6 and 3.7 present bear responses to NDVI, distance to settlements, young dense forests and open water; in estimated values for their regression coefficients. The NDVI shows a clear pattern of increasing significance in resource selection from night to midday, and decreases again from midday towards the evening.

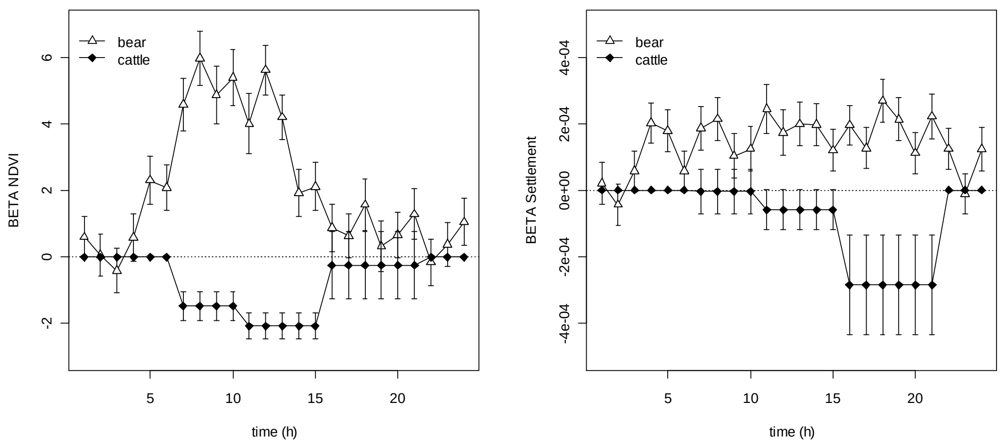


Figure 3.6: bear –and cattle- response to NDVI (left) and distance to settlements (right) during the berry season. Bars indicate standard errors of model coefficient estimates.

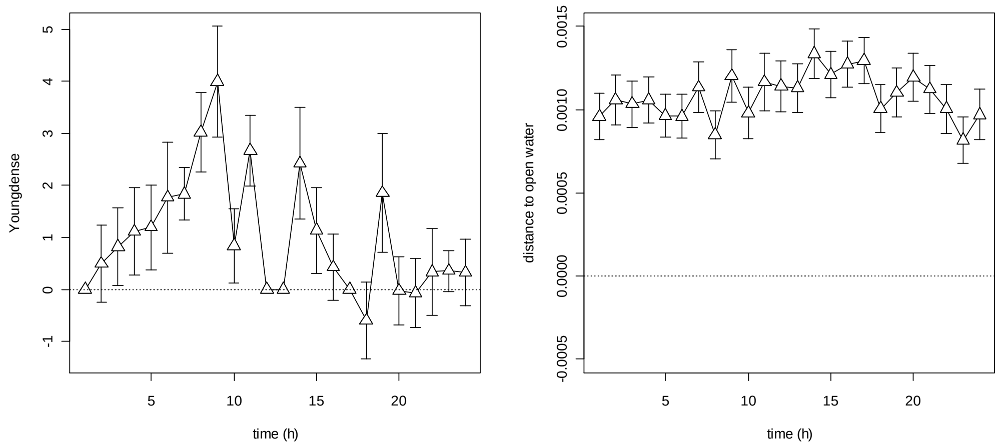


Figure 3.7: bear –and cattle- responses to young dense forests (left) and distance to open water (right) during the berry season. Bars indicate standard errors of model coefficient estimates.

Table 3.4: influence of model covariates on bear habitat use during the berry season, for hourly time steps (1- 24). -, 0 and + indicate respectively negative, none and positive influence of the covariate with a significance level of 0.05. '?' indicates unknown, as the variable was not included in the most parsimonious model.

		Night			***Late night***			***Morning***				***Afternoon***					***Evening***						***Late evening***		
	Covariate	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Distance to:	**buildings**	-	0	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0
	cattle farms	-	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	creeks	+	0	0	0	0	0	0	0	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0
	open water	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	paved roads	+	+	+	+	+	+	0	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	settlements	0	0	0	+	+	0	+	+	0	0	+	+	+	+	0	+	+	+	+	0	+	+	0	0
	tracks	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	unpaved roads	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0	+	+
Aspect	**N**	-	0	0	0	?	0	0	?	?	?	0	?	0	0	0	0	0	0	0	?	0	0	?	0
	NE	-	0	0	0	?	0	0	?	?	?	0	?	0	0	0	0	0	0	0	?	0	0	?	0
	E	-	0	0	0	?	0	0	?	?	?	0	?	0	0	0	0	0	0	0	?	0	0	?	0
	SE	-	0	0	0	?	0	0	?	?	?	0	?	0	0	0	0	0	0	0	?	0	0	?	0
	S	-	0	0	0	?	0	0	?	?	?	0	?	0	0	0	0	0	0	0	?	0	0	?	0
	SW	-	0	0	0	?	0	0	?	?	?	0	?	0	0	0	0	0	0	0	?	0	0	?	0
	W	-	0	0	0	?	0	0	?	?	?	0	?	0	0	0	0	0	0	0	?	0	0	?	0
	NW	-	0	0	0	?	0	0	?	?	?	0	?	0	0	0	0	0	0	0	?	0	0	?	0
Land cover	**Young dense forest**	?	0	0	0	0	0	+	+	+	0	+	?	?	+	0	0	?	0	0	0	0	0	0	0
	Young open forest	?	0	0	0	0	0	+	+	+	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0
	Bog	?	0	0	0	0	0	?	?	?	0	?	?	?	0	0	0	?	0	0	0	0	0	?	0
	Older forest	?	0	0	0	0	0	+	+	+	0	0	?	?	0	0	0	?	0	0	0	0	0	0	0
	Other open land	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Terrain	**Slope**	+	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	+	0	0	0	0	0	0	0
	NDVI	0	0	0	0	+	+	+	+	+	+	+	+	+	+	+	0	0	0	0	+	0	0	0	0
	Cattle RSF	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	+	0	0	0	+	+	?	?	?
	TRI	+	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	+	0	0	+	0	0
	TRI1000	+	0	0	+	0	0	0	0	+	0	0	+	+	0	0	0	0	0	0	0	0	0	0	+

3.3.4. Bear vs. cattle resource selection

Resource selection values from pixels selected by a random draw of 9848 points in a predefined > 0.05 risk probability area from cattle and bears were extracted from the resource selection maps and binned, for each time step and season. With the resulting data set, the relation between cattle and bear resource selection was tested. Table 3.5 shows the test results. The Sign tests and the progressive Marginal Homogeneity test revealed that bear and cattle resource selection strongly differed from each other, in each time step and season. The p-values of the Spearman rho correlation test as well, all showed a strong level of significance. The correlation coefficients were negative in general, except for 5 time-intervals, at evenings in the intermediate season, and at 4 time-intervals in the evening period during the berry season. During the three seasons, the correlation coefficients increased during the scope of the day (figure 3.8). Even dough the correlation coefficients all had a strong level of significance, the correlation coefficients itself were close to 0.

Table 3.5: Test results of a Spearman 's Rho correlation test (Srho), its p values and correlation coefficients (CC); and P values of a marginal homogeneity test (p. MH) and Sign test (p. S) between 0.05 binned pixel values of cattle and bear resource selection maps, in the pre-berry, intermediate and berry season (pb, I and b) during mornigs, afternoons and evenings (m, a, e) or hourly time steps (7, 8, …, 21).

Season	T	Srho CC	p, Srho	p, MH	p, S
pb	m	-0.348	< 0.001	< 0.001	< 0.001
pb	a	-0.283	< 0.001	< 0.001	< 0.001
pb	e	-0.058	< 0.001	< 0.001	< 0.001
i	m	-0.089	< 0.001	< 0.001	< 0.001
i	a	-0.126	< 0.001	< 0.001	< 0.001
i	e	0.037	< 0.001	0.006	< 0.001
b	7	-0.048	< 0.001	< 0.001	< 0.001
b	8	-0.059	< 0.001	< 0.001	< 0.001
b	9	-0.036	< 0.001	< 0.001	< 0.001
b	10	-0.139	< 0.001	< 0.001	< 0.001
b	11	-0.152	< 0.001	< 0.001	< 0.001
b	12	-0.126	< 0.001	< 0.001	< 0.001
b	13	-0.021	< 0.001	< 0.001	< 0.001
b	14	-0.042	< 0.001	< 0.001	< 0.001
b	15	-0.040	< 0.001	< 0.001	< 0.001
b	16	-0.036	< 0.001	< 0.001	< 0.001
b	17	0.044	< 0.001	< 0.001	< 0.001
b	18	0.019	< 0.001	< 0.001	< 0.001
b	19	-0.025	< 0.001	< 0.001	< 0.001
b	20	0.097	< 0.001	< 0.001	< 0.001
b	21	0.028	< 0.001	< 0.001	< 0.001

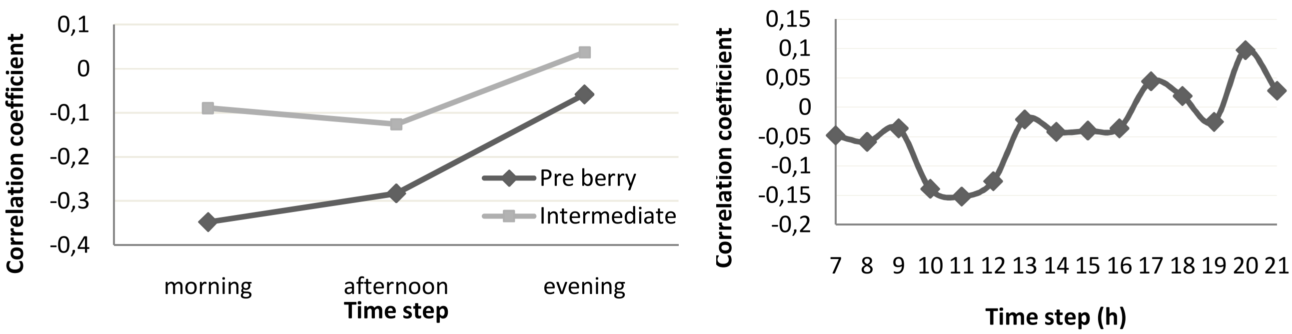


Figure 3.8: Spearman's rho correlation coefficients between cattle and bear resource selection, plotted over time during the pre-berry and intermediate season (left), and during the berry season (right).

Besides the differences in resource selection between cattle and bears observed by the correlation, the Sign and the Marginal Homogeneity test, bear and cattle responded in an inverse or different way to some of the covariates. Bear and cattle response to NDVI was inverse or strongly differed (significant for one of the species, and no strong effect for the other) during all time steps and seasons, except during evenings in the berry season. This relation was visualized for the berry season in figure 3.6. Especially during morning and afternoon hours, the relation was inverse. During late afternoon and evenings, NDVI was not a significant determinant for both bears and cattle.

A similar response behavior was observed for the distance to unpaved roads. In most of the time steps, cattle selected areas closer to unpaved roads (except pre-berry evenings, and intermediate afternoon). Bears avoided unpaved roads totally during the intermediate and berry season. During the berry season, bears only avoided unpaved roads during morning hours.

Cattle preferred areas closer than random to the cattle farms. Bears in contrast usually were not affected by the distance to cattle farms, or showed an inconsistent response regarding this covariate. In two cases (pre-berry, mornings; and intermediate, evenings), bears selected areas further than random from the cattle farms. Bears did select areas closer to cattle farms in a few time steps as well; i.e. at night during the berry and intermediate season, and during late evenings in the pre-berry season. During daytime (mornings, afternoons and evening), bears tended to be attracted by creeks. Cattle in contrast avoided these, or were not strongly influenced by the distance to creeks.

Cattle resource selection was included in bear RSFs as a covariate, in order to test whether bears' resource selection was influenced by the likelihood that a pixel was used by cattle during a given period of time. It thus served as a proxy for cattle presence and could indicate if bears were attracted by it. During the pre-berry season, bears were attracted by areas with a high probability of use by cattle during the mornings only. No strong relation was found during afternoons and evenings (fig. 3.9, upper left). During the intermediate season, bears were not attracted by cattle presence during morning time. During the evening period however, bears seemed to be attracted by areas selected by cattle. Cattle RSF was not taken into account in bear RSF during afternoons, as it was not selected as a covariate in the most parsimonious candidate model. The estimates of the covariate values of cattle resource selection values during the berry season ranged amongst both positive and negative values, but were only significantly positive in some occasions, from 15:00 – 16:00 and from 19:00 – 21:00. Bears seemed more attracted by areas with a higher cattle presence probability in the late afternoon and evening time (fig. 3.9. lower left). The responses of bears towards cattle resource selection values was however inconsistent, compared per season, and over time steps per season, which makes it a rather unreliable covariate in bear RSFs.

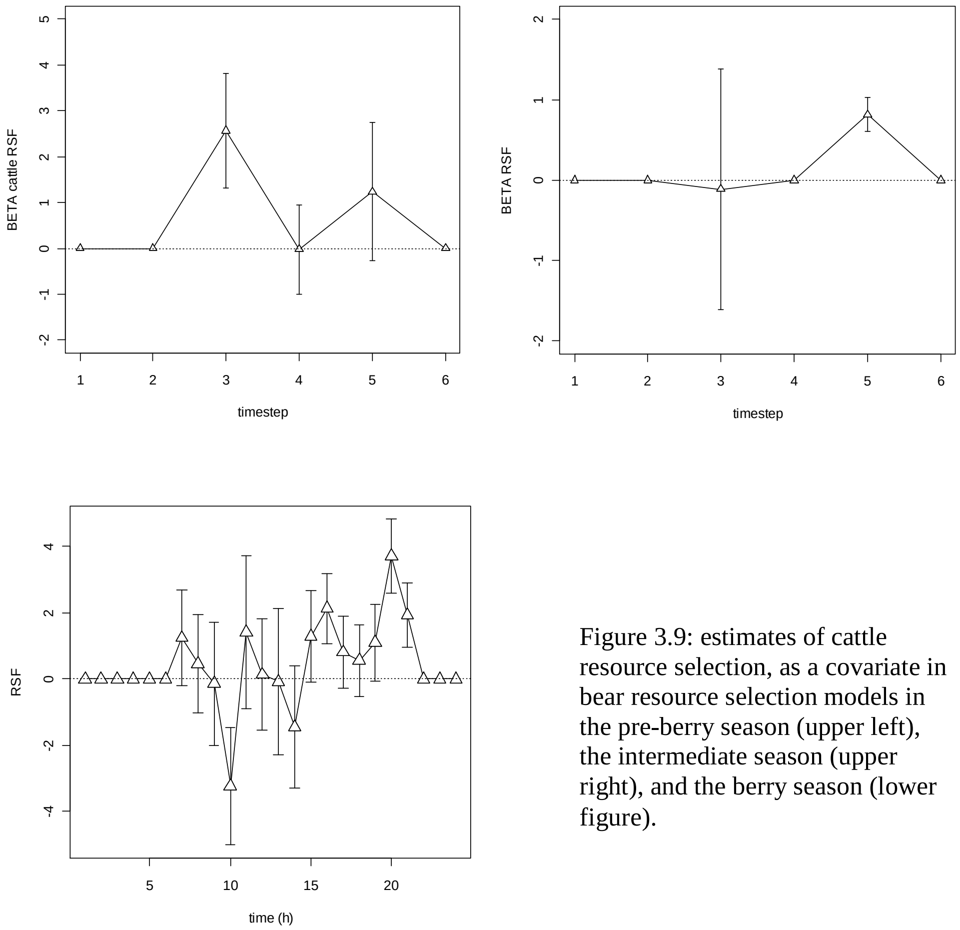


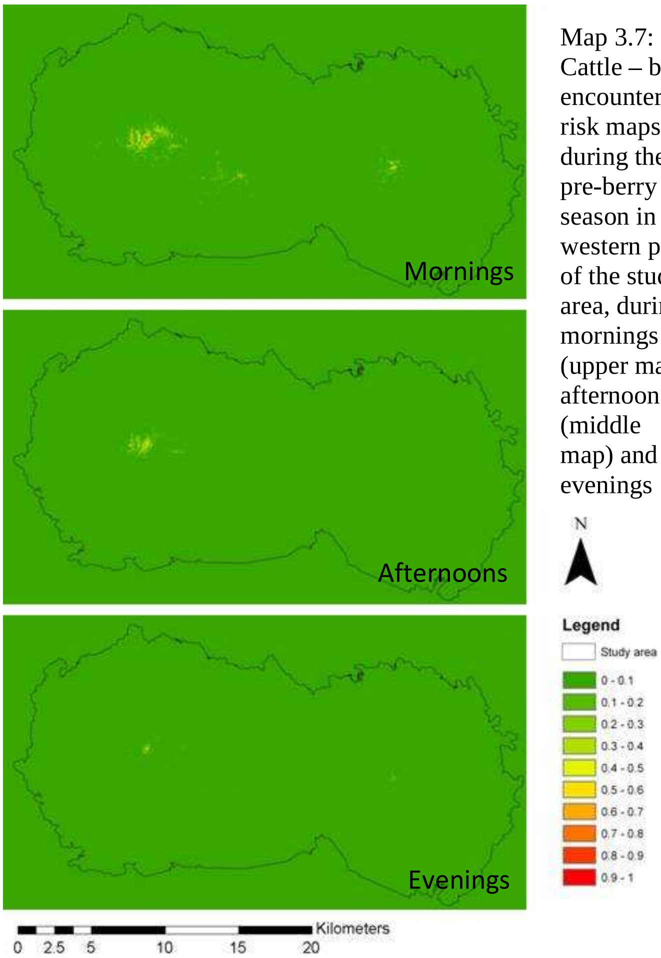
Figure 3.9: estimates of cattle resource selection, as a covariate in bear resource selection models in the pre-berry season (upper left), the intermediate season (upper right), and the berry season (lower figure).

3.4. Encounter risk

Encounter risk was defined as the relative probability of use of a pixel by both cattle and bears during the study period (i.e. time steps per season). It was calculated by multiplying resource selection probability values per pixel for bear and cattle resource selection maps per time step and season. The encounter risk maps were considered as proxies for potential conflict. Note that the actual encounter risk was undoubtely much lower as expressed in the results, as here we dealt with large time frames (mornings, afternoons or evenings, or hourly intervals), pooled over seasons.

3.4.1. Pre-berry season

Encounter risk during the pre-berry season is visualized in map 3.7. Encounter risk is centered around the cattle farms. Similar –but in lesser extent- as in the cattle resource selection maps, linear features can be observed, again representing tracks and unpaved roads. The encounter risk area decreased gradually in size and probability magnitude, from the mornings towards the evenings.



Map 3.7: Cattle – bear encounter risk maps during the pre-berry season in the western part of the study area, during mornings (upper map), afternoons (middle map) and evenings

The estimates of model covariates, evaluated as significantly (α=0.05) positive (+), negative (-) or not influencing (0) bear-cattle encounter probabilities during the pre-berry and the intermediate season were summarized in table 3.6., and provided better insight to determine encounter risk factors.

Distance to cattle farms and tracks showed an inverse relation with encounter risk during the day. This was similar for distance to single standing buildings and unpaved roads, except during the evening hours. Distance to open water and paved roads showed a positive relation with encounter risk during mornings and afternoons. Encounter risk was thus higher closer to tracks and farms, and further away than random in the study area from open water and paved roads. The distance to settlements was only positive related to encounter risk during morning time.

From the land-cover types, ‘other open land’ was the only type that did affect encounter risk; i.e. positively during mornings and evenings. The other types, as well as slope aspects and TRI500 did not strongly affected encounter risk.

Table 3.6: influence of model covariates on encounter risk for the pre-berry and the intermediate season, during mornings, afternoons and evenings. -, 0 and + indicate respectively negative, none and positive influence of the covariate with a significance level of 0.05. ? indicates unknown influence, as the variable was not included in the most parsimonious model.

		Pre-berry			*Intermediate*		
	Covariate	**Mornings**	**Afternoons**	**Evenings**	**Mornings**	**Afternoons**	**Evenings**
Distance to:	**buildings**	-	-	0	-	-	0
	cattle farms	-	-	-	-	-	0
	creeks	0	+	?	-	+	0
	open water	+	+	?	+	+	0
	paved roads	+	+	0	+	+	0
	settlements	+	0	0	+	-	0
	tracks	-	-	-	-	-	0
	unpaved roads	-	-	0	-	0	0
Aspect	**N**	0	0	?	0	0	0
	NE	0	0	?	0	0	0
	E	0	0	?	0	0	0
	SE	0	0	?	0	0	0
	S	0	0	?	0	0	0
	SW	0	0	?	0	0	0
	W	0	0	?	0	0	0
	NW	0	0	?	0	0	0
Land cover	**Young dense forest**	0	0	?	0	0	0
	Young open forest	0	0	?	0	-	0
	Bog	0	0	?	0	-	0
	Older forest	0	0	?	0	-	0
	Road	0	0	0	0	0	0
	Other open land	+	0	+	0	0	0
Terrain	**TRI**	+	+	?	+	+	0
	TRI500	0	0	?	-	0	0
	TRI1000	+	+	?	+	0	0
	NDVI	+	0	?	+	+	0
	Slope	+	+	?	-	-	0

The NDVI was determinative during mornings; otherwise its effect was unknown or not significant. Terrain ruggedness showed to be determinative on both the local, pixel scale, and the larger 1000m radius area, both during mornings and afternoons, and slope as well. Estimates of some covariates and 95% confidence intervals were visualized in figure 3.10 to give an impression on the magnitude of effect on encounter risk for each covariate during the scope of the day. The distance to single standing buildings, cattle farms, paved and unpaved roads and tracks all showed a decreasing level of significance in the scope of the day.

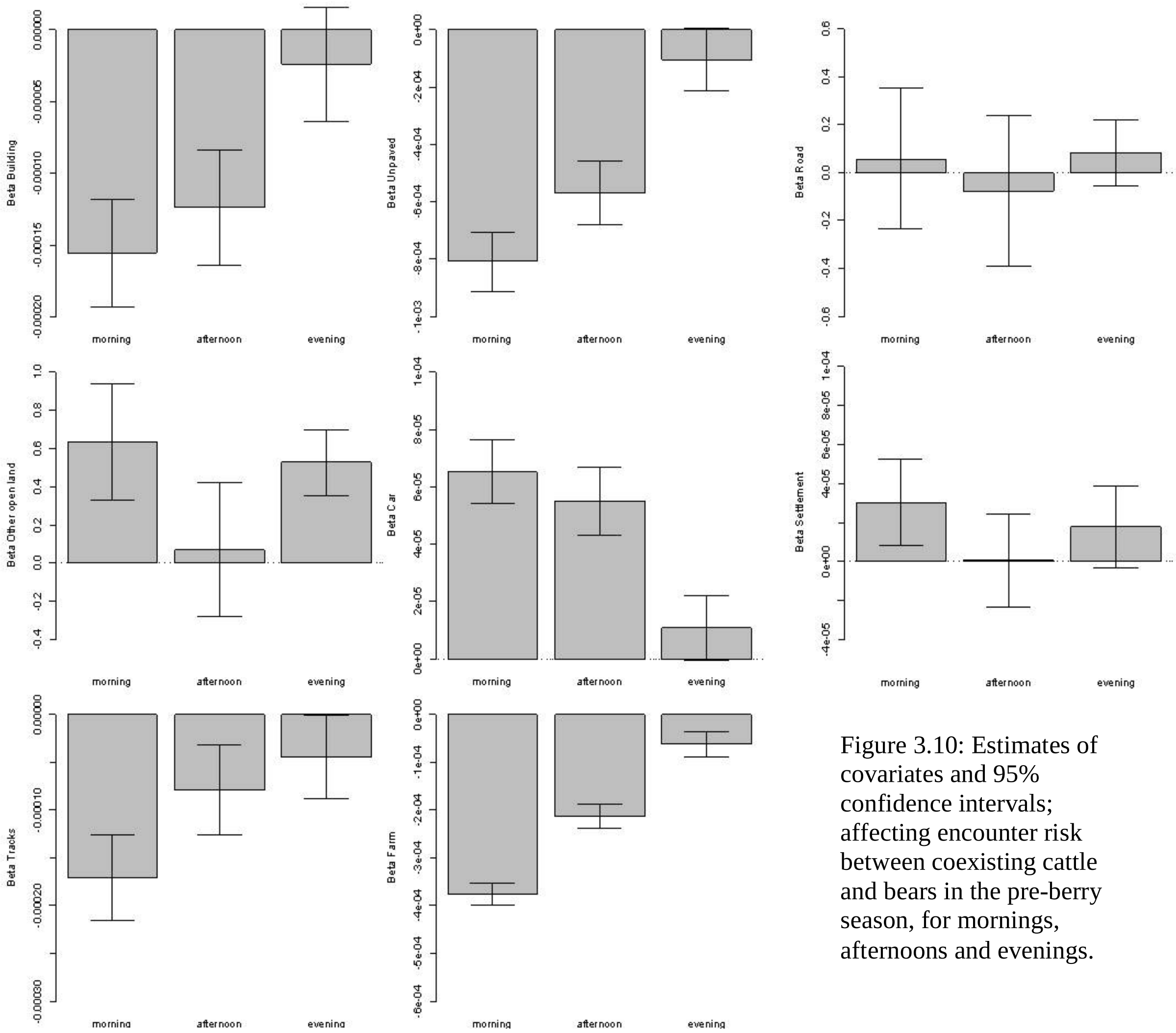
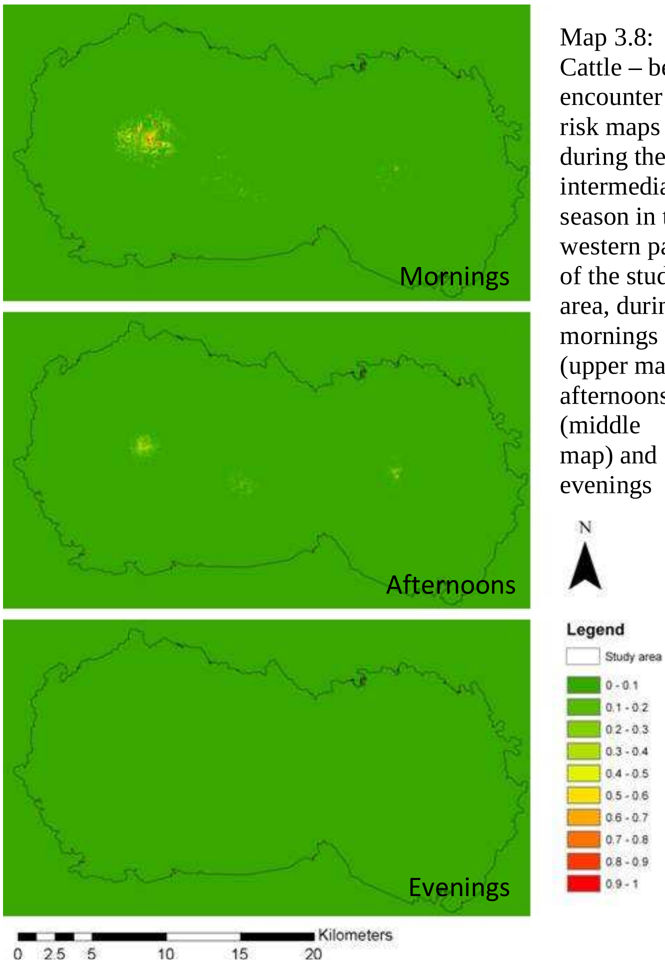


Figure 3.10: Estimates of covariates and 95% confidence intervals; affecting encounter risk between coexisting cattle and bears in the pre-berry season, for mornings, afternoons and evenings.

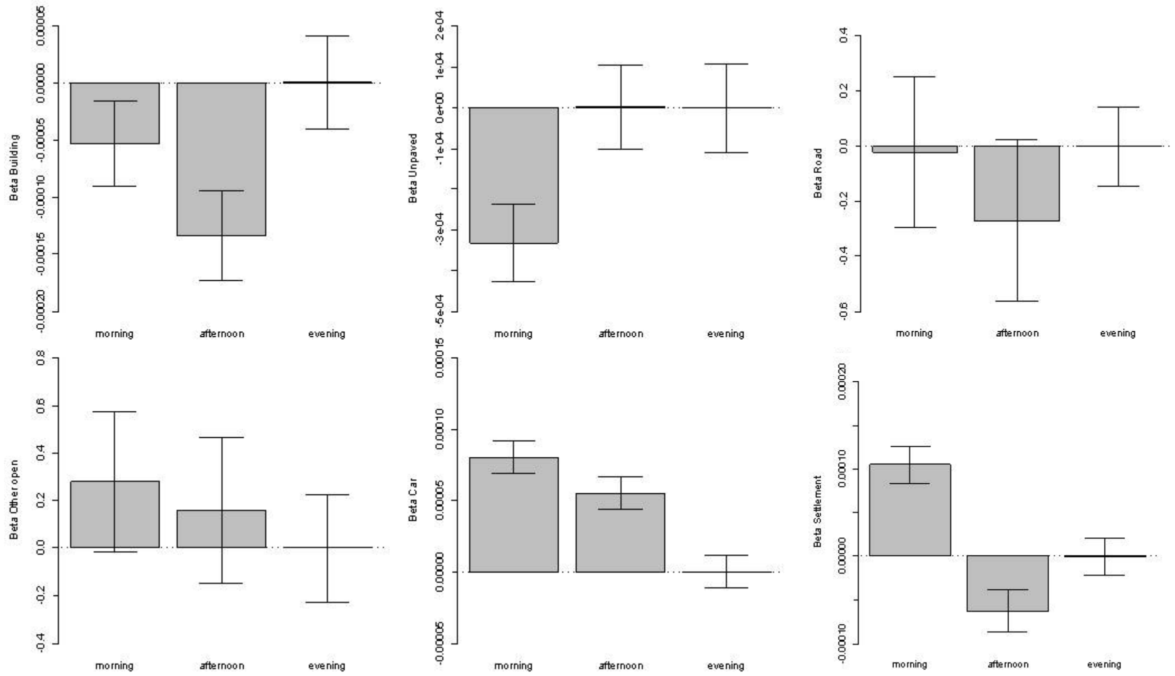
3.4.2. Intermediate season

Bear-cattle encounter risk maps during the intermediate season (Map 3.9) showed some similarity with the pre-berry season. Encounter risk was again largest during morning times, and decreased during the scope of the day until relative probabilities proportional smaller than 0.1. Again, encounter risk decreased with distance somehow concentrically around the cattle farms.



Map 3.8: Cattle – bear encounter risk maps during the intermediate season in the western part of the study area, during mornings (upper map), afternoons (middle map) and evenings

The most parsimonious model selected for the evenings of the intermediate season, was the all-inclusive model. Remarkable was that none of the variables selected in the model showed a clear significant influence on encounter risk, indicating the unpredictability of encounters at this given time step. For the morning and afternoon periods, these significant influences were found. Encounter risk was negatively related with distance to tracks, single standing building and cattle farms; and positively related with distance to open water and paved roads. Distance to settlements was positively related with encounter risk during the mornings, and negatively during the afternoons. Distance to creeks was negatively related with encounter risk during mornings, and positive during the afternoons. More open land-cover types as bogs, older forests and young open forests affected encounter risk negatively during the afternoons. Other land-cover types did not strongly affected encounter risk. TRI and NDVI both affected encounter risk in a positive way during the mornings and afternoons. In contrast to the pre-berry season, slope appeared to affect encounter risk in a negative way. Slope aspect again was not strongly affecting encounter risk. Figure 3.11 shows the estimates and their 95 % confidence intervals for some variables selected to predict encounter risk. During the evenings, the estimates were systematically very close to 0, and had a relatively large confidence interval.



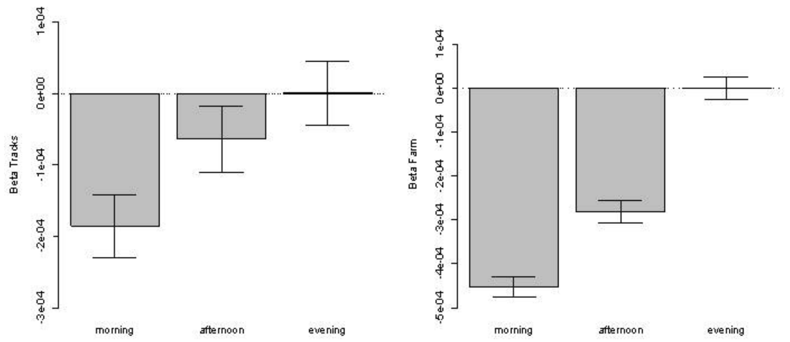
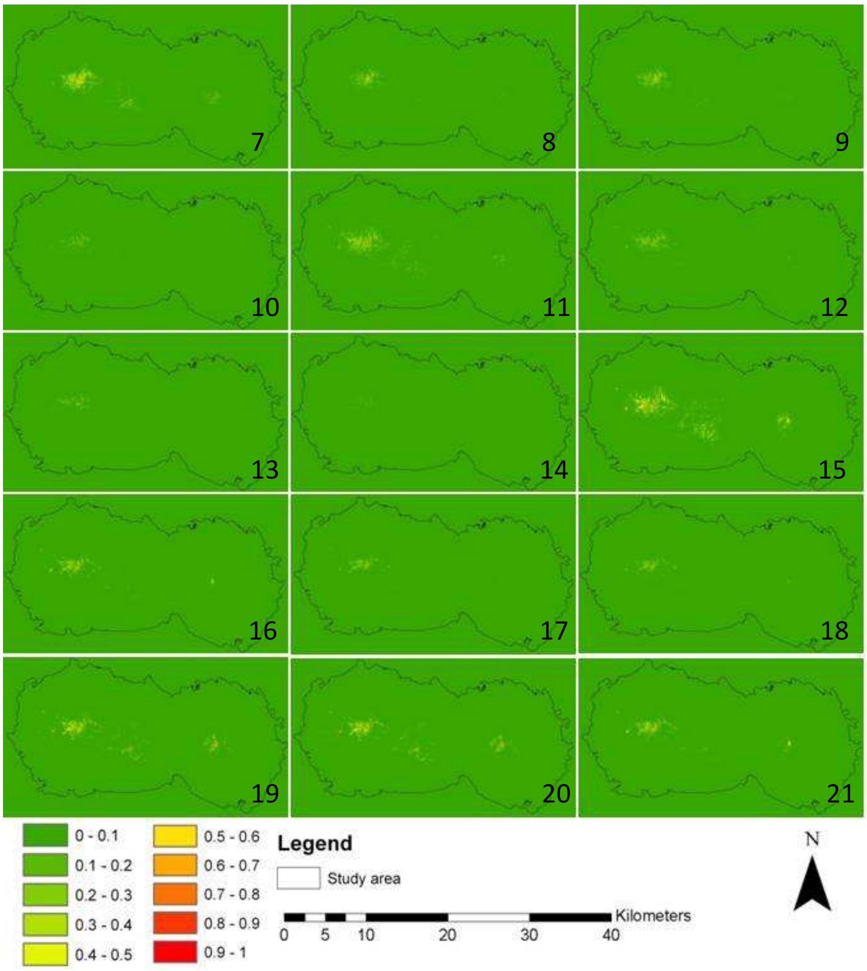


Figure 3.11: Estimates of covariates and 95% confidence intervals; affecting encounter risk between coexisting cattle and bears in the intermediate season, for mornings, afternoons and evenings.

3.4.3. Berry season

Encounter risk was predicted in hourly intervals during the berry season, starting from 6:00 - 7:00. The concentric pattern of decreasing encounter risk can be observed again. In contrast to the encounter risk maps of the pre-berry and the intermediate maps, encounter risk during the berry season appeared to be higher in afternoon and evening hours in extent and magnitude. Encounter risk seemed lower during the late mornings and early afternoon hours (10:00 ~ 15:00) than during early mornings and late afternoons/evenings.



Map 3.9: Cattle-bear encounter risk maps in the western part of the study area, during the berry season; in hourly intervals, from 6:00 – 7:00 (upper left map), to 20:00 – 21:00 (lower right map).

The distance to cattle farms, tracks and unpaved roads affected encounter risks in a negative way, over all time steps (except for unpaved roads at 14:00) in the berry season. Encounters were thus more likely to occur close to these features. The opposite was valid for the distance to open water and paved roads (table 3.7).

Table 3.7: influence of model covariates on encounter risk for the berry season, in hourly intervals, starting from time step 7 (6:00 to 7:00). -, 0 and + indicate respectively negative, none and positive influence of the covariate with a significance level of 0.05. '?' indicates unknown influence, as the variable was not included in the most parsimonious model,.

		Mornings				***Afternoons***					***Evenings***					
	Covariate	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
Distance to:	**buildings**	-	-	0	0	0	+	+	0	0	-	0	-	-	-	-
	cattle farms	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	creeks	-	-	-	-	0	0	-	?	+	+	+	+	+	+	+
	open water	+	+	+	+	+	+	+	?	+	+	+	+	+	+	+
	paved roads	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	settlements	+	+	+	+	+	+	0	+	0	-	-	0	-	-	-
	tracks	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	unpaved roads	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-
Aspect	**N**	0	0	0	0	0	0	0	?	0	0	0	0	0	-	0
	NE	0	0	0	0	0	0	0	?	0	0	0	0	0	-	0
	E	0	0	0	0	0	0	0	?	0	0	0	0	0	-	0
	SE	0	0	0	0	0	0	0	?	0	0	0	0	0	-	0
	S	0	0	0	0	0	0	0	?	0	0	0	0	0	-	0
	SW	0	0	0	0	0	0	0	?	0	0	0	0	0	-	0
	W	0	0	0	0	0	0	0	?	0	0	0	0	0	-	0
	NW	0	0	0	0	0	0	0	?	0	0	0	0	-	-	0
Land cover	**Young dense forest**	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0
	Young open forest	0	0	0	0	0	0	0	?	+	0	0	0	+	0	0
	Bog	0	0	0	0	0	0	0	?	+	0	0	0	+	+	0
	Older forest	0	0	0	0	0	0	0	?	-	0	0	0	0	0	0
	Road	0	0	0	0	0	0	0	0	+	0	0	0	+	+	0
	Other open land	0	0	0	0	+	+	0	0	+	+	+	+	+	+	+
Terrain	**TRI**	+	+	+	0	+	0	0	?	+	+	+	+	+	+	+
	TRI500	0	0	0	0	0	0	0	?	0	0	0	0	0	-	0
	TRI1000	+	+	+	+	+	+	+	?	0	+	+	+	0	+	+
	NDVI	0	+	+	0	0	0	0	?	-	-	-	0	-	-	-
	Slope	+	0	0	0	+	+	0	?	+	+	+	0	+	+	0

The distance to settlements and buildings in relation to encounter risk did not show a uniform pattern during the scope of the day. The distance to settlements strongly affected encounter risk in a positive way during mornings and afternoons until 14:00. During late afternoons and evenings, this distance became negatively related to encounter risk. The relation between distance to single standing buildings and encounter risk showed an ∩- shaped trend during the scope of the day, ranging from strong negative to strong positive estimation values for this covariate. Similar, but inverse to the distance to settlements, was the relation between distance to creeks and encounter risk. Here, encounter risk was negatively affecting risk encounter probabilities before 14:00, and positively after 14:00. The NDVI affected encounter risk in a similar, but less strong way as the distance to creeks. The relations of the above four mentioned covariates with encounter risk probabilities are visualized in figure 3.12.

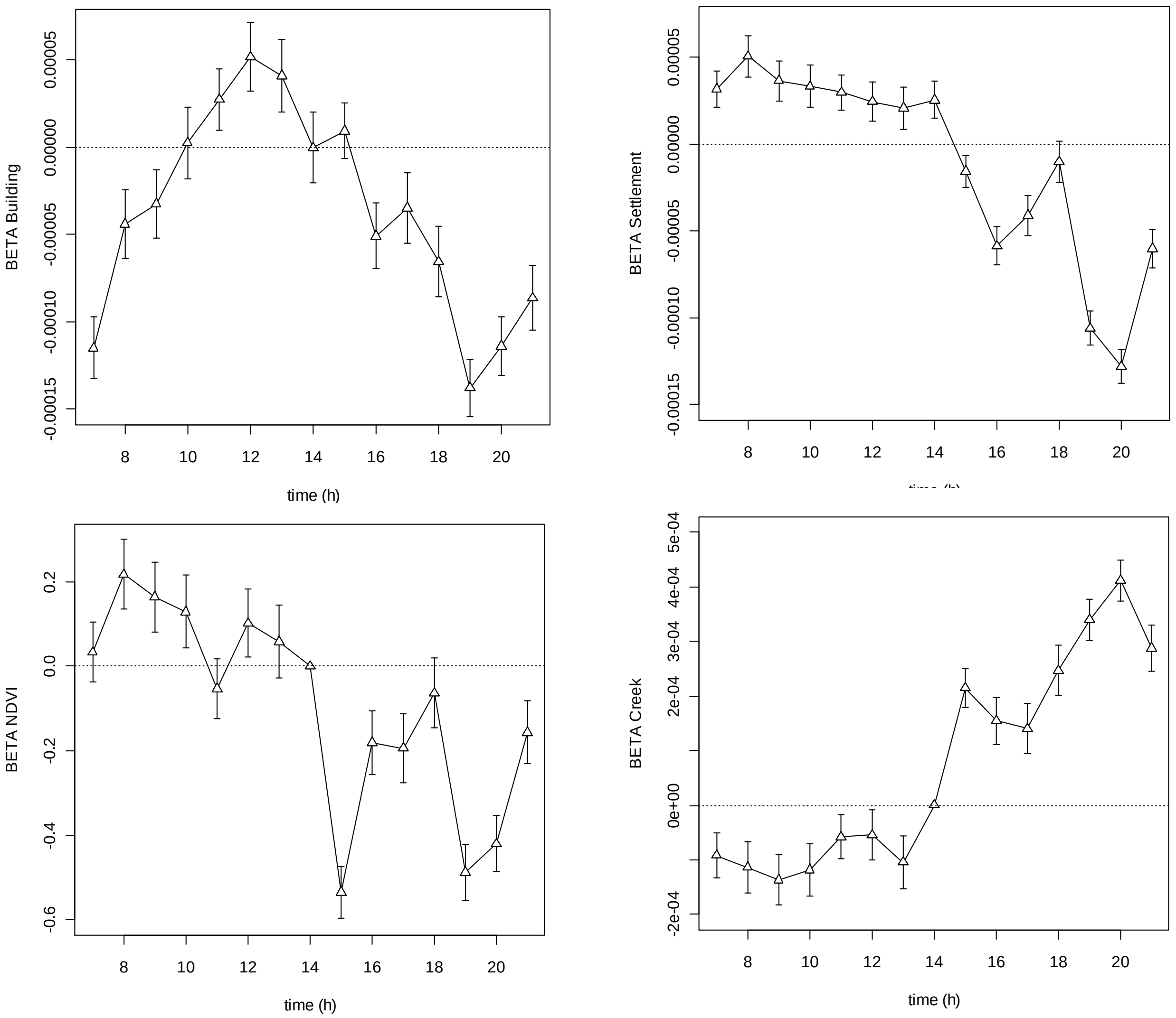


Figure 3.12: estimates of the regression coefficients of distance to single standing buildings (upper left), distance to settlements (upper right), NDVI (lower left) and distance to creeks (lower right) during the berry season. Bars indicate standard errors.

Land-cover types did generally not strongly affect encounter risk, except for the class of ‘other open land’, which affected the encounter risk in a positive way during most hourly intervals of the day. The classes ‘road’, ‘bog’ and ‘young open forest’ showed an increasing level of importance in determining encounter risk towards the evening. Figure 3.13 shows the estimates of land-cover –and distance to unpaved roads- covariates. Estimation behavior during the scope of the day for the three land-cover type was remarkably similar.

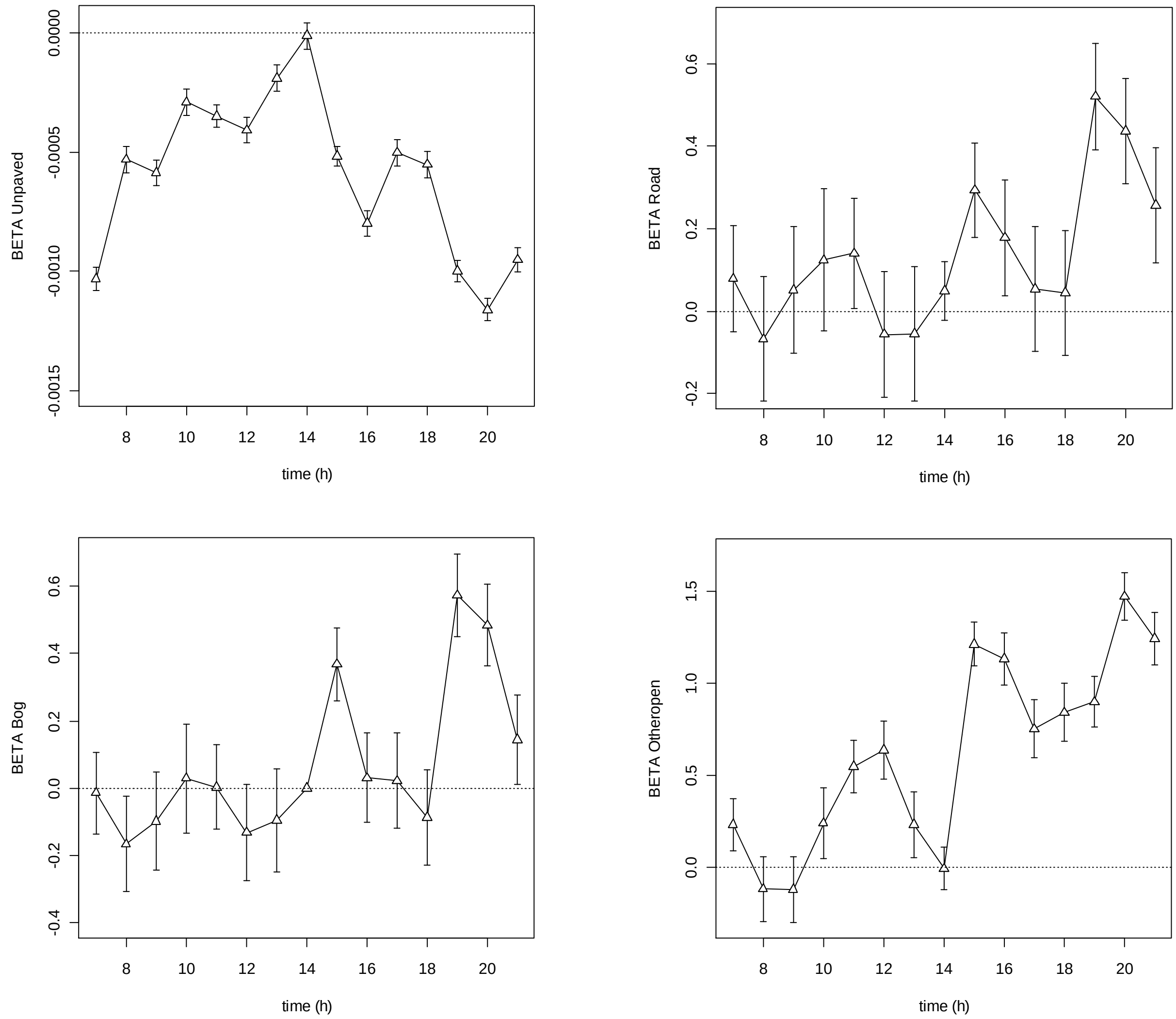


Figure 3.13: estimates of the regression coefficients of distance to unpaved roads (upper left), and the land cover types 'roads' (upper right), 'bog' (lower left) and 'other open land' (lower right) during the berry season. Bars indicate standard errors.

Terrain ruggedness at local –3*3 pixel neighborhood- scale and averaged over a circular area with 1000m radius generally affected encounter risk in a positive way, while the TRI500 did not show a clear relation with encounter risk. Slope aspect was not strongly affecting encounter risk. Slope steepness however, did affected encounter risk probabilities in general in a positive way.

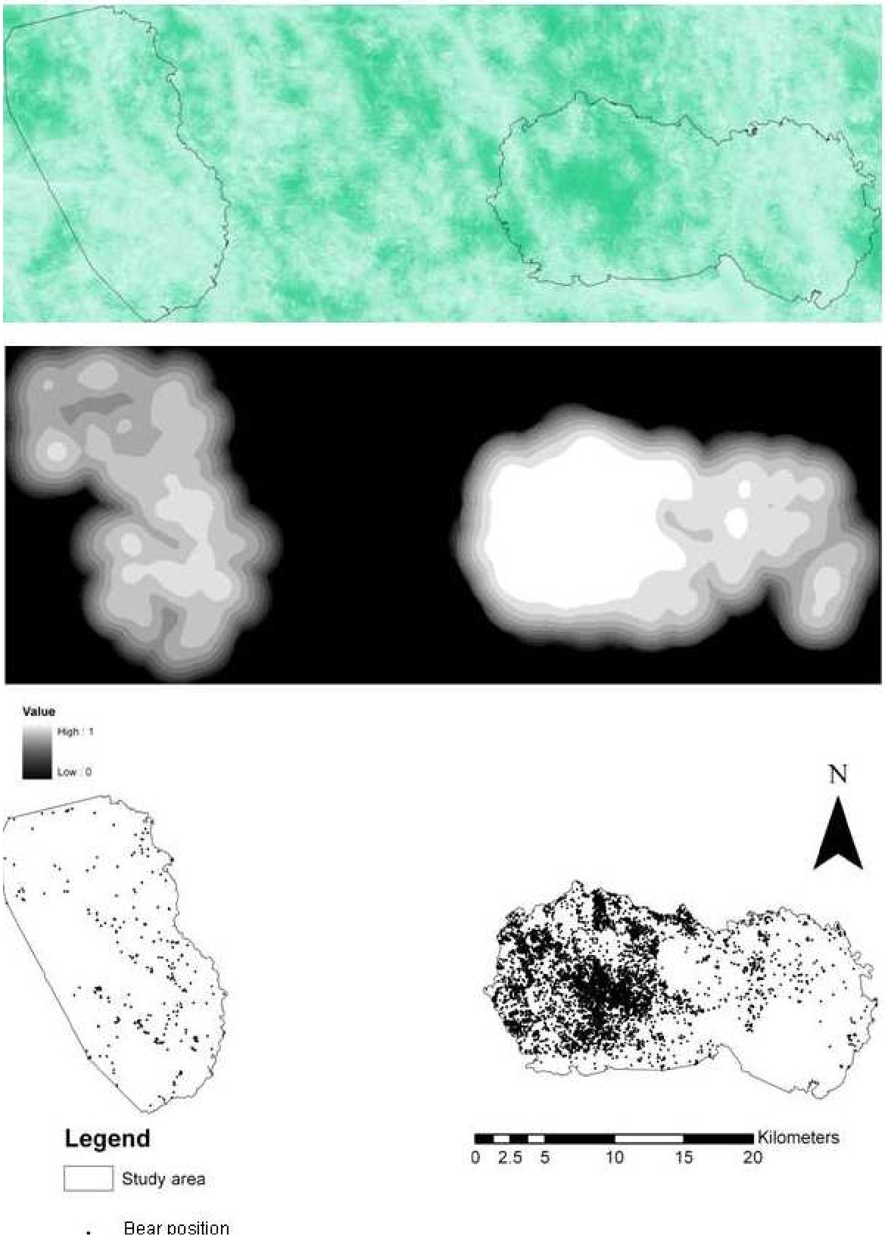
4. Conclusion, discussion and recommendations

This section discusses the methodological flaws, drawbacks and justifications of this research project, and gives an ecological interpretation of the results. It concludes with the main findings with regard to the proposed research hypothesis and aims, and gives recommendations considering management and further research needs.

4.1. Methodology

4.1.1. Point location data distribution

The main data source, on which the resource selection modeling procedure was based were the point locations of bears and cattle, obtained by satellite telemetry on a 30 minute time-interval schedule. As mentioned in the methodology, collar performance of the Vectronic collars on bears was excellent, and the data distribution over the seasons and time steps was reasonably good. It almost exclusively depended on the number of marked bears ranging in the operational study area.The distribution of bear point locations over the study area was not uniform: some areas contained a high density of point locations, while other areas had a low density. Map 4.1 gives the observed point distribution of marked bears in the study area, the derived Kernel density and a predicted standard resource selection map of bears. There are similarities: the highly frequented area by bears in the Kernel image resembles somehow with the Eastern part of the study area. In the Western part, in contrast, areas with a higher predicted resource selection were frequented less by the marked bears. The question then arises: did bears select these areas because of habitat quality an sich? Or was the bear location density skewed because of social organization reasons within the bear population in the study area? The presence of unmarked bears in the study area could have influenced bears' spatial behavior in the study area, and altered the use/availability and thus the real and the predicted resource selection of the marked bears. The presence of unmarked bears was confirmed in the operational study area, by 2 direct observations during the field season. Nevertheless habitat quality suggests to be the main drive behind resource selection rather than biases because of social organization. Field observations strengthen this idea. The area around Skadrar Djuberga and Kveksel (2 cattle farms) was, as predicted, heavily used by bears. A small area, of about 4 km^2, was simultaneously used by 2 adult males (Vattun and Bose), a female with 2 yearlings (Oda and offspring) and 2 sub adult females (Jamta and Tvaska). In addition, Scandinavian brown bears were reported to have intra- and inter sexually overlapping home ranges (Dahle and Swenson 2003, Støen et al. 2005).



Map 4.1: Bear point location distribution in the study area (lower map), bear position Kernel density (middle map) and a bear resource selection map (upper map).

Because of the poor Televilt collar performance, a significant part of potential cattle data was lost, and data of one cattle farm was excluded out of the modeling procedure. The cattle data distribution over seasons and time steps, as presented in the methodology was largely skewed.

Results were rather difficult to compare. Firstly, bear resource selection during the berry season was modeled in 24 hourly time-intervals, while all other models were on a different temporal resolution. The choice for the 24 hourly time-intervals for bear resource selection felt justified, as the data allowed for it, and covariate behavior could then be evaluated over the scope of a day. Interesting patterns, which could have been evened out in larger time frames could then be revealed. Moe et al. (2007) stressed the importance of dividing data in small time frames, especially for species that show a lot of variation in diel behavior, as is the case with the brown bear. Moreover, a more general comparison with the other time steps could still be made; be it carefully. Secondly, differences amongst the selected, most parsimonious candidate models and the exclusion of non-used dummy variables (with extreme standard errors) make RSFs difficult to compare.

Bear and cattle data was pooled, and followed Manly's resource selection design type I. Sex and age biased behavior effects –as was suggested for predation- were therefore evened out over the study population of bears and cattle. This choice felt justified, as the aim of this research was based on bear-cattle conflicts on a population level.

4.1.2. Arbitrariness

Model selection based on the information theory approach originated from a skeptical view of statisticians and mathematicians towards traditional hypothesis testing, that was considered as uninformative, its liability for type I errors, arbitrary and a priori stated false (see appendix 3) (Akaike 1973, Anderson et al. 2000, Burnham and Anderson 2002). Covariate evaluation in this research was based on traditional null hypothesis testing, with an arbitrary α-level of 0.05.This may appear as inconsistent. The null-hypothesis stated for covariate evaluation was as follows: "covariate *x* has no effect on resource selection by species *y* at a given time *z*". These hypotheses were clearly stated false, considering that covariates were initially included in the candidate models assumed to be determinative. Even dough the hypotheses were stated falsely, the significance levels were in this case informative. The estimated values and confidence intervals for covariates were evaluated over time, reflecting the importance of that covariate over time in resource selection for the study species. In an ecological context, this does contain useful information. Therefore, this approach was justified. The inconsistency feeling however remained. The information theory model choice, in combination with traditional statistical testing of covariates is the common method as presented in literature (Boyce and McDonald 1999, Boyce 2006, Ciarniello et al. 2006). Personal communications with Prof. M. Boyce (University of Alberta) did not clarify this inconsistency. He stated that model selection and covariate evaluation are different matter, and that individual covariate evaluation with its linked significance levels can be useful. Furthermore, for covariate evaluation, the use of traditional statistics is justified, as there is no real quantitative alternative.

The candidate models that were defined in advance of the analysis can be considered arbitrary as well, because of the decisions and assumptions that were made relative to the importance of covariates, and because of the dependency of the available spatial data. Spatial data or proxies for food availability, predator densities, ungulate densities, etc., most likely to affect species' resource selection, were not available.

The seasons were chosen according to Dahle and Swenson (2003) based on an important phenology in bear habitat use, i.e. the availability of berries, and berries are an important food item in the Scandinavian brown bear diet. The arbitrary selected time steps for cattle data and bear data in the pre-berry and intermediate season (mornings, afternoons and evenings) were chosen in order to get reasonable sample size per time step to create the models. To cover a complete temporal scale, it would have been ideal if the data allowed creating hourly models for cattle in all seasons and for bears in the pre-berry and intermediate season.

A major question considering the sampling scheme in the use/availability approach remains; i.e. what is the optimal sample size of random points, given the number and distribution of animal positions, and on what scale should the random sample be drawn. Boyce (2006) and Ciarniello et al. (2007) evaluated sampling schemes and scale in resource selection studies, outgoing from two fundamental considerations: 1) that the scale of the sampling scheme influences the strength of habitat associations, and 2) that ecological processes including habitat selection can occur on different spatio- temporal scales. The latter –the temporal scale- was also stressed by Moe et al. (2007). No single clear answer on this scale question could be given, as it depends on the study objective. In this case, the scale of the study area was chosen arbitrary as the area in which bears occur, with a relative probability of cattle use higher than 0.5, a level that is of course discussable. Choosing a smaller area (e.g. a relative probability of use by cattle > 0.7) would undoubtedly have led to different model coefficients estimates, and be more accurate for the small area, as less environmental variation would have been included. On the other hand, the number of bear positions would have been smaller. A trade off thus exists between scale, sample size and predictive validity. Walker et al. (2007) bypassed the 'large scale' drawback by sampling random points within a variable buffer area around each animal position and estimated track, to model Stone's sheep (*Ovis dalli stonei*) resource selection. Their approach, in contrast to this research, had a higher predictive accuracy, but on a smaller scale.

Random points were sampled with a density of 2/ha, according to Ciarniello et al. (2006), and was assumed to capture the environmental variation in the study area. In order to compare various models, the ratio on random points per animal point location was kept constant. This however was not the optimal design. An empirical power analysis in order to define the number of random points necessary to capture the environmental variation would have strengthened this research.

The dilution of precision (DOP) is a measure of accuracy that depends on satellite triangulation geometry. Multiplying the DOP value for each point with the GPS device's accuracy, indicates the standard deviation of the position (Langley 1999, Hansen and Riggs 2006). A threshold value of 5 might have been too inaccurate for this research.

4.1.2. Spatial data quality

The quality of the base spatial data layers defines the accuracy of the end result. The standard topographical map and DEM were obtained, but –despite efforts in requesting- without any measure or proof of accuracy. As both are commonly used in Sweden, for various purposes, we assumed the quality as workable, as there was no alternative. The highly dynamic character of the intensively managed forest did in some unknown extend affect the accuracy of the topographical map. Some logging roads in the study area were not yet developed at the time that the map was produced. These new logging roads, if observed, were tracked with a GPS and edited on the topographical map. Without any doubt, some of these roads have been omitted and not edited on the map, which could have resulted in an underestimation of the availability of unpaved roads in the study area.

The land-cover map created from the IRSP6-LISS 3 satellite sensor images had an estimated accuracy >85%, before topographical map features were added. 15% of the pixels used for a maximum likelihood classification were thus misclassified. This error is likely to have been propagated to the resource selection results, even dough the tests with additional ground cover points showed no significant differences between ground truth and the land-cover map (appendix 2). Furthermore, the land-cover classes were chosen arbitrary, and based on ground truth observations of various project participants. It must be stressed that land-cover is often a rather continuous than a discrete phenomenon, with often more land-cover types per pixel, and that classifying land-cover types will therefore never be error free (Foody 1995;2002, Lillesand et al. 2004). As an example, ‘young dense forest’ and ‘young open forest’ were arbitrary divided by the tree density (threshold of 10000 stems/ha) in each ground control plot. ‘Older forest’ was classified based on a tree height threshold level of 7 meter. The class of ‘bog’ included both bogs and forested bogs. This drawback might have led to the relative insignificance of land-cover types in the habitat models considering other variables. A strict sampling protocol with well defined classes and sufficient collected ground control points per class might have increased the accuracy and validity of the land-cover classification. The arbitrariness in choosing land-cover types could further be reduced, and results optimized by including non arbitrary measures for vegetation densities as the NDVI in the classification procedure.

The NDVI, one of the covariates included in the models, shows in reality temporal variation, depending on the primary production and growing season. The NDVI was derived from the satellite imagery, and thus originated from one momentum (for both image tiles), and its temporal variation was thus not captured. The NDVI layer was assumed to be valid to serve as a proxy for the complete season, and was not considered as a serious drawback.

4.1.3. Spatial autocorrelation

Autocorrelation is a property of all environmental variables, and observed to correlate over time-series or across geographical space (respectively temporal and spatial autocorrelation) (Legendre 1993). On landscape levels, spatial autocorrelation appears most common as patches or gradients. In ecological research, spatial and temporal autocorrelation are usually considered to bias the results. Autocorrelation violates the assumption of stochastical independency of, and between variables, and is considered a form of pseudo-replication. This can, if positive, increase the chance on type I errors, in which the null hypothesis of 'having no effect' is falsely rejected (Legendre 1993, Boyce 2006). Currie (2007) stated that if autocorrelation in abundance (e.g. point locations), is exogenous, resulting from environmental drivers that are spatially structured, traditional non spatial statistics describe the abundance perfectly well. In habitat studies, it is thus hoped that present autocorrelation in resource selection is the result of autocorrelation in the available covariates, and that it will be captured by the models (Aarts et al. 2008). Following the assumptions of Currie (2007) and Aarts et al. (2008), autocorrelation was not expected to have a strong effect on the model outcomes. Moe et al. (2007) tackled the 'problem' –or ecological property- of autocorrelation in the SBBRP study area for six female bears' habitat use. They reasoned as follows: the median of bears' movement distances between two 30 minute time-interval GPS fixed was 361 m and sometimes exceeded 2.5 km, while the average maximum exit distance for each habitat patch was only 85 m (< 0.1% of the habitat patches exceeded 2 km across). Bears –and cattle as well- should thus be able to move out of every habitat patch, and cross several habitat types within 2 subsequent GPS fixes, reducing the effect of spatial and temporal autocorrelation.

Despite the methodological flaws as mentioned in this section, the predictive accuracy of all RSFs was relatively high, ranging from 76.2 % to 92.4% and were considered valid and satisfactory for further analysis and interpretation.

4.2. Ecological interpretation

4.2.1. Cattle resource selection

Cattle response towards the distance to the cattle farms was consistent over the three seasons. Areas closer to the cattle farms were preferred. As it involved dairy cattle, there was an urge for the cattle to return to the farm on a daily basis. The livestock husbandry type thus restricted cattle free-ranging behavior, and most likely caused this distance to the farm response rather than a predator effect. As cattle were thus in a 'safe area' throughout the night –when bears are most active-, driven by the husbandry type, conclusions on the predator effect for this response can not be drawn. Pratt et al. (1986) and Putman (1986) reported that some free-ranging cattle herds of the large predator-free New Forest returned to the farm site at evenings, during full grazing season. This suggests that returning to the farms site is rather intrinsic behavior of domestic livestock, than predator avoidance.

There was a strong and consistent response of cattle towards distance to unpaved roads and tracks over the seasons. During most of the observations of free-ranging cattle during the field period, cattle was travelling or browsing in the roadside verges (Picture 1). The reasons behind are two folded. Roath and Krueger (1982) reported that cattle made extensively use of a dense logging road network and trails in Oregon, USA. They reported that some use of the roadside verge vegetation was made, but not intensively. They ascribed this to a travel function of roads to preferred grazing ranges. Preferred grazing habitats were even avoided when logging roads were not in the vicinity of them. The roadside verge vegetation on the other hand, was assigned as a preferred, and a main habitat type for free-ranging

Picture 1: Cattle grazing and traveling on road side verges

cattle in New Forest (Pratt et al. 1986, Putman 1986).

Cattle is classified as a preferential grazer, and have their preferred foraging grounds on green lush vegetation (Guevara et al. 1996). This was in line with results of this study, as during most time steps in all seasons, the land-cover types ‘other open land’ and ‘road’ were heavily selected, above all other land-cover types. The land-cover type of ‘other open landscape’ was extracted from the topographical map, and mainly consisted of forest meadows. The use/availability indices for other open landscapes were extremely high, and 92.7, 65.3 and 47.4 respectively for the pre-berry-, the intermediate- and the berry season. For ‘road’, the indices were respectively 7.0, 4.4 and 5.2 (values >1 indicate a preference). In other words, during the pre-berry season, 30.8% of the cattle locations were situated in other open landscapes, comprising only 0.33 % of the 100% MCP cattle home range. The strong decrease in the index level over the seasons for other open land could indicate a depletion of resources, and higher preference for other resources. This is reflected in the resource use of bogs. Bogs were significantly selected during the berry season only, and the use/availability index increased from the pre-berry season towards the berry season, from 2.1 to 3.6. This could indicate a shift towards foraging on the *Calluna* dominated vegetation on bogs and tree rich bogs. The use/availability index for land-cover type ‘roads’ remained stable and mostly significant, and could indicate that behalf their grazing function, roads were used as travel routes between cattle farms and grazing grounds. Woodlands (young dense, young open and older forest) showed no strong effect on resource selection during all time steps and seasons (with use availability indices ranging between 0.26 and 1).

Free-ranging cattle does show a diel behavior patterns (Roath and Krueger 1982, Pratt et al. 1986, Putman 1986), with two peaks of activity, during mornings and evenings. Afternoons were characterized by bedding and ruminating in the vicinity of grazing grounds and nights by bedding and ruminating in more covered habitat types as woodlands. This diurnal behavior was not reflected in this study. Seasonal changes in resource selection were reported to show little variation (Pratt et al. 1986). This is in line with our findings: responses to most covariates were consistent over seasons. Responses however towards slope steepness, terrain ruggedness and NDVI did show seasonal variety. Steeper slopes were mainly selected during the pre-berry season, while rugged terrain was more selected during the intermediate and berry season.

Responses of cattle resource selection towards NDVI tend to be negative, especially during the berry season. Adaptive learning behavior, keeping in mind the response of bears towards NDVI, leading to predator avoidance may have caused this seasonal variation.

We can conclude that cattle in the study area select their resources non randomly, preferable in the vicinity of the cattle farms, tracks and roads, driven by the livestock husbandry system of milk production. Roads and tracks were selected for both traveling between cattle farms and grazing areas, and to forage on the roadside verges. 'Other open land', including mainly forest meadows, was selected disproportionally, but showed a decreasing trend in selection over the seasons. Tree rich bogs and bogs were in contrast more selected towards the end of the grazing season. Diel behavior was not reflected in the results, and seasonal variation in resource selection, as in line with other research, was little.

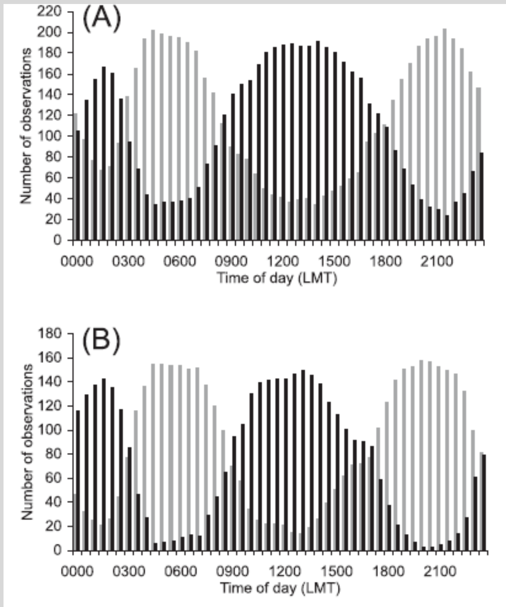
4.2.2. Bear resource selection

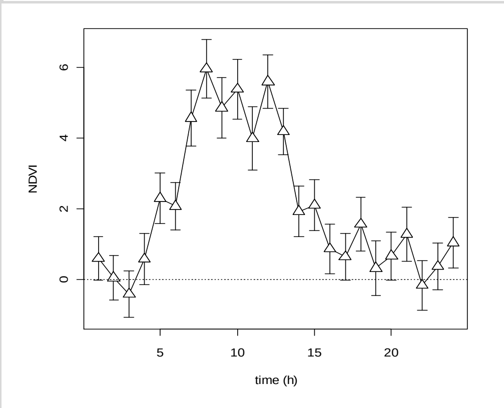
The human avoidance behavior of brown bears has been reported in the study area by Nelleman et al. (2007). Bears avoided tourist resorts and human settlements, and selected their resources further away in rather undisturbed rugged terrain. In North America, similar bear responses considering human activity were reported. Ciarnielo et al. (2006, 2007) showed that distances to logging roads and highways, as well as human induced mortality significantly negative affected bears' resource selection. Kaczensky et al. (2003) reported the negative effect of highways on bear's movement patterns in Slovenia. Numerous other authors come to the same conclusion: habitat fragmentation and related increased human activity affects bears –and wildlife in general- strongly in a negative way (Townsend et al. 2000a, Clevenger et al. 2002). In addition, a higher level of human presence is likely to correlate with hunting intensity, which could alter wildlife's wariness (Swenson 1999). Our results strongly support above mentioned research. Bears selected their resources significantly further than random from settlements, paved roads and unpaved roads. Single buildings were avoided in a lesser extent. Small tracks seemed to attract bears during the pre-berry and the berry season, most likely as travel routes. Bears used small tracks less during the berry season. This coincides with increased outdoor activities as hunting, fishing, berry and mushroom picking, when these tracks are frequented more by humans (Nellemann et al. 2007). Bears selected their resources on larger distances from open water (lakes and rivers), during all but one time step over the three seasons. Reasons behind could again be an increased human activity close to water (because of the idyllic settings for summer cabins and related tourism), or simply because open water does not offer any supplementary resource for bears, especially as small creeks and wet bogs are abundant in the area to fulfill in the needs of water.

Moe et al. (2007) showed that bears in the study area show a strong diel behavior, and stressed the importance of selecting time frames as small as possible in habitat selection studies. They monitored bears activity patterns with activity data loggers, and found that bears' activity peaked twice a day, from around 3:00 – 7:00, and from 19:00 – 12:00. The active periods –mainly crepuscular and nocturnal hours- are followed by a bedding period, in which bears show low activity. Bear day beds are typically located under dense vegetation, in woodlands (Moe et al. 2007). The day bed locations are as a consequence characterized with high NDVI values. Vegetation density seemed to be less determinative for bedding locations during the night rest (SBBRP personal communication, and personal observations). Rather than the habitat types, as we expected dense forest types to be selected by bears during daytime, the NDVI showed to be a strong determinative covariate in bear resource selection. Moreover, bear response towards NDVI followed the midday-dip in bear activity. During nighttime and night rest, the NDVI did not appear to be significant in bear resource selection (see Box 1). NDVI was also shown to be a strong predictor in bear resource selection in grizzly bear resource selection in British Columbia (Ciarniello et al. 2006). The land-cover classes as defined in this study did show very little effect on bear resource selection. Forests (young dense, young open and older forests) were selected in some occasions, while bogs and older forests were avoided in some occasions. The classes 'roads' and 'other

Picture 2: Typical daybed (center picture) with bear scats.

open landscape' were excluded from most of the models, due to extreme standard errors, as these dummy variables were not selected at all.





Box 1: diel bear behavior and relation with NDVI

Graph (A) and (B) are scanned from Moe et al. (2007)

Graph A and B illustrate diel behavior of five female brown bears in the study area during the pre-berry season (A) and the berry season (B). Activity was measured with activity sensors that register the number of two directional head movements, during 5 minute time intervals. Data was pooled per season and 30 minute interval for the 5 female bears. When the mean index value exceeded 50, bears were assumed active. The shaded bars indicate activity; the full bars indicate the inactivity.

The lower graph shows bear response to NDVI during the berry season. It follows the pattern of daytime low activity of the five female brown bears in the berry season (B) as presented by Moe et al. (2007). It indicates that bears select locations with high NDVI values during the day rest, and do not specifically select high NDVI locations during the night rest and night activity.

Terrain characteristics as slope steepness and aspect did not show to be straight forward predictors in bear habitat selection. In a few occasions, steeper slopes appeared to be selected, and in some occasions, less steep slopes were selected. Generally, slope steepness was of non-significant influence on bear resource selection. It must be stated, that with the arbitrariness of the chosen α-level, covariates will sometimes appear to be significant because of type I errors (in 5% of the occasions).Terrain ruggedness revealed to be a significant habitat use altering factor for 106 bears monitored by radio tracking in the study area as presented by Nelleman et al (2007).

In this study, terrain ruggedness was not found to be a strong predictor for resource selection. The reason for this might lay in the different terrain ruggedness index that was used in this study.

Bears in the study area showed a rather unpredictable response towards the distance to the cattle farms. In general, no effect was found. In some occasions however, bears did select areas closer than random to the cattle farms, while in others further. Again here, the type I error might have caused this significant responses. The same was valid for the response of bears to cattle resource selection values. No clear answer can be given on the question whether bears were attracted by or avoided areas with a high probability of use by cattle.

We can conclude that bear resource selection in the study area is driven by avoiding human activity, i.e. selecting resources further than random from settlements, unpaved and paved roads. During the day rest, bears strongly select locations with high NVDI values, while during night rest, NDVI appears to have no strong effect on their resource selection.

4.2.3. Research question I: How does bears' and cattle resource selection relates?

Human activity was shown to strongly affect both coexisting bears' and free-ranging cattle resource selection, but in an inverse way. Bears avoided human activity (settlements, single buildings, unpaved and paved roads), while cattle were attracted by unpaved roads for forage and travel, and showed no avoidance of human related landscape features whatsoever. Open land-cover types, as forest meadows, roads and bogs –the latter during the berry season- were preferred habitat for cattle during daytime hours, when cattle was active, and tended to avoid dense vegetation. Bears in contrast, showed preferences for dense vegetation during day rest. The correlation coefficients for resource selection values were negative during mornings and afternoons during all seasons, and showed an increase towards slightly positive values during the evenings. This indicates spatial avoidance during daytime, when bears are inactive, and less avoidance towards the evenings, when bears start to be active and roam to fulfill in their resource needs. The Sign and Marginal homogeneity test showed however that bears and cattle strongly differ in resource selection during all time steps. To answer the first research question: spatiotemporal overlap in resource selection between coexisting free-ranging cattle and bears in the study area is very low because of inverse responses towards human activity proxies and vegetation density.

The reverse situation, at nocturnal and crepuscular hours, when cattle were reported to be less active and select denser vegetation to ruminate and rest, and bears are active (Pratt et al. 1986, Putman 1986, Moe et al. 2007) would probably show a different picture, in which spatial and temporal overlap in resource selection occurs more. Kaczensky (1999) mentioned higher rates of depredation of large predators on livestock during nocturnal hours. However, the husbandry practice of dairy cattle which restricted free-ranging prevented from this hypothetical situation in the study area.

This study did not reveal any social or behavioral insight in cattle anti-predator or avoidance behavior, and how this could affect cattle resource selection. Predation induced altered resource selection was proven in the Yellowstone National Park (Brown et al. 1999, Ripple and Beschta 2004). After reintroduction wolves in 1995, elk numbers were expected to drop, but did not. Elk shifted their foraging strategy, and formerly preferred lush river banks (open areas with a high predation risk) became avoided and developed to woody browse due to natural succession. This process is referred to as the ecology of fear. Other fear- ecology research pointed in the same direction. Shrader et al (2008) found that predator presence altered resource selection of free-ranging goats and other free-ranging domestic species, in a experimental setup with predator urine and dung. Similar, owls affected gerbils' foraging behavior in Israel, and many more examples are found in literature (Brown et al. 2000). On the other hand, how fear- ecology could alter resource selection of bears in the study area remains unknown, as there is no reference for human absence, or a hunting-ban.

4.2.4. Research question II: Which factors determine encounter risk probability?

Despite the low spatiotemporal overlap in resource selection between bears and free-ranging cattle, the low conflict rate in Sweden in general (Kaczensky 1999, Viltskadecenter 2008;2009) and the assumption that bears do not actively prey on free-ranging cattle (Knight and Judd 1983), encounters and predation risk in the study area are not excluded. In line with the hypothesis of

Linnell et al. (1999), that individuals of large carnivores will at least occasionally kill accessible livestock, the factors that do influence encounter risk were determinmed, in order to optimize the predation aspect in cattle management.

The general trends in resource selection by bears and cattle are as a logical consequence reflected in bear-cattle encounter risk probabilities. Encounter risk was highest –with a few exceptions- in areas close to cattle farms, single standing buildings, tracks and unpaved roads, which are situated on larger distances from paved roads and open water during all seasons. Land-cover types did not appear to strongly affect encounter probabilities. Open landscapes (bogs, roads and other open land) were the only land-cover types that occasionally showed to have a positive effect on encounter risk. NDVI strongly affected encounter risk during the three seasons. During mornings, NDVI positively affected encounter risk, and in a lesser extend as well during afternoons. During evening periods, NDVI had no strong effect on encounter risk in the pre-berry and intermediate season, but did affect encounter risk in a strong negative way during the berry season. Again, this seems to coincide with bears' diel behavior. Risk appeared to be higher in rugged terrain, both on local scale, and larger landscape scale over all seasons. No consistent response of encounter risk towards the distance to creeks, –remarkably- to settlements and slope steepness was observed. Aspect did not show to be determinative.

It is important to stress, that the encounter risks as presented here are relative and not absolute, for each time step and season. Moreover, an encounter does not necessarily result in an attack and an attack not necessarily in a kill. Actual predation risk is without any doubt much lower than the encounter risk relative probabilities. Hebblewhite et al. (2005) decomposed the predation chain from encounter to potential attack and kill, based on radio- and continuous ground tracking data in a wolf-elk predator-prey system in Banff National Park. Encounter risk was similarly as in this study, determined with RSF. They however, had references of true encounters and attacks (based on track patterns), and actual kills due to ground tracking. In this study, we did not track continuously on ground, and did not have the reference of true kills.

We conclude that bear-cattle encounter risk in the study period during daytime was very low. The determinative factors reflect important covariates for both cattle and bear resource selection, as human activity proxies and vegetation densities. Seasonal differences in covariate response of encounter risk appeared to be relatively low. Variation in response during the day was observed for vegetation density only. Terrain ruggedness was not strongly determining resource selection for both cattle and bears, but it positively affected encounter risk relative probabilities. Encounter risk is the first step in the predation chain and should be considered as a predation proxy, when reference materials on true conflicts (attacks/kills) are not available.

4.3. General conclusion

The low spatiotemporal overlap in resource selection and thus encounter risk between bears and free-ranging cattle, in addition with the absence of actual predation events during the study period support the hypothesis that bears in the study area do not actively prey on free-ranging cattle during daytime, and if conflicts would occur, it would rather be by chance after an encounter.

According to the expectations, we observed inverse relations between cattle and bears considering human activity proxies, in which bears avoided human activity, and cattle were attracted to it, be it for cattle rather for traveling and foraging purposes than for predator avoidance. Encounter risk was further minimized because of the strong preference for dense vegetation by bears during daytime, while dense vegetation was rather avoided by free-ranging cattle.

Spatial overlap in resource selection was low during daytime, but remains unknown during nighttime, as cattle stayed at the farm site overnight. The livestock husbandry practice of dairy cattle in the Dalarna –Gavleborg region, which restricts free-ranging of cattle, can therefore be considered suitable for the area, where bears and cattle coexist during daytime only. Conflicts can however not be excluded, and livestock husbandry managers, coexisting with large carnivores should be willing to accept potential livestock losses and secondary effects due to depredation.

4.4. Management implications and recommendations

This research showed that a dairy cattle livestock husbandry system, that restricts free-ranging during nighttime, can coexist with a bear population in Scandinavia, with a minimum of direct predation losses. Therefore, it suggests that cattle livestock managers can minimize depredation losses by adapting to this particular system, in which cattle is kept at the farm site overnight.

As suggested by Zimmerman et al. (2003), and with the findings of this research, cattle is not very liable for bear depredation. It can therefore serve as an alternative for other livestock husbandry systems, like sheep and goat herding, for managers that do face direct depredation losses.

The efficiency of preventive measures, as already discussed (section 1.2.) varies conditionally. For farmers facing depredation losses, experimenting with deterrents, electric fencing or livestock guarding animals in order to minimize losses is therefore recommended, but they should keep in mind the cost-balance between actual losses (and compensation regulations) and preventative measures.

The recolonization of wolves in central Sweden –which is great from a conservational point of view-, will most likely question further coexistence between large carnivores and free-ranging livestock husbandry. Therefore, it is highly recommended to focus research on this new predator, and its potential impacts on free-ranging livestock and people's perception of large carnivores.

This study was rather descriptive than explanatory. Explanatory studies are however a necessity to gain more knowledge about secondary depredation effects. Experimental setups, in which e.g. stress-hormone levels, a milk production volumes, disease occurrence etc. are measured and compared between a study population coexisting with large carnivores, and a reference population could reveal more knowledge about production related secondary depredation effects. On a landscape level, these secondary effects could be determined with experimental trails with e.g. predator scent (dung and urine).

As a methodological research suggestion: the arbitrariness in land-cover classification class definition can probably be minimized by adding non arbitrary measures as the NDVI in the classification process.

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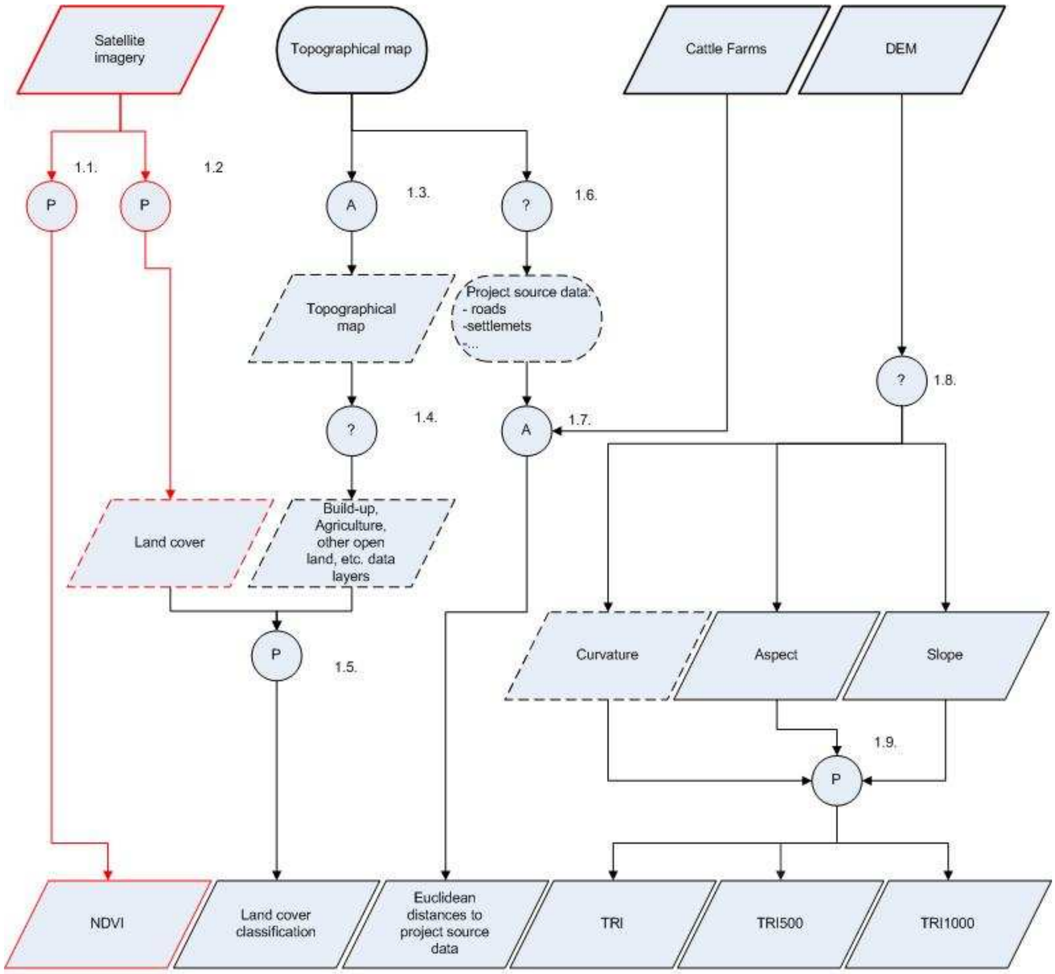
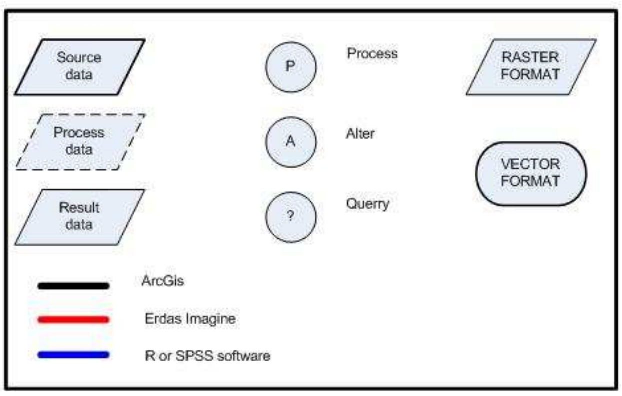
Appendix 1: Data action model

Step 1: derivation of the project source data.





GIS and RS data derivation:

1.1.Derive the NDVI from the satellite imagery according to equation 2 (section 2.2.2.2.).

1.2.A maximum likelihood supervised classification from the satellite imagery.

1.3.Topographical map: from vector to raster.

1.4.Derive relevant data layers from the topographical raster map.

1.5. Merge the classified satellite images with the rasterized topographical map. The result is a land-cover classification.

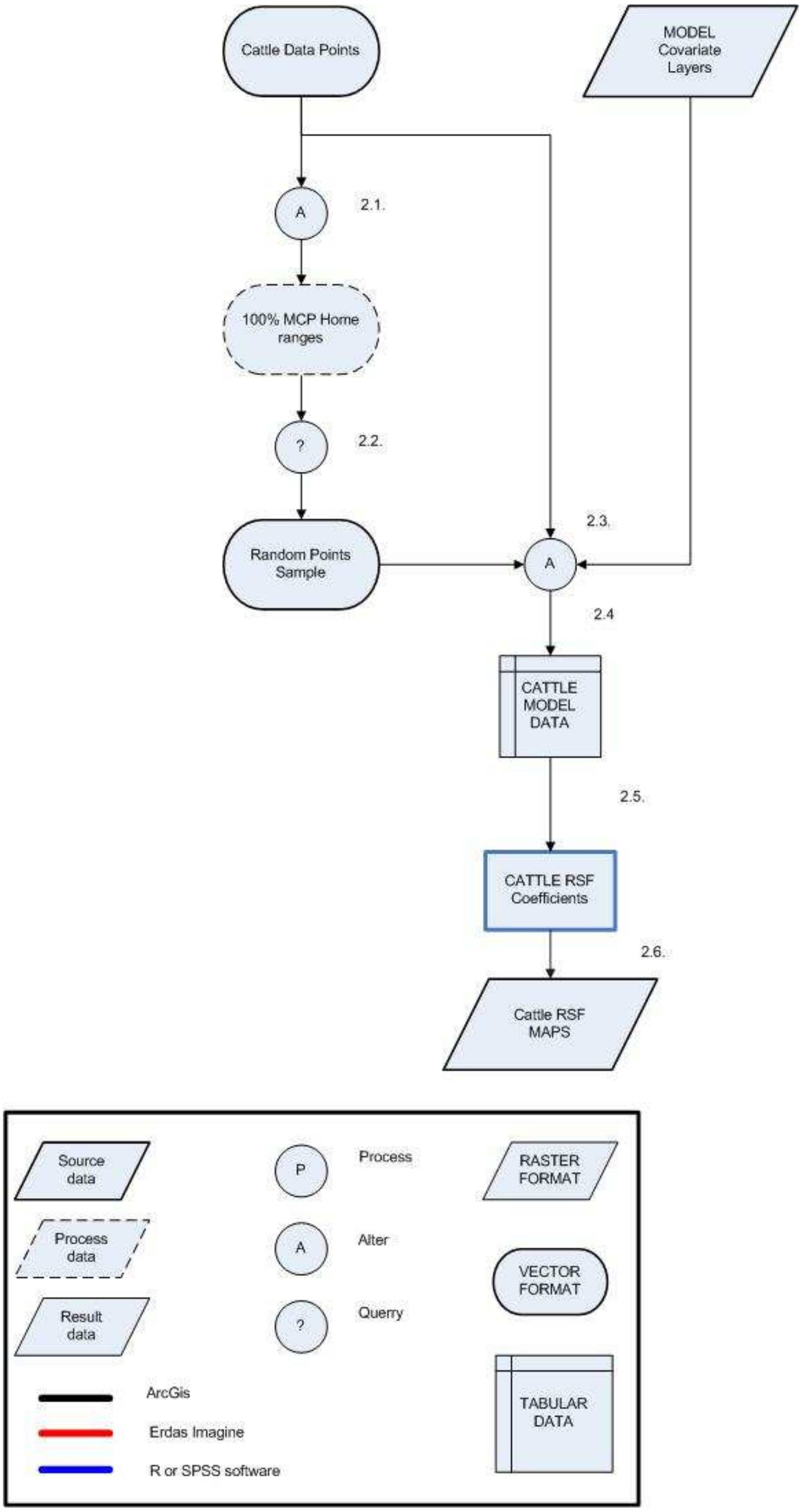
1.6.Query relevant data layers from the topographical map.

1.7.Create Euclidean distance maps from the source data. Each pixel value gives the distance to the source data (e.g. roads).

1.8.Derive the slope, curvature and aspect out of the DEM.

1.9.Single map algebra expressions to create the terrain ruggedness indices at local level (equation 1). Focal statistics were used to average the TRI values in a circular area with a radius of 500m and of 1000m for respectively TRI500 and TRI1000.

Step 2: create resource selection functions for cattle



Create resource selection functions for cattle.

2.1. Create a 100% MCP home range around the positions of each cattle herd

2.2. Sample a number of random points in the MCP (here, with a density of 2/ha)

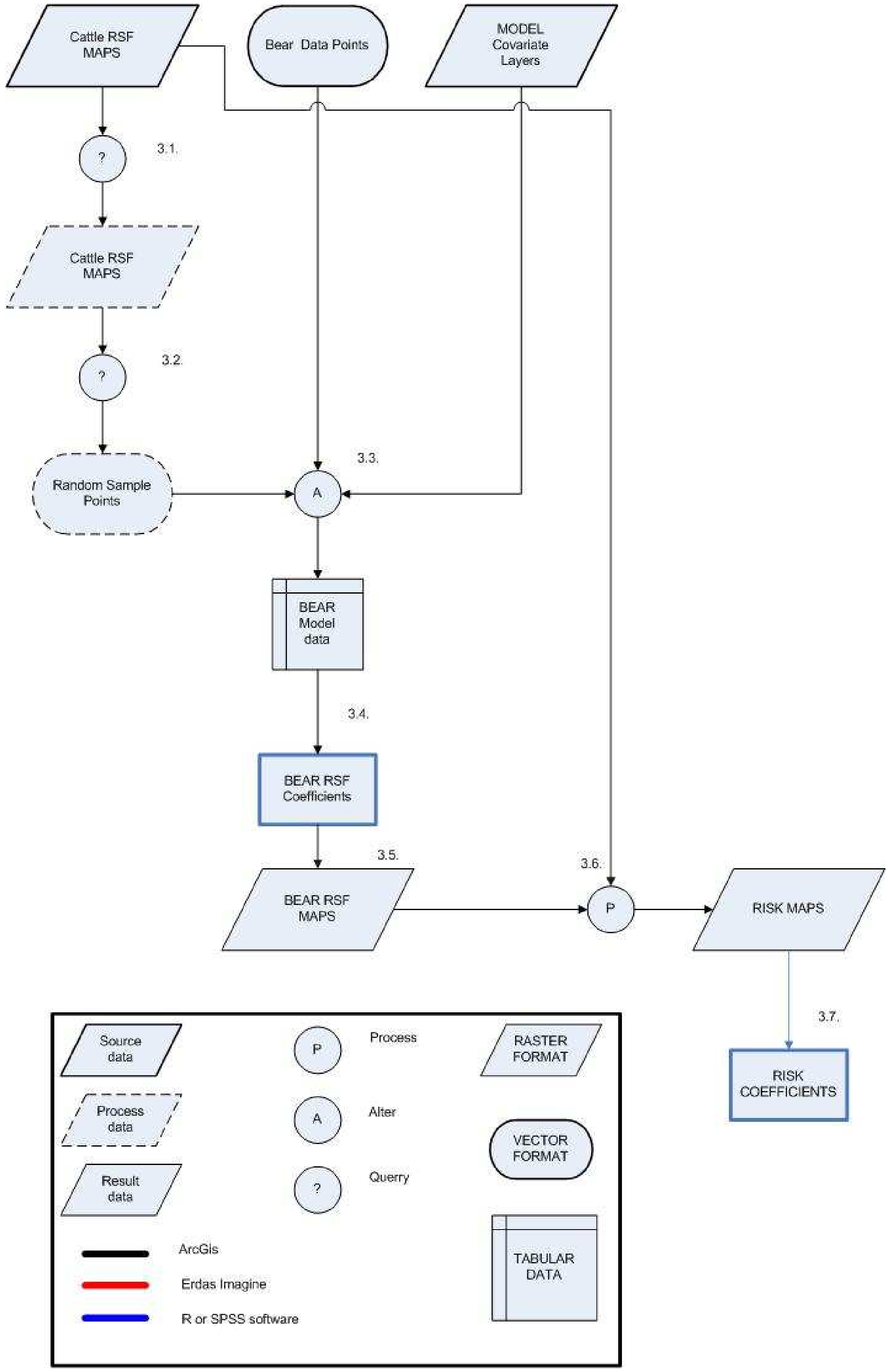
2.3. Extract data values for each covariate derived in step 1 –assumed necessary for the modeling purpose- for each random point and for each cattle point location.

2.4. Create appropriate datasets, with all covariates and the dependent variable (0/1)

2.5. Export the datasets from Arcgis to a statistical software package (here R) and run the appropriate GLM (here binomial, logistic regression)

2.6. Enter the estimates of covariances in the appropriate regression form in GIS or RS software to create the RSF maps.

Step 3: create bear RSFs and determine encounter risk variables.



Create Bear RSF and encounter risk maps, and derive determinative encounter risk factors.

3.1. Define a coexistence area (RSF cattle > 0.5) based on the average cattle RSF map.
3.2. Draw a random sample of data points in the coexistence area, and interest the co existence area with all bear positions.
3.3. Extract the covariate data for each random and bear point, and create a tabular dataset.
3.4. Export the dataset to a statistical software package and run the appropriate GLM.
3.5. Enter the resulting estimates of covariates in bear resource selection in a map single map algebra expression according to the form of the GLM to create bear resource selection maps.
3.6. Multiply the bear and the cattle resource selection maps to obtain risk maps.
3.7. Extract all covariates assumed important in predicting conflict risk with a random number of points. Fit an appropriate GML through the data (here it was a Poisson GLM, as binned risk data can be considered count data).

Appendix 2: Model selection

Selecting variables to include in a model that best describes reality is a critical step in a modeling procedure (Hosmer and Lemeshow 1989). Traditional statistical ways of variable selection – stepwise methods based on statistical significance testing- increasingly face criticism considering the strength and validity of these selection procedures. Anderson et al. (2000) present a range of shortcomings and problems considering null hypothesis testing for variable selection for modeling purposes and statistics in general. They claim that almost all null hypotheses are a priori stated false, and results are often completely uninformative. They thus question the scientific meaning of null hypothesis states as “differs”, “correlates”, “equals”, etc based on a completely arbitrary α – level (usually 0.1, 0.05 or 0.01) lacking any theoretical background. Shifting the arbitrary α – level, from e.g. 0.01 to 0.05 can as a consequence alter results, and as p – values depend on sample size, ‘significant’ results can always be obtained with large enough samples. The debate on the validity of traditional statistics is still ongoing in the scientific community. As an example, the authors of Anderson et al. (2000) listed citations on pro’s and con’s about traditional statistics in null hypothesis testing and model selection. An impressive list of over 400 citations and references can be found on: *www.cnr.colostate.edu/~anderson/thom-pson1.html* and *www.cnr.colostate.edu/~anderson/nester.html*. Their focus is mainly on variable selection in modeling procedures, and they confirm that the use of traditional statistics after the most parsimonious model has been selected can be justified if hypothesis are at least stated correctly (Burnham and Anderson 2002).

The information – theoretic approach bypasses these traditional statistical shortcomings, and is based on a priori reasoning and defining a set of scientifically sound candidate models. Hirotugu Akaike developed a method to quantify the loss of information of candidate models in relation to reality. He published his findings in his pioneering 1973 publication: “Information theory and an extension of the maximum likelihood principle”. With his method, further on referred to as Akaike’s Information Criteria (AIC), he linked Fisher’s maximum likelihood theory –a maximized log likelihood function- with the Kullback-Leiber information, and so found a sound mathematical and statistical way of quantifying information losses in modeling (Akaike 1973, Anderson et al. 2000, Burnham and Anderson 2002). The mathematical derivation of the AIC goes way beyond the scope of this study, but some key concepts of AIC are given below, following Akaike (1974) and Anderson et al. (2000).

The Kullback-Leiber information, between conceptual truth *f* and model *g* attempting to approximate *f*, quantifies the amount of information lost by this approximation, and is denoted as *I*(*f*,*g*) [eq. 5].

$$I(f,g) = \int f(x)\log_e\left(\frac{f(x)}{g(x\mid\theta)}\right)dx \qquad \text{[eq. 5]}$$

The integral can be interpreted as the statistical expectation of the natural logarithm of the ratio of full reality (*f*) and the model (*g*), and thus be written as [eq. 6]:

$$I(f,g) = \mathrm{E}_f\left[\log_e\left(\frac{f(x)}{g(x\mid\theta)}\right)\right] \qquad \text{[eq. 6]}$$

and transformed due to logarithmic properties to [eq. 7]:

$$I(f,g) = \mathrm{E}_f[\log_e(f(x))] - \mathrm{E}_f[\log_e(g(x\mid\theta))] \qquad \text{[eq. 7]}$$

as full reality *f* is unknown, kept constant *C* across all models [eq. 8]:

$$I(f,g) = C - \mathrm{E}_f[\log_e(g(x\mid\theta))] \qquad \text{[eq. 8]}$$

The $\mathrm{E}_f[\log_e(g(x|\theta))]$ term of the equation is the part to focus on in selecting a model out of a set of candidate models in order to minimize the information loss *I*(*f*,*g*). The theoretical Kullback-Leiber information however, is based on true reality and its parameters, and is thus unknown. An estimation of the expected or relative Kullback-Leiber information was obtained by linking it with a maximum log likelihood function (Akaike 1973) and is referred to as AIC and written as [eq. 9]:

$$AIC = -2\log_e(\ell(\theta \mid data)) + 2K \quad \text{[eq. 9]}$$

Where $\log_e(\ell(\theta|data))$ is the value of the maximized log likelihood over the unknown parameters θ, with given data and a –candidate- model. K represents the number of variables included in the model. When applied on a set of a priori defined candidate models, the candidate model with lowest AIC value loses least information in respect to reality and can be considered as the 'best' model out of the candidates.

The AIC is known to be biased when the number of parameters K is large in respect to the sample size n ($n/K < 40$). Sugiura derived a modified AIC, named AIC_c, or a small sample AIC in 1978. Burnham et al. (2002) suggested being conservative and applying AIC_c in case of any doubt [eq. 10]. n Represents the sample size of the data set.

$$AIC_c = -2\log_e(\ell(\theta \mid data)) + 2K + \frac{2K(K+1)}{n-K-1} \quad \text{[eq. 10]}$$

As no single 'best' model exists, the candidate models each need to be evaluated and ranked. The simplest way doing that is by taking the AIC (or AIC_c) differences between each model and the model with the lowest AIC score [eq. 11]. The absolute sizes of the AIC values are thus practically meaningless, it are the differences between AIC scores that determine model suitability given the candidate model and the dataset. A rule of thumb suggests that models with $\Delta_i < 2$ gives substantial empirical support to the 'best' selected model, and should thus be ranked relatively high.

$$\Delta_i = AIC_i - AIC_{\min} \quad \text{[eq. 11]}$$

The likelihood (L) of a model (g), given the data (x), is a measure that quantifies the plausibility of each candidate model, of being the actual Kulback-Leiber model. It is calculated as follows:

$$L(g_i \mid x) = \exp\left(-\frac{1}{2}\Delta_i\right) \qquad \text{[eq. 12]}$$

The likelihood (L) of each model, normalized over *R* candidate models is defined as the Akaike's Weight, ω(*i*). The weights are considered as the weight of evidence in favor of each model i, being the best model amongst the set of candidates and is calculated as [eq. 13]:

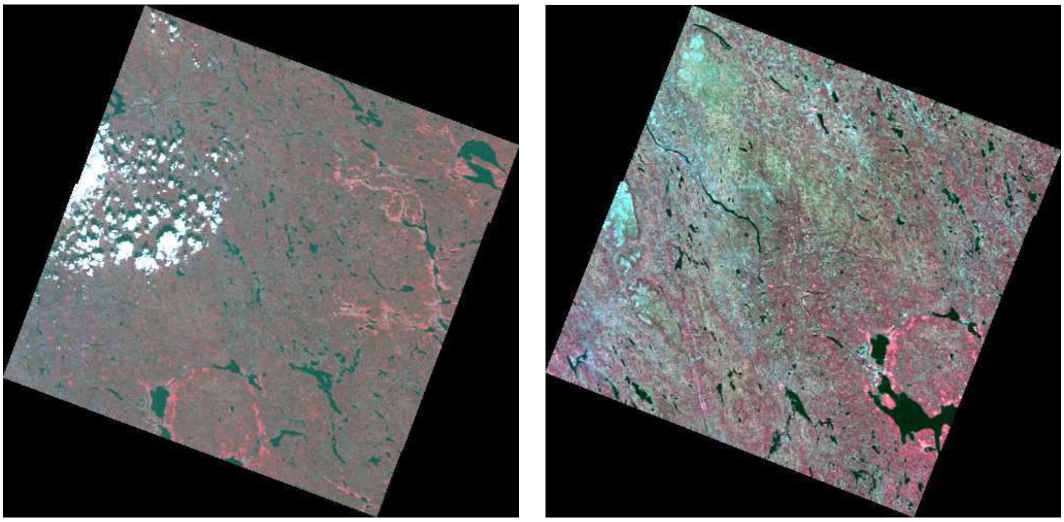
$$\omega_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_r\right)} \qquad \text{[eq. 13]}$$

Appendix 3: Creating the Land-cover Map

Introduction

In habitat modeling studies, up-to-date land-cover maps are a necessity, especially when the study area consists of a highly dynamic ecosystem (e.g. intensively managed forest area). The most recent land-cover maps covering the study area are the Swedish Corine Land-cover, the Corine Land-cover and the detailed Svenska Marktäckedata (Ahlcrona et al. 2002). These land-cover classifications date from 2000. The time lag between their publication and this study is relatively large: during these 8 years, habitat patches were liable to natural succession, disturbances or management measures; with differences in resource availability as a consequence. An example: during this period clear-cut areas can evolve from poorly productive almost bare soils to young primary forests with a high primary production; or old grown forests could have been harvested. These changes in habitat types and resource availability consequently alter animals' decisions in habitat and resource selection (Townsend et al. 2000b).

To bypass this time lag problem, an up-to-date land-cover map of the study area was decided to be created, by merging non or less dynamic landscape features (e.g. roads, build up, agriculture, …) from a topographical map and more dynamic landscape features (e.g. forest types) from a satellite imagery based supervised classification.



Picture A11: the 2 IRS-P6-LISS3 images covering the study area.

Methodology

GIS and Remote sensing data acquisition

The SBBRP obtained a 1:50.000 GSD-Topographic Map (GSD - Geographical data for Sweden) and 2 IRS-P6-LISS3 satellite images from the study area through the "Saccess" clearinghouse (Hosmer and Lemeshow 1989)(Hosmer and Lemeshow 1989)(Hosmer and Lemeshow 1989)(Hosmer and Lemeshow 1989)(Hosmer and Lemeshow 1989)of the Swedish Land Survey (Lantmateriet). The satellite imagery originated from the Indian Remote sensing Satellites IRS-P6 (RESOURCESAT1). This sun synchronous satellite orbits 14 times per day at 817 km height at an inclination of 98.7 degrees. Its payload consists of 3 sensors, of which the LISS3. The swath width of the LISS 3 sensor covers 141 km, and it has a spatial resolution of 23.5 m and a repetition time of 24 days. The sensor operates in 3 spectral bands in the VNIR (green: 0.52-0.59 μm, red: 0.62-0.68 μm, and near infrared: 0.77-0.86 μm) and in 1 spectral band in the SWIR region (1.55-1.70 μm). The band selection and spatial resolution of this sensor make it a comparable with LANDSAT imagery and suitable for vegetation and land-cover mapping (Furby and Wu 2007). Both the satellite imagery and the topographical maps were obtained in the local Swedish RT90 2.5 gon West projection reference system. The partly overlapping IRS-P6_LISS3 images were acquired on respectively July 2nd and 7th 2007. Both images were needed for a classification of the complete study area, because of the extent and some could cover on one of the images. The images were geometrically corrected by Lantmateriet.

Ground truth data collection

From late spring to late autumn 2008, 395 ground control points (GCP's) were collected in the study area. A GCP was considered valuable when it consisted of a single habitat type (>95%) in a radius of minimum 30m. For each GCP, tree density, average tree height and tree species composition was measured or estimated, and the location classified in a predefined habitat type (initial forest categories defined by (Karlsson and Westman 1991). The field procedure followed the habitat assessment protocol of the SBBRP. Based on these habitat assessments, the following classes were defined to initiate a supervised classification:

- S1 p, s and m: Old grown forest ca. 10 years before final harvest, consisting of >90 % pine (p, N = 11) or spruce(s, N=13). Class S1m refers to old grown mixed forest, and was defined when 1 species group was represented a maximum of 70% in the habitat patch (N=22).
- G1 p, s and m: A broad class of medium aged forest, where the medium tree diameter at breast height exceeded 10 cm and tree height on average exceeded 7m. Definition of "p", "s", and "m" are equivalent to these of class S1 (N_p= 40, N_s= 26 and N_m= 77).
- SF: Swamp forest; a forested waterlogged ground (not on peat), often with broadleaf tree species, grasses, herbs and sedges, with in- and outflow of groundwater (N=11).
- B: Bog; often very wet ground, on peat with low productivity. Lacking trees or just very few trees, without any in-or out flow of ground water (N= 5).
- TRB: Tree rich bog; similar as a bog, but sparsely forested (N= 13).
- R2 vd, d and nd: Young forest, prior to primary thinning. Vd, d and nd refer to the tree density (vd, > 5 stems/m^2, N=26; d, <5 and >1 stem/m^2, N=60 and nd, <1 stem/m^2, N=78).
- K= Clear-cut areas or bare soil, with trees <1.3m (N=13).

An additional number of GCP's were derived from a topographical map and field knowledge of the classes Bog (N=20), Build-up (N=20), Water (N=20) and Agriculture (N=15). A similar dataset, dating from 2007 with 498 GCP's was available and kept for validation.

The classification procedure

We followed the procedure for a supervised classification as explained in Lillesand et al. (2004) with the Erdas Imagine 9.1 software package of Leica Geosystems Inc; after the images were atmospherically corrected through the "darkest pixel" method. Training areas were defined by the GCP's, and both satellite images were classified with a maximum likelihood classifier. Class separability was assessed visually through histogram check, a Euclidean Distance separability measure and through the error or contingency matrix results. The classification and class merging process was iterated until the highest total accuracy for each image was reached.

Making the map complete: GIS and RS integration

After the best classification results were obtained, the classified images were resampled to 10x10m raster cell size, made a mosaic off, and clipped according to the extent of the study area. Non dynamic anthropogenic classes like roads build up area and agricultural land and pastures, which have a high accuracy on topographical maps, were derived from the Gronkarta data and converted to a raster (10x10m). Combining the Gronkarta with the classified images would undoubtedly increase general end result accuracy. The final result was then validated towards the validation dataset from 2007 with a nonparametric paired sample test for homogeneity in the SPSS 16.0 software package.

Results

The best classification result obtained was after merging S1 and G1 forests together in a class “Older”, TRB and B into “Bog”, R2vd, R2d into the class “young dense (Y dense)” and K and R2nd into “young open”. The easternmost image contained a relatively large amount of cloud cover, which was classified as well, to be extracted later. The overall accuracy for the easternmost image was 95%, and 85% after clouds were excluded. The overall accuracy for the western image was 87%. The results are summarized in the contingency matrix of table A 3.1.

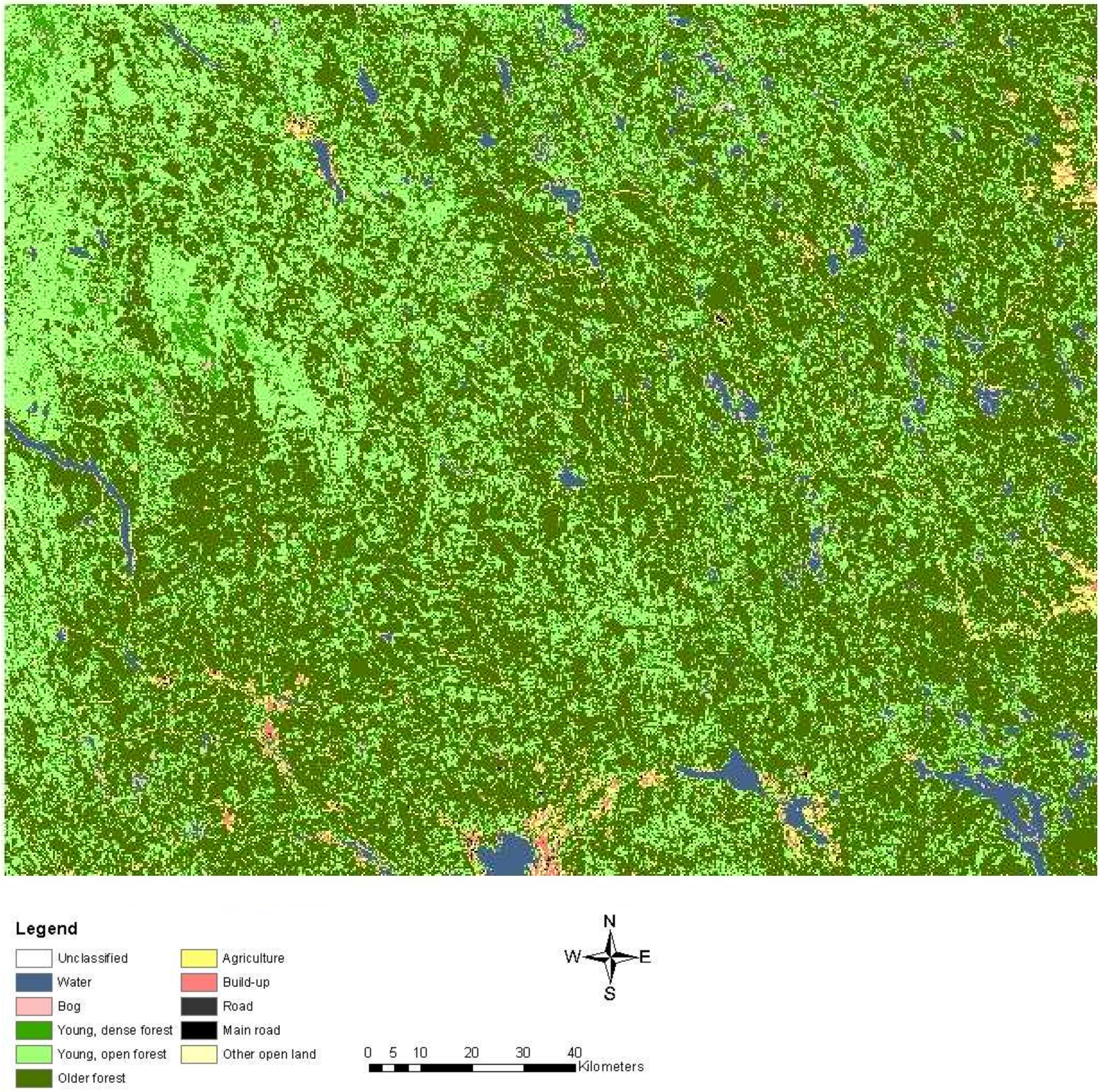
The relatively high training data accuracy levels do not mean an overall high accuracy. It indicates that the chosen training classes are homogenous and spectrally separable, and that the classification procedure worked well for the training pixels (Lillesand et al. 2004, Chang 2008). The users’ accuracy (the number of correctly classified pixels of a category divided by the total number of pixels classified in that category) was in both images highest for the category “water” (1) and lowest in both pictures for the category “young open forest” (0.67 and 0.72). The producers’ accuracy (the proportion of correctly classified pixels of each category) was in both images highest for the category “water” (0.99 in the western image and 1 in the eastern image), and lowest for “young open forest” in the western image (0.66) and for both “bog” and “young open forest” in the eastern image (both 0.77). It should be mentioned that 0.05% of the pixels were classified as “unclassified” or “cloud” in the end result. These two classes were merged into the class “unclassified”.

Table A 3.1: Contingency matrix of the classification results of the IRS-P6-LISS3 images (abbreviations: acc. = accuracy, Y = young).

Westernmost image		**Reference data**							
		Cloud	Bog	Y open	Y dense	Water	Older	Row Total	Users' acc.
Classified data	Cloud	-	-	-	-	-	-	-	
	Bog	-	632	13	0	0	4	649	0.97
	Y open	-	28	148	24	0	22	222	0.67
	Y dense	-	0	29	159	0	8	196	0.81
	Water	-	0	0	0	154	0	154	1.00
	Older	-	0	35	23	1	194	253	0.77
	Column Total	-	660	225	206	155	228	1474	
	Producers' acc.	-	0.96	0.66	0.77	0.99	0.85	**ACC.**	0.87
Easternmost image		**Reference data**							
		Cloud	Water	Bog	Y dense	Y open	Older	Row Total	Users' acc.
Classified data	Cloud	2640	0	0	0	0	0	2640	1.00
	Water	0	173	0	0	0	0	173	1.00
	Bog	6	0	140	0	16	3	165	0.85
	Y dense	0	0	0	113	10	21	144	0.78
	Y open	0	0	33	6	200	39	278	0.72
	Older	0	0	9	2	34	368	413	0.89
	Column Total	2646	173	182	121	260	431	3813	
	Producers' acc.	1.00	1.00	0.77	0.93	0.77	0.85	**ACC.**	0.95
								excl. cloud	0.85

The classes "agriculture", "build-up", "main road", "road" and "other open land" were derived out of the topographical map and added to the classification. "Agriculture" and "build-up" were derived and each aggregated (polygons separated <100m away from each other) in order to prevent misclassification of non-anthropogenic land use classes within these areas. Other open land was chosen to include as well, because open land-cover types like pastures, forest meadows and some grasslands in and around settlements –which are interesting for grazers as cattle- were not represented in the classified images. Map A 3.1 shows the final result of the classification process.

The 498 GCP's dating from 2007 were projected on the newly created map. 77% of the GCP's were correctly identified by the new map. A Marginal Homogeneity test revealed no significant differences between the 2007 validation data and the land-cover types as expected by the 2008 map (N=498, p= 0.649).



Map A11: Land-cover classification of the study area, a result of combining image classification and GIS data derivation.

Figure 1 shows details of the community of Orsa and a summer farm "Skadar Djuberga" on both a topographical map and on the newly created land-cover map. Road networks, build-up area and agriculture resemble –logically- very well on both maps; and open water and other open land as well. On the topographical map, the striped forest patterns –due to forest management- are less visible than on the land-cover map, as well as the different non anthropogenic land-cover types.

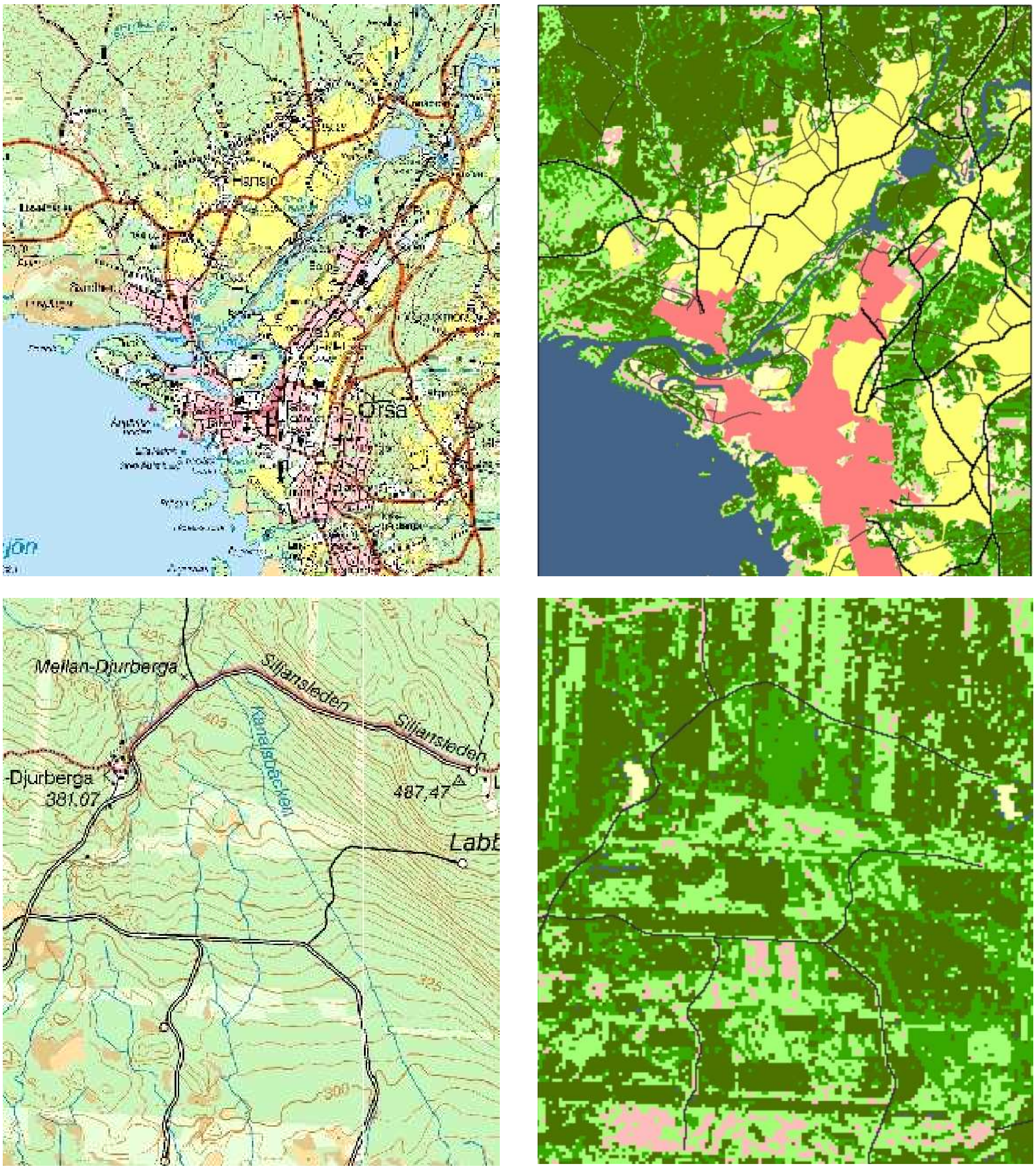


Figure A11: Orsa community (upper two maps) and Skadar Djuberga area (lower two maps) on the topographical map (left) and on the newly created land-cover classification map (right).

Discussion

Considering the high classification accuracy and the validation results, we consider the land-cover classification as workable for our purposes. 100% accuracy cannot, or maybe never be obtained through remote sensing and imagery classification. The sensor characteristics, like temporal and spatial resolution play an important role in this, as well as the on ground dynamics (Foody 2002, Lillesand et al. 2004).

The initial defined set of classes eventually resulted in a classification of only 3 forest types: older, young dense, and young open forest. We could not classify according to species or species composition. The three classes we defined were thus a continuum of forest ages and density, and arbitrary defined. Bogs and tree rich bogs were merged as well. If bogs were misclassified according to the confusion matrix, the missed pixels fell in the class of young open forest. A priori definition of non arbitrary classes can be seen as ideal, but is very difficult in semi-natural ecosystems, where habitat types are varying more in e.g. stand age, species composition, soil water content and tree stem density (Lieng et al. 2005).

The number of GCP's per class differed considerably. Only a small part of the GCP's originated from a randomly drawn sample (N= 36) of points over the study area. The other GCP's were collected during bear habitat related fieldwork. Thus, GCP's were taken relative to bear habitat use. Avoided habitat types were thus underrepresented in the sample of GCP's. This problem was partly bypassed through extracting additional GCP's from topographical maps. Another obstacle is that the GCP's were clustered in areas with concentrated fieldwork activities. These areas were thus relatively well represented in the classification process, but other parts of the – large, 12500 km^2- study area were not sampled at all. A stratified random sampling plan to cover most of the variation in the area of interest would have improved results.

We can conclude that the map is suitable for this study, i.e. as a variable in modeling cattle and bear habitat use, and to predict high encounter risk areas. However, care has to be taken with the map interpretation of land-cover and habitat results (e.g. misclassified bogs). As long as no up-to-date land-cover classification with proven high accuracy is available, land-cover mapping from freely available satellite imagery in combination with topographical GIS data can provide a good and cheap alternative.

Appendix 4: Model selection results

Model selection: Cattle in the pre-berry (pb), intermediate (i) and berry season (b), for mornings (m), afternoons (a) and evenings (e).

RSF_c_pb_m

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	Accuracy	N
ALL	764.77	16	0.41	765.18	0.0	1.0000	0.9993	0.883	1345
Expert	779.69	9	0.13	779.82	14.6	0.0007	0.0007	0.876	
Human P.	968.68	6	0.06	968.74	203.6	0.0000	0.0000	0.866	
Land-cover	1038.5	7	0.08	1038.58	273.4	0.0000	0.0000	0.849	
						1.0007			

RSF_c_pb_a

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	Cvbinary	N
ALL	462.3	16	0.62	462.92	0	1.0000	1.0000	0.889	900
Expert	496.68	9	0.20	496.88	33.97	0.0000	0.0000	0.884	
Human P.	589.38	6	0.09	589.47	126.6	0.0000	0.0000	0.866	
Land-cover	637.41	7	0.13	637.54	174.6	0.0000	0.0000		
						1.0000			

RSF_c_pb_e

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	Cvbinary	N
ALL	54.144	16	4.25	58.39	7.0	0.0304	0.0295	0.883	145
Expert	50.076	9	1.33	51.41	0.0	1.0000	0.9705	0.924	
Human P.	74.38	6	0.61	74.99	23.6	0.0000	0.0000	0.917	
Land-cover	82.916	7	0.82	83.73	32.3	0.0000	0.0000	0.931	
						1.0304			

RSF_c_i_m

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	Cvbinary	N
ALL	1006.9	16	0.31	1007.21	0	2.7183	1.0000	0.887	1800
Expert	1037.4	9	0.10	1037.50	30.3	0.0000	0.0000	0.883	
Human P.	1094.5	6	0.05	1094.55	87.34	0.0000	0.0000	0.816	
Land-cover	1600.4	7	0.06	1600.46	593.3	0.0000	0.0000	0.827	
						2.7183			

RSF_c_i_a

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	Cvbinary	N
ALL	923	10	0.12	923.12	0	1.0000	1.0000	0.882	1445
Expert	962.01	6	0.05	962.06	38.93	0.0000	0.0000	0.841	
Human P.	1439.3	2	0.01	1439.31	516.2	0.0000	0.0000	0.8	
Land-cover	1230.1	6	0.05	1230.15	307	0.0000	0.0000	0.807	
						1.0000	1.0000		

RSF_c_i_e

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	Cvbinary	N
ALL	187.16	16	1.50	188.66	1.262	0.5320	0.3473	0.892	380
Expert	186.91	9	0.49	187.40	0	1.0000	0.6527	0.903	
Human P.	215.55	6	0.23	215.78	28.38	0.0000	0.0000	0.895	
Land-cover	279.25	7	0.30	279.55	92.15	0.0000	0.0000	0.863	
						1.5320			

RSF_c_b_m

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	Cvbinary	N
ALL	2210	16	0.15	2210.15	0	1.0000	1.0000	0.872	3655
Expert	2275.9	9	0.05	2275.95	65.8	0.0000	0.0000	0.867	
Human P.	2666.2	6	0.02	2666.22	456.1	0.0000	0.0000	0.844	
Land-cover	2942.7	7	0.03	2942.73	732.6	0.0000	0.0000	0.836	
						1.0000			

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	Cvbinary	N
RSF_c_b_a	ALL	2843.2	16	0.12	2843.32	0	1.0000	1.0000	0.864	4565
	Expert	2968.5	9	0.04	2968.54	125.2	0.0000	0.0000	0.858	
	Human P.	3771.7	6	0.02	3771.72	928.4	0.0000	0.0000	0.808	
	Land-cover	3486.2	7	0.02	3486.22	642.9	0.0000	0.0000	0.832	
							1.0000			

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	Cvbinary	N
RSF_c_b_e	ALL	527.42	16	0.67	528.09	0	1.0000	0.9882	0.863	825
	Expert	536.73	9	0.22	536.95	8.858	0.0119	0.0118	0.862	
	Human P.	663.13	6	0.10	663.23	135.1	0.0000	0.0000	0.842	
	Land-cover	650.22	7	0.14	650.36	122.3	0.0000	0.0000	0.848	
							1.0119			

Model selection: bear in the pre-berry season, for 6 time steps (in hours, indicated behind the model name)

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	accuracy	N
RSF_b_pb_1-3	ALL	886.21	25	1.175	887.385	0.000	1.000	1.000	0.82	1135
	Human P.	1016	7	0.101	1016.101	128.716	0.000	0.000	0.799	
	Land-cover	1023.3	6	0.076	1023.376	135.991	0.000	0.000	0.797	
	Expert	931.94	11	0.239	932.179	44.793	0.000	0.000	0.814	
							1.000			

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
RSF_b_pb_4_6	ALL	905.75	21	0.796	906.546	0.000	1.000	1.000	0.831	1190
	Human P.	1131.8	7	0.096	1131.896	225.351	0.000	0.000	0.797	
	Land-cover	1054.6	2	0.010	1054.610	148.064	0.000	0.000	0.793	
	Expert	1016.8	7	0.096	1016.896	110.351	0.000	0.000	0.8	
							1.000			

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
RSF_b_pb_7_10	ALL	1116.3	18	0.351	1116.651	0.000	1.000	1.000	0.882	1980
	Human P.	1717.4	7	0.057	1717.457	600.807	0.000	0.000	0.784	
	Land-cover	1314.9	6	0.043	1314.943	198.292	0.000	0.000	0.852	
	Expert	1217.8	11	0.135	1217.935	101.285	0.000	0.000	0.86	
							1.000			

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
RSF_b_pb_11_15	ALL	1960.5	26	0.547	1961.047	0.000	1.000	1.000	0.847	2595
	Human P.	2407.2	7	0.044	2407.244	446.196	0.000	0.000	0.793	
	Land-cover	2271.4	6	0.033	2271.433	310.386	0.000	0.000	0.813	
	Expert	2169.8	11	0.103	2169.903	208.856	0.000	0.000	0.811	
							1.000			

RSF_b_pb_16_21

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1064.4	27	1.162	1065.562	0.000	1.000	1.000	0.828	1330
Human P.	1148.6	7	0.086	1148.686	83.124	0.000	0.000	0.813	
Land-cover	1239.8	7	0.086	1239.886	174.324	0.000	0.000	0.799	
Expert	1129.9	11	0.203	1130.103	64.541	0.000	0.000	0.804	
						1.000			

RSF_b_pb_22_00

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1063.1	26	1.079	1064.179	0.000	1.000	1.000	0.829	1330
Human P.	1148.6	7	0.086	1148.686	84.507	0.000	0.000	0.812	
Land-cover	1239.8	7	0.086	1239.886	175.707	0.000	0.000	0.797	
Expert	1129.9	11	0.203	1130.103	65.924	0.000	0.000	0.804	
						1.000			

Model selection: bear in the intermediate season, for 6 time steps (in hours, indicated behind the model name)

RSF_b_i_1_3

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	510	21	0.835	510.835	0.000	1.000	0.987	0.777	575
Human P.	519.58	7	0.101	519.681	8.846	0.012	0.012	0.803	
Land-cover	570.04	2	0.011	570.051	59.215	0.000	0.000	0.8	
Expert	523.62	7	0.101	523.721	12.886	0.002	0.002	0.807	
						1.014			

RSF_b_ic_4_6

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	484.73	13	0.314	485.044	0.000	1.000	1.000	0.803	600
Human P.	554.24	7	0.096	554.336	69.293	0.000	0.000	0.795	
Land-cover	546.85	2	0.010	546.860	61.817	0.000	0.000	0.805	
Expert	514.54	7	0.096	514.636	29.593	0.000	0.000	0.8	
						1.000			

RSF_b_ic_7_10

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	498.99	14	0.215	499.205	0.000	1.000	1.000	0.866	770
Human P.	665.77	7	0.057	665.827	166.622	0.000	0.000	0.782	
Land-cover	631.61	2	0.006	631.616	132.411	0.000	0.000	0.791	
Expert	558.86	7	0.057	558.917	59.712	0.000	0.000	0.83	
						1.000			

RSF_b_ic_11_15

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	567.45	14	0.164	567.614	27.760	0.000	0.000	0.82	745
Human P.	655.44	7	0.044	655.484	115.630	0.000	0.000	0.783	
Land-cover	606.39	2	0.005	606.395	66.541	0.000	0.000	0.799	
Expert	539.81	7	0.044	539.854	0.000	1.000	1.000	0.836	
						1.000			

RSF_b_ic_16_21

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	989.78	26	1.079	990.859	0.000	1.000	1.000	0.813	1305
Human P.	1153	7	0.086	1153.086	162.227	0.000	0.000	0.792	
Land-cover	1223.4	6	0.065	1223.465	232.605	0.000	0.000	0.789	
Expert	1104.1	12	0.240	1104.340	113.481	0.000	0.000	0.802	
						1.000			

RSF_b_ic_22_00

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	545.45	13	0.280	545.730	0.000	1.000	1.000	0.762	565
Human P.	575.83	7	0.086	575.916	30.186	0.000	0.000	0.755	
Land-cover	624.23	2	0.009	624.239	78.509	0.000	0.000	0.759	
Expert	584.88	7	0.086	584.966	39.236	0.000	0.000	0.743	
						1.000			

Model selection: bear in the berry season, for hourly time steps

RSF_b_b_1

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1141.4	21	0.7345	1142.1	0.00	1.000	1.000	0.818	1280
Human P.	1207.1	7	0.0881	1207.2	65.05	0.000	0.000	0.78	
Land-cover	1330.5	2	0.0094	1330.5	188.37	0.000	0.000	0.784	
Expert	1207.9	11	0.2082	1208.1	65.97	0.000	0.000	0.775	
						1.000			

RSF_b_b_2

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1135.9	25	0.9496	1136.8	0.00	1.000	1.000	0.824	1395
Human P.	1221	7	0.0807	1221.1	84.23	0.000	0.000	0.797	
Land-cover	1396.1	6	0.0605	1396.2	259.31	0.000	0.000	0.8	
Expert	1216.2	11	0.1909	1216.4	79.54	0.000	0.000	0.787	
						1.000			

RSF_b_b_3

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1155.3	25	0.9427	1156.2	0.00	1.000	1.000	0.825	1405
Human P.	1260.1	7	0.0802	1260.2	103.94	0.000	0.000	0.802	
Land-cover	1368.2	6	0.0601	1368.3	212.02	0.000	0.000	0.8	
Expert	1245.4	11	0.1895	1245.6	89.35	0.000	0.000	0.802	
						1.000			

RSF_b_b_4

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1182.8	25	0.8850	1183.7	0.00	1.000	1.000	0.833	1495
Human P.	1276.6	7	0.0753	1276.7	92.99	0.000	0.000	0.809	
Land-cover	1427.8	6	0.0565	1427.9	244.17	0.000	0.000	0.797	
Expert	1270	11	0.1780	1270.2	86.49	0.000	0.000	0.801	
						1.000			

RSF_b_b_5

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1137.2	17	0.4274	1137.6	0.00	1.000	1.000	0.83	1450
Human P.	1253.5	7	0.0777	1253.6	115.95	0.000	0.000	0.803	
Land-cover	1348.6	6	0.0582	1348.7	211.03	0.000	0.000	0.794	
Expert	1220.9	11	0.1836	1221.1	83.46	0.000	0.000	0.806	
						1.000			

RSF_b_b_6

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1128	25	0.9292	1128.9	0.00	1.000	1.000	0.84	1425
Human P.	1248.4	7	0.0790	1248.5	119.55	0.000	0.000	0.801	
Land-cover	1320.2	6	0.0592	1320.3	191.33	0.000	0.000	0.804	
Expert	1194.9	11	0.1868	1195.1	66.16	0.000	0.000	0.818	
						1.000			

RSF_b_b_7

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	992.93	25	0.9782	993.9	0.00	1.000	1.000	0.845	1355
Human P.	1246.5	7	0.0831	1246.6	252.67	0.000	0.000	0.795	
Land-cover	1116.4	5	0.0445	1116.4	122.54	0.000	0.000	0.83	
Expert	1079.8	10	0.1637	1080.0	86.06	0.000	0.000	0.835	
						1.000			

RSF_b_b_8

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	981.53	17	0.4412	982.0	0.00	1.000	1.000	0.852	1405
Human P.	1257.1	7	0.0802	1257.2	275.21	0.000	0.000	0.805	
Land-cover	1105.2	5	0.0429	1105.2	123.27	0.000	0.000	0.823	
Expert	1027	10	0.1578	1027.2	45.19	0.000	0.000	0.834	
						1.000			

RSF_b_b_9

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	883.92	16	0.4377	884.4	0.00	1.000	1.000	0.854	1260
Human P.	1141	7	0.0895	1141.1	256.73	0.000	0.000	0.8	
Land-cover	977.27	5	0.0478	977.3	92.96	0.000	0.000	0.844	
Expert	927.63	10	0.1761	927.8	43.45	0.000	0.000	0.851	
						1.000			

RSF_b_b_10

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	869.06	17	0.4888	869.5	0.00	1.000	1.000	0.863	1270
Human P.	1151.5	7	0.0887	1151.6	282.04	0.000	0.000	0.791	
Land-cover	982.72	6	0.0665	982.8	113.24	0.000	0.000	0.845	
Expert	922.97	11	0.2099	923.2	53.63	0.000	0.000	0.857	
						1.000			

RSF_b_b_11

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	779.45	27	1.3298	780.8	0.00	1.000	1.000	0.87	1165
Human P.	1034.3	7	0.0968	1034.4	253.62	0.000	0.000	0.812	
Land-cover	939.17	5	0.0518	939.2	158.44	0.000	0.000	0.839	
Expert	871.89	10	0.1906	872.1	91.30	0.000	0.000	0.838	
						1.000			

RSF_b_b_12

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	865.27	14	0.3750	865.6	0.00	1.000	1.000	0.824	1135
Human P.	1029.5	7	0.0994	1029.6	163.95	0.000	0.000	0.804	
Land-cover	1027.7	2	0.0106	1027.7	162.07	0.000	0.000	0.793	
Expert	942.98	7	0.0994	943.1	77.43	0.000	0.000	0.814	
						1.000			

RSF_b_b_13

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1013.9	21	0.7230	1014.6	0.00	1.000	1.000	0.843	1300
Human P.	1189.7	7	0.0867	1189.8	175.16	0.000	0.000	0.812	
Land-cover	1253.5	2	0.0093	1253.5	238.89	0.000	0.000	0.797	
Expert	1144.2	7	0.0867	1144.3	129.66	0.000	0.000	0.815	
						1.000			

RSF_b_b_14

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1080.2	26	1.0007	1081.2	0.00	1.000	1.000	0.838	1430
Human P.	1256.5	7	0.0788	1256.6	175.38	0.000	0.000	0.81	
Land-cover	1301.3	6	0.0590	1301.4	220.16	0.000	0.000	0.806	
Expert	1192	11	0.1862	1192.2	110.99	0.000	0.000	0.812	
						1.000			

RSF_b_b_15

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1114	26	0.9663	1115.0	0.00	1.000	1.000	0.852	1480
Human P.	1290.8	7	0.0761	1290.9	175.91	0.000	0.000	0.806	
Land-cover	1358	6	0.0570	1358.1	243.09	0.000	0.000	0.808	
Expert	1227.1	11	0.1798	1227.3	112.31	0.000	0.000	0.814	
						1.000			

RSF_b_b_16

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1172.8	26	0.9696	1173.8	0.00	1.000	1.000	0.835	1475
Human P.	1299.5	7	0.0763	1299.6	125.81	0.000	0.000	0.804	
Land-cover	1410.9	6	0.0572	1411.0	237.19	0.000	0.000	0.798	
Expert	1276.4	11	0.1805	1276.6	102.81	0.000	0.000	0.801	
						1.000			

RSF_b_b_17

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1111.9	22	0.7458	1112.6	0.00	1.000	1.000	0.828	1380
Human P.	1225.1	7	0.0816	1225.2	112.54	0.000	0.000	0.802	
Land-cover	1370	2	0.0087	1370.0	257.36	0.000	0.000	0.8	
Expert	1230.8	7	0.0816	1230.9	118.24	0.000	0.000	0.793	
						1.000			

RSF_b_b_18

Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
ALL	1056.4	26	1.0817	1057.5	0.00	1.000	1.000	0.827	1325
Human P.	1127.2	7	0.0850	1127.3	69.80	0.000	0.000	0.81	
Land-cover	1282.9	6	0.0637	1283.0	225.48	0.000	0.000	0.798	
Expert	1120.5	11	0.2011	1120.7	63.22	0.000	0.000	0.808	
						1.000			

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
RSF_b_b_19	ALL	1040	26	1.1480	1041.1	0.00	1.000	1.000	0.832	1250
	Human P.	1116.7	7	0.0902	1116.8	75.64	0.000	0.000	0.8	
	Land-cover	1233.3	6	0.0676	1233.4	192.22	0.000	0.000	0.8	
	Expert	1118.5	11	0.2132	1118.7	77.57	0.000	0.000	0.795	
							1.000			

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
RSF_b_b_20	ALL	1102.2	18	0.4971	1102.7	0.00	1.000	1.000	0.843	1395
	Human P.	1200.9	7	0.0807	1201.0	98.28	0.000	0.000	0.814	
	Land-cover	1376.2	6	0.0605	1376.3	273.56	0.000	0.000	0.8	
	Expert	1212.8	11	0.1909	1213.0	110.29	0.000	0.000	0.799	
							1.000			

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
RSF_b_b_21	ALL	1050.5	26	1.1250	1051.6	0.00	1.000	1.000	0.839	1275
	Human P.	1122.2	7	0.0884	1122.3	70.66	0.000	0.000	0.823	
	Land-cover	1243.5	6	0.0662	1243.6	191.94	0.000	0.000	0.801	
	Expert	1130.9	11	0.2090	1131.1	79.48	0.000	0.000	0.801	
							1.000			

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
RSF_b_b_22	ALL	1089.1	25	1.0621	1090.2	0.00	1.000	1.000	0.813	1250
	Human P.	1133.8	7	0.0902	1133.9	43.73	0.000	0.000	0.801	
	Land-cover	1244.9	6	0.0676	1245.0	154.81	0.000	0.000	0.8	
	Expert	1142.4	11	0.2132	1142.6	52.45	0.000	0.000	0.798	
							1.000			

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
RSF_b_b_23	ALL	1071	24	1.0042	1072.0	0.00	1.000	1.000	0.789	1220
	Human P.	1104.9	7	0.0924	1105.0	32.99	0.000	0.000	0.792	
	Land-cover	1205.6	5	0.0494	1205.6	133.65	0.000	0.000	0.801	
	Expert	1103	10	0.1820	1103.2	31.18	0.000	0.000	0.788	
							1.000			

	Model Type	AIC	K	c	AICc	ΔAICc	Likelihood	Probability	CV accuracy	N
RSF_b_b_0	ALL	986.51	25	1.1464	987.7	0.00	1.000	1.000	0.81	1160
	Human P.	1057.3	7	0.0972	1057.4	69.74	0.000	0.000	0.796	
	Land-cover	1134.9	6	0.0729	1135.0	147.32	0.000	0.000	0.8	
	Expert	1045.7	11	0.2300	1045.9	58.27	0.000	0.000	0.794	
							1.000			

Model selection: risk in the pre-berry season (N = 9848 for all risk model)

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_PB_M	ALL	23739	0	1.0000	1.0000	0.861
	HP	24273	534	0.0000	0.0000	
	LC	25088	1349	0.0000	0.0000	
	Expert	24171	432	0.0000	0.0000	
				1.0000		

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_PB_A	ALL	21309	0	1.0000	1.0000	0.258
	HP	21468	159	0.0000	0.0000	
	LC	21729	420	0.0000	0.0000	
	Expert	24171	2862	0.0000	0.0000	
				1.0000		

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_PB_E	ALL	20206	27	0.0000	0.0000	
	HP	20179	0	1.0000	0.8808	0.083
	LC	20223	44	0.0000	0.0000	
	Expert	20183	4	0.1353	0.1192	
				1.1353		

Model selection: risk in the intermediate season (N = 9848 for all risk models)

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_I_M	ALL	25591	25591	1.0000	1.0000	1.694
	HP	26434	26434	0.0000	0.0000	
	LC	27301	27301	0.0000	0.0000	
	Expert	26595	26595	0.0000	0.0000	
				1.0000		

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_I_A	ALL	22045	22045	1.0000	1.0000	0.337
	HP	22169	22169	0.0000	0.0000	
	LC	22578	22578	0.0000	0.0000	
	Expert	22192	22192	0.0000	0.0000	
				1.0000		

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_I_E	ALL	19753	19753	0.0000	0.0000	
	HP	19715	19715	1.0000	0.7311	0.001
	LC	19745	19745	0.0000	0.0000	
	Expert	19717	19717	0.3679	0.2689	
				1.3679		

Model selection: risk in the berry season (N = 9848 for all risk models)

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_B_7	ALL	25348	0	1.0000	1.0000	0.948
	HP	26029	681	0.0000	0.0000	
	LC	27861	2513	0.0000	0.0000	
	Expert	26372	1024	0.0000	0.0000	
				1.0000		
	Model Type	**AIC**	**ΔAIC**	**Likelihood**	**Probability**	**CV k=10**
R_B_8	ALL	22160	0	1.0000	1.0000	0.369
	HP	22398	238	0.0000	0.0000	
	LC	22820	660	0.0000	0.0000	
	Expert	22532	372	0.0000	0.0000	
				1.0000		
	Model Type	**AIC**	**ΔAIC**	**Likelihood**	**Probability**	**CV k=10**
R_B_9	ALL	22429	0	1.0000	1.0000	0.429
	HP	22776	347	0.0000	0.0000	
	LC	23179	750	0.0000	0.0000	
	Expert	22904	475	0.0000	0.0000	
				1.0000		
	Model Type	**AIC**	**ΔAIC**	**Likelihood**	**Probability**	**CV k=10**
R_B_10	ALL	21328	0	1.0000	1.0000	0.213
	HP	21425	97	0.0000	0.0000	
	LC	21532	204	0.0000	0.0000	
	Expert	21458	130	0.0000	0.0000	
				1.0000		
	Model Type	**AIC**	**ΔAIC**	**Likelihood**	**Probability**	**CV k=10**
R_B_11	ALL	26123	0	1.0000	1.0000	1.104
	HP	26935	812	0.0000	0.0000	
	LC	27215	1092	0.0000	0.0000	
	Expert	27278	1155	0.0000	0.0000	
				1.0000		
	Model Type	**AIC**	**ΔAIC**	**Likelihood**	**Probability**	**CV k=10**
R_B_12	ALL	22437	0	1.0000	1.0000	0.397
	HP	22796	359	0.0000	0.0000	
	LC	23032	595	0.0000	0.0000	
	Expert	22997	560	0.0000	0.0000	
				1.0000		
	Model Type	**AIC**	**ΔAIC**	**Likelihood**	**Probability**	**CV k=10**
R_B_13	ALL	21021	0	1.0000	1.0000	0.158
	HP	21109	88	0.0000	0.0000	
	LC	21201	180	0.0000	0.0000	
	Expert	21174	153	0.0000	0.0000	
				1.0000		
	Model Type	**AIC**	**ΔAIC**	**Likelihood**	**Probability**	**CV k=10**
R_B_14	ALL	20283	9	0.0111	0.0108	
	HP	20274	0	1.0000	0.9714	0.059
	LC	20307	33	0.0000	0.0000	
	Expert	20282	8	0.0183	0.0178	
				1.0294		
	Model Type	**AIC**	**ΔAIC**	**Likelihood**	**Probability**	**CV k=10**
R_B_15	ALL	29566	0	1.0000	1.0000	2.087
	HP	31860	2294	0.0000	0.0000	
	LC	31796	2230	0.0000	0.0000	
	Expert	32144	2578	0.0000	0.0000	
				1.0000		

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_B_16	ALL	23282	0	1.0000	1.0000	0.605
	HP	23947	665	0.0000	0.0000	
	LC	24149	867	0.0000	0.0000	
	Expert	24022	740	0.0000	0.0000	
				1.0000		

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_B_17	ALL	21669	0	1.0000	1.0000	0.267
	HP	22010	341	0.0000	0.0000	
	LC	22075	406	0.0000	0.0000	
	Expert	22020	351	0.0000	0.0000	
				1.0000		

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_B_18	ALL	21759	0	1.0000	1.0000	0.308
	HP	22002	243	0.0000	0.0000	
	LC	22187	428	0.0000	0.0000	
	Expert	22083	324	0.0000	0.0000	
				1.0000		

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_B_19	ALL	27048	0	1.0000	1.0000	1.359
	HP	29083	2035	0.0000	0.0000	
	LC	28880	1832	0.0000	0.0000	
	Expert	29176	2128	0.0000	0.0000	
				1.0000		

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_B_20	ALL	26766	0	1.0000	1.0000	1.607
	HP	28385	1619	0.0000	0.0000	
	LC	28645	1879	0.0000	0.0000	
	Expert	28560	1794	0.0000	0.0000	
				1.0000		

	Model Type	AIC	ΔAIC	Likelihood	Probability	CV k=10
R_B_21	ALL	23805	0	1.0000	1.0000	0.746
	HP	24603	798	0.0000	0.0000	
	LC	24926	1121	0.0000	0.0000	
	Expert	24756	951	0.0000	0.0000	
				1.0000		

Appendix 5: Model coefficients

I. Cattle RSF

Covariate	RSF_c_pb_m β	SE	RSF_c_pb_a β	SE	RSF_c_pb_e β	SE	RSF_c_i_m β	SE	RSF_c_i_a β	SE
(Intercept)	1.445000	1.062000	0.848263	1.041110	0.797900	2.385000	-0.537500	1.182000	1.419071	0.460532
TRI	0.069730	0.115600	0.259062	0.150191	0.136600	0.488000	0.144800	0.099000	0.258209	0.096865
Slope	0.088560	0.041110	0.134005	0.054935	0.000000	0.000000	-0.118000	0.041520	-0.034256	0.042527
Tracks	-0.000456	0.000217	-0.000295	0.000263	0.000000	0.000000	-0.000186	0.000173	0.000382	0.000171
Unpaved	-0.003161	0.000627	-0.003972	0.000988	-0.002679	0.003840	-0.003123	0.000583	-0.001029	0.000527
Farm	-0.001597	0.000195	-0.001484	0.000252	-0.003822	0.001386	-0.002719	0.000228	-0.002674	0.000229
Building	-0.000354	0.000179	-0.001106	0.000235	0.000000	0.000000	-0.000168	0.000147	-0.000529	0.000134
Settlement	0.000072	0.000116	-0.000183	0.000159	0.000000	0.000000	-0.000036	0.000113	-0.000196	0.000115
Creeks	0.001018	0.000408	0.001560	0.000502	0.000000	0.000000	0.001307	0.000335	0.002020	0.000382
NDVI	-1.346000	0.842700	-0.771684	0.947223	0.000000	0.000000	0.036630	0.717000	-1.281917	0.568515
Bog	1.022000	1.002000	1.405772	0.990556	0.000000	0.000000	3.281000	1.148000	0.000000	0.000000
Young dense	-0.709700	1.031000	-0.279439	0.997136	0.000000	0.000000	2.347000	1.116000	0.000000	0.000000
Young open	-0.168300	0.987600	-0.194023	0.947487	-0.095360	1.443000	2.836000	1.106000	0.000000	0.000000
Older	-1.463000	0.993400	-1.015322	0.944254	-0.923900	1.514000	1.740000	1.102000	0.000000	0.000000
Road	2.312000	1.148000	0.877398	1.047351	10.290000	6.656000	3.682000	1.181000	0.000000	0.000000
Other open	2.448000	1.114000	2.782049	1.071357	5.262000	3.112000	4.246000	1.205000	0.000000	0.000000

Covariate	***RSF_c_i_e*** ***β***	***SE***	***RSF_c_b_m*** ***β***	***SE***	***RSF_c_b_a*** ***β***	***SE***	***RSF_c_b_e*** ***β***	***SE***
(Intercept)	1.165955	0.891952	0.321100	0.529500	-0.452900	0.579500	-0.675100	0.999900
TRI	0.502791	**0.214479**	0.161600	**0.064050**	0.239900	**0.057150**	0.286100	**0.143200**
Slope	0.000000	0.000000	0.046680	0.025950	0.035230	0.023780	0.031680	0.052700
Tracks	0.000000	0.000000	-0.000795	**0.000117**	-0.000923	**0.000104**	-0.000763	**0.000261**
Unpaved	-0.005264	**0.001612**	-0.002723	**0.000360**	-0.001265	**0.000285**	-0.001946	**0.000772**
Farm	-0.002135	**0.000385**	-0.001382	**0.000111**	-0.000970	**0.000081**	-0.000934	**0.000187**
Building	0.000000	0.000000	0.000034	0.000096	0.000170	**0.000082**	0.000026	0.000214
Settlement	0.000000	0.000000	-0.000004	0.000068	-0.000059	0.000060	-0.000285	0.000150
Creeks	0.000000	0.000000	-0.000228	0.000234	0.000303	0.000190	0.000499	0.000424
NDVI	0.000000	0.000000	-1.479000	**0.433700**	-2.078000	**0.392900**	-0.256600	1.012000
Bog	0.000000	0.000000	2.081000	**0.495000**	2.194000	**0.547700**	2.137000	**0.874300**
Young dense	-0.812877	0.872237	0.266800	0.518400	0.456300	0.577700	0.465200	0.905800
Young open	-2.338813	**0.817077**	1.101000	**0.484100**	1.042000	0.546200	0.226200	0.834700
Older	-1.307283	**0.608375**	-0.192700	0.487300	-0.386900	0.553500	-0.150300	0.828700
Road	0.643498	0.951364	2.556000	**0.554100**	2.524000	**0.593300**	3.713000	**1.021000**
Other open	2.164304	**1.088478**	3.353000	**0.572000**	4.283000	**0.626600**	4.253000	**1.207000**

II. Bear, pre-berry season

Covariate	RSF_b_pbc_1_3 β	SE	RSF_b_pbc_4_6 β	SE	RSF_b_pbc_7_10 β	SE	RSF_b_pbc_11_15 β	SE	RSF_b_pbc_16_21 β	SE	RSF_b_pbc_22_24 β	SE
(Intercept)	-4.61600	1.42800	-7.97100	1.31600	-9.04700	0.92820	-4.40600	0.88330	-2.49400	1.28700	-2.28300	1.38800
Building	0.00016	0.00016	0.00046	0.00018	0.00010	0.00013	0.00008	0.00010	-0.00001	0.00015	-0.00004	0.00014
Settlement	0.00008	0.00007	0.00015	0.00007	0.00004	0.00006	0.00021	0.00006	0.00014	0.00007	0.00014	0.00007
RSF	0.00000	0.00000	0.00000	0.00000	2.96800	1.24700	-0.02067	0.97220	1.23300	1.50600	0.00000	0.00000
TRI	-0.00945	0.11250	-0.10290	0.11000	-0.05312	0.10150	-0.10740	0.07226	-0.04762	0.10120	-0.04288	0.10090
TRI1000	-0.07006	0.11700	-0.14180	0.11690	-0.14610	0.10100	0.06409	0.07804	0.13670	0.10640	0.16720	0.10640
Tracks	-0.00074	0.00017	0.00014	0.00014	0.00006	0.00013	-0.00023	0.00019	-0.00078	0.00016	-0.00078	0.00016
Unpaved	0.00041	0.00040	0.00041	0.00041	0.00148	0.00033	0.00020	0.00027	0.00052	0.00037	0.00049	0.00037
Cut	0.00024	0.00006	0.00018	0.00006	0.00026	0.00004	0.00011	0.00013	0.00015	0.00004	0.00015	0.00004
Slope	0.05301	0.03744	0.04264	0.03200	0.03960	0.03535	0.00906	0.02493	0.01451	0.03557	0.01871	0.03501
Creek	0.00145	0.00044	0.00004	0.00000	0.00140	0.00000	0.00022	0.00024	0.00040	0.00035	0.00043	0.00035
Water	0.00091	0.00017	0.00122	0.00018	0.00116	0.00016	0.00121	0.00011	0.00078	0.00014	0.00078	0.00014
NDVI	0.20130	0.74220	0.06200	0.70700	0.07300	0.00470	0.50000	0.62710	1.03200	0.77744	1.50000	0.77070
N	0.82570	1.15100	0.21960	1.24500	0.00000	0.00000	-0.56500	0.67330	-0.63780	0.94790	-0.68090	0.94970
NE	0.37630	1.12100	0.62140	1.14100	0.00000	0.00000	-0.79070	0.66110	-1.12300	0.92190	-1.17400	0.92360
E	0.92310	1.09800	0.91570	1.13900	0.00000	0.00000	-0.38100	0.63420	-1.06400	0.91680	-1.07600	0.91870
SE	0.99690	1.09500	1.11600	1.13000	0.00000	0.00000	-0.15790	0.62710	-0.77790	0.91410	-0.73490	0.91600
S	0.81440	1.09600	1.44200	1.12400	0.00000	0.00000	-0.06097	0.62530	-0.63280	0.91310	-0.62750	0.91490
SW	1.08200	1.09600	1.07100	1.12700	0.00000	0.00000	-0.44050	0.63230	-0.59400	0.91580	-0.58640	0.91740
W	0.62730	1.12500	0.40130	1.16500	0.00000	0.00000	-0.50410	0.64950	-0.53490	0.92070	-0.54680	0.92290
NW	0.96040	1.17000	0.04750	1.20000	0.00000	0.00000	-0.89210	0.67400	-1.84700	1.01100	-1.86100	1.01200
Bog	0.44520	0.90040	0.00000	0.00000	-1.00800	0.85010	-1.00000	0.62740	0.29700	0.80020	0.22980	0.79020
Youngdense	1.96200	0.83660	0.00000	0.00000	1.68400	0.68970	0.62300	0.42300	0.79460	0.74730	0.74620	0.73710
Youngopen	1.77200	0.81410	0.00000	0.00000	0.76420	0.69600	0.23290	0.40820	0.97660	0.71690	0.91990	0.70480
Older	0.20940	0.81980	0.00000	0.00000	-0.23410	0.68750	-0.80810	0.40910	-0.29950	0.72040	-0.36020	0.70710
Otheropenland	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.39810	1.52100	0.51690	1.46100
Farm	-0.00003	0.00006	0.00007	0.00006	0.00011	0.00006	0.00000	0.00004	-0.00019	0.00006	-0.00021	0.00008

III. Bear, intermediate season

	RSF_b_ic_1-3		RSF_b_ic_4-6		RSF_b_ic_7_10		RSF_b_ic_11-15		RSF_b_ic_16_21		RSF_b_ic_22_24	
Covariate	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
(Intercept)	-4.567000	1.436000	-6.319000	0.947800	-9.859000	1.048000	-8.612000	0.779800	-8.423000	1.276000	-2.836000	0.766100
Building	-0.000199	0.000223	0.000387	0.000211	0.000256	0.000236	0.000024	0.000195	0.000524	0.000162	0.000302	0.000211
Settlement	0.000096	0.000093	0.000113	0.000096	0.000284	0.000087	0.000117	0.000084	0.000402	0.000067	0.000233	0.000089
RSF	0.000000	0.000000	0.000000	0.000000	-0.112100	1.493000	0.000000	0.00000C	0.815700	0.211000	0.000000	0.000000
TRI	-0.034670	0.152700	0.043910	0.156100	0.303400	0.144100	0.000000	0.00000C	0.215000	0.108100	0.173300	0.134800
TRI1000	-0.064650	0.154000	0.066820	0.161500	0.234200	0.146800	0.000000	0.00000C	-0.020950	0.107400	-0.442900	0.148100
Tracks	-0.000120	0.000195	-0.000275	0.000223	-0.000711	0.000217	-0.000309	0.000195	-0.000386	0.000189	-0.000352	0.000182
Unpaved	0.001429	0.000622	0.000954	0.000618	0.002488	0.000628	0.002686	0.000462	0.001060	0.000346	0.001223	0.000436
Car	0.000293	0.000063	0.000186	0.000058	0.000144	0.000060	0.000303	0.000061	0.000175	0.000046	0.000294	0.000082
Slope	-0.011530	0.052330	-0.071800	0.052440	-0.117100	0.067440	0.000000	0.00000C	-0.045010	0.039680	-0.032240	0.050460
Creek	-0.001554	0.000662	-0.001878	0.000676	-0.002041	0.000662	0.000000	0.00000C	-0.001436	0.000388	-0.001148	0.000461
Water	0.000598	0.000220	0.000908	0.000218	0.001548	0.000230	0.000000	0.00000C	0.001376	0.000164	0.000641	0.000188
NDVI	1.424000	0.959100	6.320000	1.173000	8.403000	1.167000	10.200000	1.087000	2.681000	0.774000	0.400200	0.854800
N	1.712000	1.231000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	-0.875900	0.898200	0.000000	0.000000
NE	1.203000	1.219000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	-0.013150	0.797100	0.000000	0.000000
E	1.254000	1.209000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	0.276200	0.784000	0.000000	0.000000
SE	1.826000	1.194000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	0.503700	0.770700	0.000000	0.000000
S	1.829000	1.177000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	0.762900	0.771100	0.000000	0.000000
SW	1.706000	1.193000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	0.664700	0.770600	0.000000	0.000000
W	1.308000	1.220000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	0.427900	0.797400	0.000000	0.000000
NW	2.108000	1.241000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	-0.627400	0.928100	0.000000	0.000000
Bog	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	0.050900	0.895600	0.000000	0.000000
Youngdense	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	0.736000	0.829900	0.000000	0.000000
Youngopen	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	0.720900	0.813800	0.000000	0.000000
Older	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	0.333700	0.809000	0.000000	0.000000
Otheropenland	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.00000C	0.000000	0.000000	0.000000	0.000000
Farm	-0.000148	0.000081	-0.000007	0.000086	0.000146	0.000091	0.000000	0.00000C	0.000180	0.000063	-0.000054	0.000083

IV. Bear, berry season

	RSF_b_bc_1		RSF_b_bc_2		RSF_b_bc_3		RSF_b_bc_4		RSF_b_bc_5		RSF_b_bc_6	
Covariate	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*
(Intercept)	-3.31200	0.87710	-4.285000	1.070000	-4.819000	1.049000	-4.956000	1.256000	-5.255000	0.930400	-6.191000	1.430000
Building	-0.00025	0.00014	-0.000192	0.000141	-0.000072	0.000140	0.000049	0.000142	-0.000055	0.000141	-0.000154	0.000141
Settlement	0.00002	0.00006	-0.000044	0.000062	0.000058	0.000060	0.000203	0.000060	0.000178	0.000063	0.000058	0.000061
TRI	0.14140	0.09253	0.047580	0.096320	0.102200	0.095800	-0.167100	0.097330	-0.063920	0.093480	-0.128800	0.096600
TRI1000	0.25590	0.10720	0.254100	0.110400	0.090790	0.108600	0.289500	0.105400	0.101200	0.105000	0.095100	0.103100
Tracks	0.00000	0.00012	0.000014	0.000120	-0.000079	0.000124	-0.000173	0.000114	-0.000176	0.000125	-0.000098	0.000125
Unpaved	0.00086	0.00033	0.001340	0.000344	0.001112	0.000351	0.001299	0.000339	0.001862	0.000344	0.001660	0.000331
Car	0.00023	0.00004	0.000281	0.000041	0.000254	0.000041	0.000244	0.000039	0.000175	0.000040	0.000208	0.000041
Slope	0.05050	0.02746	0.029270	0.030170	0.040800	0.029740	0.051230	0.030080	0.010400	0.030950	-0.014860	0.034850
Creek	-0.00035	0.00031	-0.000180	0.000328	0.000173	0.000304	0.000077	0.000304	-0.000080	0.000308	-0.000423	0.000334
Water	0.00096	0.00014	0.001059	0.000148	0.001034	0.000140	0.001058	0.000141	0.000962	0.000129	0.000960	0.000131
NDVI	0.60010	0.61940	0.056850	0.628000	-0.411900	0.667400	0.578800	0.717600	2.296000	0.715200	2.076000	0.670100
N	-1.14900	0.79980	-0.941700	0.798300	-0.011650	0.665500	-0.697600	0.910000	0.000000	0.000000	0.052340	0.924600
NE	-1.64400	0.78750	-1.152000	0.779500	-1.229000	0.674900	-0.957800	0.871700	0.000000	0.000000	0.318300	0.892800
E	-1.24600	0.77010	-0.509200	0.757600	0.157100	0.616900	-0.385400	0.853900	0.000000	0.000000	0.791400	0.862700
SE	-1.06200	0.76020	-0.588200	0.758000	0.080290	0.618800	-0.429100	0.852200	0.000000	0.000000	0.848700	0.860400
S	-0.99860	0.75330	-1.137000	0.758200	-0.117800	0.607600	-0.515000	0.853500	0.000000	0.000000	0.732200	0.856500
SW	-1.13500	0.75570	-0.415400	0.749700	0.289000	0.607500	-0.597800	0.852100	0.000000	0.000000	0.580300	0.860200
W	-1.30100	0.77640	-1.105000	0.785000	-0.199800	0.659400	-0.914900	0.869400	0.000000	0.000000	0.505500	0.882800
NW	-1.53600	0.83280	-0.733500	0.802800	-0.348200	0.705100	-1.287000	0.913900	0.000000	0.000000	-0.457300	0.966800
Bog	0.00000	0.00000	0.369400	0.737400	-0.175700	0.765000	-0.509200	0.905000	-0.880800	0.924900	0.137900	1.131000
Youngdense	0.000000	0.000000	0.497200	0.739200	0.823000	0.738600	1.117000	0.840600	1.198000	0.813500	1.766000	1.067000
Youngopen	0.000000	0.000000	1.059000	0.690300	0.834600	0.713200	0.688300	0.815700	0.492200	0.796000	1.229000	1.059000
Older	0.000000	0.000000	0.077460	0.690000	0.059360	0.712600	0.249500	0.812700	0.453600	0.790300	0.974100	1.055000
Farm	-0.00010	0.00005	-0.000088	0.000055	-0.000043	0.000052	-0.000080	0.000053	-0.000147	0.000057	0.000010	0.000054
rsf	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000

	RSF_b_bc_7		RSF_b_bc_8		RSF_b_bc_9		RSF_b_bc_10		RSF_b_bc_11		RSF_b_bc_12	
Covariate	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*
(Intercept)	-7.4520000	1.4080000	-8.709000	0.984200	-8.949000	1.269000	-5.746000	0.953000	-8.823000	1.489000000	-6.962000	0.738800
Building	0.0001980	0.0001507	0.000078	0.000147	0.000176	0.000162	0.000180	0.000161	0.000049	0.000178000	0.000129	0.000165
Settlement	0.0001497	0.0000644	0.000214	0.000063	0.000103	0.000067	0.000124	0.000067	0.000173	0.000074540	0.000173	0.000067
TRI	-0.1033000	0.1037000	-0.030230	0.105600	-0.141500	0.114400	-0.185100	0.112200	-0.241200	0.125400000	-0.325000	0.114500
TRI1000	0.1094000	0.1100000	0.146700	0.107300	0.271700	0.114800	0.131000	0.114600	0.220700	0.125700000	0.251700	0.119300
Tracks	-0.0001754	0.0001384	-0.000014	0.000141	-0.000075	0.000154	-0.000138	0.000147	-0.000118	0.000160200	-0.000132	0.000147
Unpaved	0.0007305	0.0003853	0.001563	0.000357	0.000998	0.000426	0.001492	0.000412	0.001724	0.000441700	0.001150	0.000390
Car	0.0001755	0.0000444	0.000141	0.000042	0.000157	0.000046	0.000157	0.000045	0.000225	0.000051110	0.000196	0.000046
Slope	-0.0378800	0.0374600	-0.069040	0.041030	-0.073320	0.043740	-0.005366	0.039580	-0.029370	0.046730000	0.031870	0.032150
Creek	-0.0005527	0.0003792	-0.000600	0.000361	-0.001026	0.000393	-0.001003	0.000389	-0.000853	0.000419300	-0.000923	0.000370
Water	0.0010970	0.0001552	0.000848	0.000143	0.001202	0.000156	0.000981	0.000154	0.001098	0.000172500	0.001141	0.000153
NDVI	4.3760000	0.7856000	5.966000	0.817600	4.866000	0.863200	5.391000	0.845200	4.690000	0.910100000	5.607000	0.756300
N	0.2517000	1.1990000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.017890	1.285000000	0.000000	0.000000
NE	-0.3096000	1.1920000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	1.206000	1.205000000	0.000000	0.000000
E	0.7286000	1.1700000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.714900	1.200000000	0.000000	0.000000
SE	0.8942000	1.1700000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	1.556000	1.181000000	0.000000	0.000000
S	0.8153000	1.1620000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	1.493000	1.179000000	0.000000	0.000000
SW	0.3541000	1.1720000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.740100	1.188000000	0.000000	0.000000
W	0.1287000	1.1960000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	0.697100	1.212000000	0.000000	0.000000
NW	-0.1994000	1.2380000	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000	-0.844000	1.392000000	0.000000	0.000000
Bog	0.0000000	0.0000000	0.000000	0.000000	0.000000	0.000000	-2.486000	1.280000	0.000000	0.000000000	0.000000	0.000000
Youngdense	2.1560000	0.4951000	3.022000	0.758400	3.991000	1.061000	0.840400	0.708500	2.471000	0.655300000	0.000000	0.000000
Youngopen	1.1400000	0.4850000	2.080000	0.745000	2.516000	1.051000	-0.386100	0.701400	1.042000	0.639500000	0.000000	0.000000
Older	0.9605000	0.4743000	1.544000	0.743200	2.099000	1.048000	-0.993000	0.697800	0.829300	0.631100000	0.000000	0.000000
Farm	-0.0000022	0.0000632	-0.000021	0.000064	0.000035	0.000069	0.000027	0.000066	0.000054	0.000073280	0.000060	0.000067
rsf	-1.1080000	1.3550000	0.464300	1.489000	-0.139600	1.855000	-3.226000	1.777000	-2.077000	1.982000000	0.138200	1.688000

	RSF_b_bc_13		RSF_b_bc_14		RSF_b_bc_15		RSF_b_bc_16		RSF_b_bc_17		RSF_b_bc_18	
Covariate	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*
(Intercept)	-6.257000	0.962900	-6.005000	1.464000	-6.218000	1.332000	-5.533000	1.493000	-4.914000	1.325000	-4.600000	1.180000
Building	0.000375	0.000154	-0.000022	0.000147	-0.000052	0.000155	0.000120	0.000143	0.000121	0.000147	-0.000041	0.000154
Settlement	0.000199	0.000066	0.000197	0.000064	0.000120	0.000063	0.000196	0.000059	0.000126	0.000062	0.000269	0.000065
TRI	-0.268500	0.103000	-0.144800	0.100700	-0.054690	0.097190	-0.073950	0.096980	0.002192	0.101400	0.057280	0.100900
TRI1000	0.216800	0.107800	0.205700	0.106100	0.048750	0.104300	0.174800	0.098830	0.074440	0.103600	-0.067630	0.110000
Tracks	-0.000194	0.000142	-0.000118	0.000130	-0.000181	0.000126	-0.000130	0.000126	-0.000108	0.000127	-0.000041	0.000126
Unpaved	0.001446	0.000361	0.001603	0.000323	0.001578	0.000338	0.001642	0.000337	0.001530	0.000338	0.001499	0.000310
Car	0.000196	0.000044	0.000178	0.000043	0.000225	0.000042	0.000190	0.000039	0.000225	0.000040	0.000265	0.000044
Slope	0.019160	0.036890	-0.107300	0.038650	-0.026200	0.034250	0.044380	0.032290	0.076990	0.030710	0.017540	0.031860
Creek	-0.001338	0.000357	-0.000361	0.000341	-0.000146	0.000335	-0.000593	0.000313	-0.000252	0.000310	0.000477	0.000319
Water	0.001131	0.000147	0.001337	0.000152	0.001212	0.000140	0.001272	0.000139	0.001294	0.000139	0.001005	0.000145
NDVI	4.188000	0.665900	1.926000	0.714100	2.107000	0.721100	0.869800	0.698600	0.639100	0.661700	1.566000	0.766100
N	-0.168100	0.813000	-0.916700	0.922000	-0.013210	0.950300	-0.236100	1.272000	-0.693400	1.234000	-0.130900	0.894400
NE	-0.347300	0.779300	-1.004000	0.879100	0.464800	0.883400	-0.232500	1.246000	-0.983500	1.219000	-0.365200	0.834400
E	-0.452200	0.758100	-0.605000	0.857600	0.693900	0.876900	-0.037460	1.243000	-0.325700	1.207000	-0.273400	0.832900
SE	0.135700	0.742800	-0.534300	0.854100	0.159100	0.875600	-0.006445	1.245000	-0.225800	1.203000	0.012460	0.826200
S	0.222800	0.734500	-0.651400	0.848000	0.965600	0.864400	-0.243300	1.241000	-0.633600	1.202000	-0.134900	0.822900
SW	0.179100	0.739900	-0.850900	0.856400	0.736100	0.872400	-0.200000	1.244000	-0.646600	1.205000	-0.275300	0.829000
W	-0.695000	0.792300	-0.584400	0.868600	-0.095980	0.920600	-0.496000	1.261000	-0.745800	1.218000	-0.875200	0.860300
NW	-0.964400	0.952200	-1.841000	0.987700	-0.041820	0.937600	-0.353700	1.280000	-1.604000	1.301000	-0.397700	0.887700
Bog	0.000000	0.000000	0.100200	1.209000	-0.968000	1.001000	-1.413000	0.744700	0.000000	0.000000	-1.379000	0.793800
Youngdense	0.000000	0.000000	2.424000	1.079000	1.136000	0.817600	0.429000	0.643100	0.000000	0.000000	-0.596100	0.742700
Youngopen	0.000000	0.000000	1.265000	1.069000	0.384600	0.808700	0.139600	0.612500	0.000000	0.000000	-0.219900	0.698900
Older	0.000000	0.000000	1.317000	1.064000	0.091730	0.804100	-0.154000	0.610400	0.000000	0.000000	-0.870400	0.699600
Farm	-0.000008	0.000066	0.000048	0.000064	0.000050	0.000060	0.000073	0.000061	0.000014	0.000061	-0.000068	0.000066
rsf	-0.076860	2.207000	-1.447000	1.853000	1.279000	1.384000	2.127000	1.054000	0.807400	1.086000	0.556900	1.080000

	RSF_b_bc_19		RSF_b_bc_20		RSF_b_bc_21		RSF_b_bc_22		RSF_b_bc_23		RSF_b_bc_24	
Covariate	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*
(Intercept)	-7.057000	1.683000	-5.137000	0.816200	-5.133000	1.419000	-4.021000	1.261000	-4.066000	0.589400	-5.548000	1.061000
Building	-0.000293	0.000151	-0.000271	0.000145	-0.000051	0.000148	0.000138	0.000147	0.000018	0.000143	-0.000051	0.000151
Settlement	0.000213	0.000064	0.000111	0.000062	0.000222	0.000066	0.000124	0.000062	-0.000011	0.000061	0.000124	0.000066
TRI	0.227200	0.101300	0.003353	0.095710	0.102800	0.101400	0.204800	0.097890	-0.036360	0.098040	-0.002907	0.101400
TRI1000	0.062570	0.107100	0.145100	0.111100	0.116000	0.110600	0.084490	0.107800	0.133000	0.108000	0.269300	0.118100
Tracks	-0.000101	0.000125	-0.000178	0.000122	-0.000108	0.000126	-0.000226	0.000126	-0.000148	0.000123	-0.000136	0.000128
Unpaved	0.001448	0.000348	0.001038	0.000341	0.000810	0.000355	0.000428	0.000360	0.001288	0.000338	0.000899	0.000367
Car	0.000194	0.000041	0.000250	0.000040	0.000191	0.000042	0.000224	0.000040	0.000248	0.000041	0.000240	0.000045
Slope	0.003267	0.030170	0.003081	0.029810	0.011040	0.029480	0.046170	0.031650	0.030040	0.029080	0.012840	0.030210
Creek	0.000136	0.000319	0.000170	0.000314	0.000078	0.000335	-0.000430	0.000323	-0.000398	0.000318	0.000000	0.000337
Water	0.001103	0.000147	0.001194	0.000144	0.001123	0.000144	0.001005	0.000148	0.000816	0.000140	0.000970	0.000152
NDVI	0.321300	0.767000	0.666000	0.678600	1.280000	0.757200	-0.166800	0.706700	0.374700	0.662000	1.045000	0.706100
N	-0.587700	1.230000	0.000000	0.000000	0.106800	1.213000	-1.407000	0.931300	0.000000	0.000000	-0.531700	0.815300
NE	0.084370	1.185000	0.000000	0.000000	0.196700	1.185000	-1.039000	0.900800	0.000000	0.000000	-0.771600	0.755500
E	0.482100	1.175000	0.000000	0.000000	-0.081750	1.186000	-0.862900	0.891400	0.000000	0.000000	-0.343300	0.749700
SE	0.084930	1.176000	0.000000	0.000000	0.146300	1.183000	-0.908800	0.892100	0.000000	0.000000	0.264500	0.740900
S	0.449000	1.166000	0.000000	0.000000	-0.092720	1.182000	-1.119000	0.884600	0.000000	0.000000	-0.095420	0.733000
SW	0.286600	1.172000	0.000000	0.000000	0.244200	1.182000	-0.789200	0.882000	0.000000	0.000000	0.153000	0.733900
W	0.978400	1.179000	0.000000	0.000000	0.126000	1.193000	-0.827900	0.896800	0.000000	0.000000	-0.742500	0.776600
NW	-0.787500	1.254000	0.000000	0.000000	-0.388600	1.246000	-1.153000	0.951400	0.000000	0.000000	-1.537000	0.940400
Bog	1.256000	1.158000	-0.147200	0.646600	-1.027000	0.716500	0.200700	0.852700	0.000000	0.000000	-0.007864	0.667400
Youngdense	1.855000	1.140000	-0.029110	0.655400	-0.069910	0.665500	0.336700	0.838200	0.357400	0.398100	0.324200	0.633300
Youngopen	1.907000	1.113000	0.579700	0.595200	-0.047340	0.622200	0.831500	0.795800	0.142300	0.308800	0.937700	0.591500
Older	1.519000	1.116000	0.041510	0.596500	-0.409700	0.622400	0.295200	0.792000	-0.233700	0.307700	0.166700	0.588100
Farm	-0.000007	0.000064	0.000028	0.000063	-0.000047	0.000064	-0.000038	0.000056	0.000012	0.000054	0.000020	0.000057
rsf	1.095000	1.153000	3.701000	1.118000	1.932000	0.958300	0.000000	0.000000	0.000000	0.000000	0.000000	0.000000

V. Risk functions, pre-berry season

	R_PB_M		R_PB_A		R_PB_E	
Covariate	*β*	*se*	*β*	*se*	*β*	*se*
(Intercept)	0.377500000	0.229700000	0.015760000	0.236500000	**0.107100000**	0.040600000
building	**-0.000155700**	0.000019320	**-0.000124100**	0.000020520	-0.000023900	0.000020430
settlement	**0.000030450**	0.000011360	0.000000780	0.000012200	0.000018230	0.000010650
tri	**0.027580000**	0.011020000	**0.034220000**	0.012020000	0.000000000	0.000000000
tri500	-0.031890000	0.017070000	-0.003138000	0.018450000	0.000000000	0.000000000
tri1000	**0.067990000**	0.017720000	**0.056190000**	0.019070000	0.000000000	0.000000000
tracks	**-0.000170500**	0.000022760	**-0.000078740**	0.000024290	**-0.000044010**	0.000022280
unpaved	**-0.000807500**	0.000052500	**-0.000567500**	0.000055840	-0.000104100	0.000055760
car	**0.000065190**	0.000005660	**0.000055100**	0.000006085	0.000010890	0.000005763
slope	**0.028270000**	0.004115000	**0.009147000**	0.004506000	0.000000000	0.000000000
creek	-0.000008319	0.000044180	**0.000124800**	0.000046920	0.000000000	0.000000000
water	**0.000195400**	0.000016680	**0.000173200**	0.000017740	0.000000000	0.000000000
ndvi	**0.525000000**	0.079350000	0.108200000	0.085980000	0.000000000	0.000000000
N	-0.134100000	0.185400000	-0.057800000	0.188200000	0.000000000	0.000000000
NE	-0.051810000	0.179000000	-0.018120000	0.181900000	0.000000000	0.000000000
E	-0.086090000	0.176900000	-0.032630000	0.179800000	0.000000000	0.000000000
SE	-0.081610000	0.175800000	-0.033030000	0.178700000	0.000000000	0.000000000
S	-0.105100000	0.175500000	-0.070290000	0.178500000	0.000000000	0.000000000
SW	-0.079620000	0.175800000	-0.081430000	0.178800000	0.000000000	0.000000000
W	-0.143300000	0.178300000	-0.106000000	0.181600000	0.000000000	0.000000000
NW	-0.195400000	0.185000000	-0.101100000	0.188000000	0.000000000	0.000000000
farm	**-0.000375900**	0.000012090	**-0.000212000**	0.000012880	**-0.000061380**	0.000012940
Road	0.058980000	0.150000000	-0.076080000	0.161300000	0.083950000	0.069720000
Bog	-0.136400000	0.142800000	-0.072960000	0.150500000	0.000000000	0.000000000
Youngdense	0.015850000	0.143600000	-0.023160000	0.153900000	0.000000000	0.000000000
Youngopen	-0.164800000	0.140900000	-0.083380000	0.149600000	0.000000000	0.000000000
Older	-0.251900000	0.140900000	-0.113100000	0.149900000	0.000000000	0.000000000
Otheropen	**0.636800000**	0.154500000	0.072760000	0.178600000	**0.530000000**	0.088480000

VI. Risk functions, intermediate season

	R_I_M		*R_I_A*		*R_I_E*	
Covariate	*β*	*se*	*β*	*se*	*β*	*se*
(Intercept)	-0.338500000	0.222100000	0.411700000	0.228400000	-0.000659300	0.041420000
building	**-0.000053380**	0.000018940	**-0.000133700**	0.000020230	0.000000766	0.000020620
settlement	**0.000105000**	0.000010960	**-0.000062450**	0.000012170	-0.000000077	0.000010800
tri	**0.077890000**	0.010600000	**0.046000000**	0.011720000	0.000000000	0.000000000
tri500	**-0.045840000**	0.016310000	-0.009522000	0.018080000	0.000000000	0.000000000
tri1000	**0.177100000**	0.017130000	0.021890000	0.018490000	0.000000000	0.000000000
tracks	**-0.000186000**	0.000022500	**-0.000063350**	0.000023660	0.000000869	0.000022500
unpaved	**-0.000333000**	0.000048640	0.000002317	0.000052710	-0.000000718	0.000055970
car	**0.000080490**	0.000005716	**0.000055240**	0.000005890	0.000000060	0.000005820
slope	**-0.022510000**	0.004349000	-0.004065000	0.004494000	0.000000000	0.000000000
creek	**-0.000240100**	0.000043530	**0.000226200**	0.000046070	0.000000000	0.000000000
water	**0.000328200**	0.000016250	**0.000081710**	0.000017480	0.000000000	0.000000000
ndvi	**0.313800000**	0.075930000	**0.469500000**	0.084550000	0.000000000	0.000000000
N	0.047380000	0.185100000	-0.026830000	0.187300000	0.000000000	0.000000000
NE	0.147400000	0.178700000	0.016420000	0.181700000	0.000000000	0.000000000
E	0.113600000	0.176800000	0.026420000	0.179600000	0.000000000	0.000000000
SE	0.059950000	0.175800000	0.023330000	0.178500000	0.000000000	0.000000000
S	0.068310000	0.175500000	-0.003503000	0.178300000	0.000000000	0.000000000
SW	0.034690000	0.175800000	-0.034050000	0.178600000	0.000000000	0.000000000
W	0.111300000	0.178000000	-0.051470000	0.181200000	0.000000000	0.000000000
NW	0.094570000	0.183400000	-0.059980000	0.187800000	0.000000000	0.000000000
farm	**-0.000452700**	0.000012070	**-0.000281600**	0.000012860	-0.000000276	0.000013210
Road	-0.023300000	0.140200000	-0.269900000	0.149500000	-0.000612700	0.073390000
Bog	-0.111900000	0.130800000	**-0.336000000**	0.136600000	0.000000000	0.000000000
Youngdense	-0.206900000	0.132200000	-0.254200000	0.138700000	0.000000000	0.000000000
Youngopen	0.012510000	0.128800000	**-0.343100000**	0.134800000	0.000000000	0.000000000
Older	-0.221700000	0.129000000	**-0.307300000**	0.134800000	0.000000000	0.000000000
Otheropen	0.281300000	0.150600000	0.158900000	0.156100000	0.000120700	0.115600000

VII. Risk functions, berry season

	R_B_7		R_B_8		R_B_9		R_B_10		R_B_11		R_B_12		R_B_13		R_B_14	
Covariates	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE	β	SE
(intercept)	0.636200	0.213400	0.016380	0.231100	-0.088510	0.232400	-0.178500	0.248600	-0.054280	0.216000	-0.192900	0.230700	-0.108700	0.237100	0.041240	0.040740
building	0.000115	0.000018	0.000044	0.000020	-0.000088	0.000020	0.000008	0.000020	0.000027	0.000018	0.000052	0.000020	0.000041	0.000021	0.000000	0.000020
settlement	0.000032	0.000010	0.000050	0.000012	0.000036	0.000012	0.000033	0.000012	0.000030	0.000010	0.000024	0.000011	0.000021	0.000012	0.000025	0.000011
tri	0.054620	0.009998	0.039650	0.011550	0.028520	0.011410	0.005640	0.012000	0.054140	0.010120	0.014220	0.011870	-0.001455	0.012090	0.000000	0.000000
tri500	-0.017420	0.015570	-0.022610	0.017700	-0.092580	0.017520	-0.019990	0.018300	-0.028080	0.015690	-0.024050	0.017560	-0.016360	0.018470	0.000000	0.000000
tri1000	0.056350	0.016200	0.099750	0.018870	0.130700	0.018230	0.074750	0.018890	0.076980	0.016310	0.089440	0.018240	0.063160	0.019070	0.000000	0.000000
tracks	0.000333	0.000021	0.000166	0.000024	0.000184	0.000024	0.000131	0.000024	0.000311	0.000021	0.000229	0.000024	0.000133	0.000025	0.000072	0.000022
unpaved	0.001025	0.000048	0.000532	0.000054	0.000587	0.000058	0.000292	0.000055	0.000350	0.000046	0.000409	0.000052	0.000192	0.000055	-0.000014	0.000055
car	0.000074	0.000005	0.000056	0.000006	0.000061	0.000006	0.000038	0.000006	0.000080	0.000005	0.000076	0.000006	0.000046	0.000006	0.000024	0.000006
slope	0.011030	0.008950	0.004896	0.004426	0.004467	0.004408	0.006904	0.004585	0.010730	0.008882	0.012290	0.004290	0.008009	0.004568	0.000000	0.000000
creek	0.000092	0.000041	0.000114	0.000046	0.000137	0.000046	0.000118	0.000048	-0.000078	0.000041	-0.000054	0.000045	0.000105	0.000048	0.000000	0.000000
water	0.000271	0.000015	0.000194	0.000017	0.000241	0.000017	0.000136	0.000018	0.000272	0.000015	0.000274	0.000017	0.000161	0.000018	0.000000	0.000000
ndvi	0.088480	0.070280	0.216200	0.082540	0.164200	0.081680	0.129300	0.086310	-0.058400	0.071610	0.102400	0.080760	0.058020	0.086850	0.000000	0.000000
N	0.086810	0.181400	-0.027990	0.188100	-0.008257	0.188000	-0.008595	0.188300	0.045870	0.182100	0.028610	0.188100	0.026090	0.188200	0.000000	0.000000
NE	0.069010	0.176200	0.088170	0.181800	0.045620	0.181800	0.007140	0.181900	0.176500	0.175800	0.054800	0.181700	0.019060	0.181900	0.000000	0.000000
E	0.040860	0.174100	0.006595	0.179700	0.013860	0.179700	-0.006702	0.179900	0.124200	0.174100	0.042750	0.179700	0.008737	0.179900	0.000000	0.000000
SE	0.141800	0.173000	-0.014580	0.178700	-0.016660	0.178700	-0.085840	0.178800	0.230600	0.173000	0.010840	0.178700	-0.014940	0.178800	0.000000	0.000000
S	0.137700	0.172800	-0.022310	0.178400	-0.019440	0.178400	-0.020740	0.178500	0.223600	0.172800	-0.013170	0.178400	-0.025140	0.178600	0.000000	0.000000
SW	0.098480	0.173000	0.002823	0.178700	0.011770	0.178700	0.000737	0.178800	0.150200	0.173100	0.019370	0.178700	-0.008555	0.178900	0.000000	0.000000
W	0.042190	0.175100	-0.008794	0.181200	-0.008072	0.181100	-0.022750	0.181500	0.155800	0.175100	0.030720	0.181000	-0.017200	0.181600	0.000000	0.000000
NW	-0.058830	0.180900	-0.084610	0.187800	-0.098290	0.187800	-0.080800	0.187900	-0.085830	0.181800	0.022830	0.187000	-0.088980	0.188300	0.000000	0.000000
farm	0.000471	0.000011	0.000285	0.000013	0.000294	0.000012	0.000169	0.000013	0.000322	0.000011	0.000253	0.000012	0.000159	0.000013	0.000078	0.000013
Road	0.078000	0.128600	-0.087220	0.151700	0.051590	0.158100	0.128500	0.171700	0.189900	0.134200	-0.056710	0.151600	-0.054460	0.168400	0.048760	0.070960
Bog	-0.013820	0.121400	-0.166200	0.142200	-0.097830	0.144600	0.029420	0.162100	0.002819	0.126300	-0.131800	0.141900	-0.095490	0.152300	0.000000	0.000000
Young dense	-0.125600	0.128800	-0.146800	0.144800	-0.065840	0.147200	0.084650	0.165700	-0.218800	0.128500	-0.208700	0.145800	-0.141200	0.156700	0.000000	0.000000
Young open	0.023940	0.120400	-0.118900	0.140800	-0.087880	0.148300	0.062850	0.161400	0.093850	0.125700	-0.081160	0.141000	-0.063270	0.151800	0.000000	0.000000
Older	-0.234800	0.120700	-0.231000	0.141100	-0.162200	0.148600	-0.012360	0.161800	-0.282500	0.126200	-0.247600	0.141400	-0.149700	0.152200	0.000000	0.000000
Other open	0.231800	0.140000	-0.116500	0.178500	-0.119000	0.177300	0.240400	0.190100	0.546800	0.142700	0.636400	0.158300	0.232900	0.179400	-0.005518	0.114800

	R_B_15		R_B_16		R_B_17		R_B_18		R_B_19		R_B_20		R_B_21	
Covariates	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*	*β*	*SE*
(Intercept)	0.854700	0.182400	0.134800	0.216900	-0.093930	0.230800	-0.033980	0.231000	0.662400	0.192200	0.931500	0.182600	0.278900	0.209400
building	0.000009	0.000016	-0.000051	0.000019	-0.000035	0.000020	-0.000066	0.000020	-0.000138	0.000017	-0.000114	0.000017	-0.000086	0.000019
settlement	-0.000016	0.000009	-0.000059	0.000011	-0.000041	0.000012	-0.000010	0.000012	-0.000106	0.000010	-0.000128	0.000010	-0.000060	0.000011
tri	0.118200	0.009009	0.074840	0.011090	0.045150	0.011790	0.057550	0.011790	0.173900	0.009705	0.135100	0.009972	0.111800	0.010880
tri500	-0.023150	0.014160	-0.032830	0.017330	-0.024970	0.018230	-0.021670	0.018190	-0.025970	0.015310	-0.036110	0.015850	-0.028530	0.017040
tri1000	-0.018460	0.014540	0.082020	0.017910	0.054920	0.018820	0.036840	0.018750	0.018280	0.015660	0.065450	0.016220	0.072060	0.017560
tracks	-0.000456	0.000019	-0.000233	0.000023	-0.000145	0.000024	-0.000139	0.000024	-0.000340	0.000020	-0.000350	0.000021	-0.000249	0.000022
unpaved	-0.000518	0.000041	-0.000798	0.000052	-0.000503	0.000054	-0.000553	0.000054	-0.000997	0.000046	-0.001155	0.000048	-0.000952	0.000051
car	0.000059	0.000005	0.000073	0.000006	0.000070	0.000006	0.000068	0.000006	0.000058	0.000005	0.000063	0.000005	0.000068	0.000005
slope	0.009382	0.003405	0.015450	0.004075	0.014010	0.004358	0.004858	0.004398	0.017550	0.003513	0.011010	0.003635	0.007147	0.004006
creek	0.000215	0.000036	0.000155	0.000043	0.000140	0.000046	0.000247	0.000045	0.000340	0.000038	0.000412	0.000038	0.000288	0.000042
water	0.000269	0.000013	0.000337	0.000016	0.000282	0.000017	0.000227	0.000017	0.000310	0.000014	0.000306	0.000015	0.000323	0.000016
ndvi	-0.534600	0.060660	-0.180500	0.076150	-0.194400	0.082290	-0.063490	0.082400	-0.487800	0.065790	-0.420400	0.066300	-0.157100	0.074490
N	-0.090790	0.154000	-0.037120	0.177400	0.033100	0.187900	0.030090	0.187800	-0.191400	0.154100	-0.287300	0.141200	-0.142000	0.166900
NE	0.057530	0.148500	-0.018220	0.171600	0.043560	0.181800	0.051480	0.181700	-0.117700	0.149100	-0.280000	0.136400	-0.111500	0.161200
E	-0.023050	0.146800	-0.045250	0.169500	0.044610	0.179700	0.043130	0.179700	-0.151600	0.147000	-0.342100	0.134200	-0.168200	0.159200
SE	-0.005218	0.146000	-0.070940	0.168500	0.036470	0.178700	0.051530	0.178700	-0.133500	0.146000	-0.381600	0.133300	-0.174900	0.158100
S	0.130300	0.145600	-0.114200	0.168300	-0.046510	0.178500	-0.014700	0.178500	-0.089920	0.145700	-0.347800	0.132900	-0.213900	0.157800
SW	0.140000	0.145800	-0.089250	0.168500	-0.052440	0.178800	-0.010860	0.178800	-0.081970	0.145900	-0.356500	0.133200	-0.150800	0.158000
W	0.016380	0.147700	-0.146700	0.171100	-0.030500	0.181300	-0.038900	0.181500	0.066060	0.147300	-0.380900	0.135400	-0.178500	0.160400
NW	-0.055370	0.153100	-0.157500	0.177300	-0.071380	0.188000	-0.048440	0.187700	-0.324200	0.154800	-0.443600	0.141800	-0.289400	0.167300
farm	-0.000413	0.000010	-0.000258	0.000012	-0.000192	0.000012	-0.000196	0.000012	-0.000349	0.000010	-0.000344	0.000010	-0.000287	0.000011
Road	0.293500	0.115100	0.177800	0.139900	0.053470	0.151900	0.044320	0.151200	0.519700	0.128300	0.436700	0.127800	0.256800	0.139900
Bog	0.368400	0.107800	0.031030	0.132500	0.021810	0.142100	-0.086240	0.142200	0.573000	0.122100	0.483600	0.121400	0.144200	0.133100
Youngdense	-0.055830	0.112700	-0.136400	0.136700	-0.125700	0.147200	-0.160300	0.146500	0.132000	0.126900	0.035530	0.126300	-0.076530	0.137000
Youngopen	0.273200	0.108600	-0.053780	0.132400	-0.072350	0.142300	-0.106200	0.141800	0.320800	0.123000	0.219900	0.122300	0.022990	0.133000
Older	-0.232100	0.109300	-0.199000	0.132700	-0.137900	0.142700	-0.189500	0.142100	0.007023	0.123400	-0.081260	0.122700	-0.145800	0.133300
Otheropen	1.212000	0.117800	1.132000	0.142900	0.751400	0.158700	0.840100	0.156200	0.898300	0.135400	1.466000	0.129600	1.242000	0.142200