

**FACULTE DES SCIENCES**

Institut d'Ecologie

**Habitat and corridor selection of an expanding red deer  
(*Cervus elaphus*) population**

**Thèse de doctorat**

présentée à la

Faculté des Sciences de  
l'Université de Lausanne

par

**Patrick Patthey**

Biologiste diplômé  
Université de Lausanne

**Jury**

Prof. Jacques Hausser, Président  
Dr. Cornelis Neet, Directeur de thèse  
Prof. Jean-Michel Gaillard, Expert  
Prof. Antoine Guisan, Expert  
Dr. François Klein, Expert

LAUSANNE  
2003

# Imprimatur

Vu le rapport présenté par le jury d'examen, composé de

Président	Monsieur Prof. Jacques Hausser
Directeur de thèse	Monsieur Dr Cornelis Neet
Rapporteur	Monsieur Prof. Jacques Hausser
Experts	Monsieur Prof. Jean-Michel Gaillard
	Monsieur Prof. Antoine Guisan
	Monsieur Dr François Klein

le Conseil de Faculté autorise l'impression de la thèse de

**Monsieur Patrick Patthey**

Biologiste diplômé de l'Université de Lausanne

intitulée

**Habitat and corridor selection of an expanding red deer  
(Cervus elaphus) population**

Lausanne, le 19 juin 2003

pour Le Doyen de la Faculté des Sciences

  
Prof. Jacques Hausser

## SUMMARY

Red deer (*Cervus elaphus*) are currently recolonizing the Jura Mountains and the Geneva Bassin, a highly fragmented area, from releases during the 1950's. This picturesque icon of wildlife provides recreational opportunities for hunters, artists and large public but, on the other hand, red deer may have serious negative impacts on forests and meadows. It may be also a threat to human safety (e.g. vehicle collisions). Therefore, local managers have required wildlife management options that consider spatial and temporal colonization possibilities to handle the risks associated with an expanding red deer population. The aim of this work is to understand red deer recovery in a spatially explicit manner in order to improve future red deer population management.

Our first objectives are to describe current red deer habitat use and to construct habitat suitability (HS) maps. Firstly, our habitat analyses are based on a hierarchical summer and winter habitat selection framework. Our results reveal that red deer populations are established in the less disturbed open forests (away from inhabited area and open roads) both in the Geneva Bassin and Jura Mountains. Secondly, inside their population range, red deer bedding sites are settled in the less disturbed open forest stands characterized, in the summer, by a high grass cover (sedges, *Festuca altissima* and red raspberry). Moreover, our findings highlight the importance of thermoregulation as a habitat feature, especially during winter mornings. As a result, red deer ecological requirements may be integrated into forest, recreation and road management planning. We have also constructed reliable HS maps for red deer populations based on habitat factors derived from Geographic information systems (GIS) and have shown that other areas predicted as favorable are not currently occupied.

Habitat selection analyses have allowed us to rank and point out the important habitat factors and to construct habitat suitability maps. To achieve our goals, our last objectives have been to answer the following question; can red deer reach areas predicted as suitable and if so, where will the corridors be located? Therefore, we compared habitat features on observed linear corridors to average landscape habitat. The comparison, based on GIS, allowed us to build a corridor suitability model that helped us to construct a corridor suitability map. Corridors are depicted by a high density of trees (i.e. forest, thickets) and are distant from inhabited areas. The corridor suitability map locates the potential corridors and the red deer-road conflict areas. We next developed DeerDisperser, a software that simulates spatially-explicit random walks and applied it to the corridor suitability map. We successfully parameterized it to estimate between-habitat patch colonization probabilities. Thus, we may assess whether suitable habitat patches not yet occupied may be colonized in the future. Moreover, urban planners and wildlife managers may test effects of their management scenario on the connectivity network by virtually altering the landscape, for example by constructing new roads. Our dispersal models differ from previous known models, and are the first that are not based on expert knowledge.

Our predictive models and tools that allow habitat-based management, are likely to become critical tools for insuring forestry, recreation and landscape options to be taken into account in the management of red deer in the Geneva Bassin and the nearby Jura Mountains. As DeerDisperser needs to be calibrated, our dispersal framework might also be extended to other animal species.



## RESUME

Le cerf élaphe (*Cervus elaphus*) recolonise progressivement le bassin genevois et les montagnes jurassiennes à partir de lâchers effectués au milieu des années cinquante. Le cerf est un gibier exceptionnel, un symbole de la nature, et sa présence constitue un enrichissement incontestable de la faune sauvage. Cependant, il est reconnu que cet ongulé peut avoir un impact négatif et important sur les forêts et les cultures. De plus, le cerf est une espèce à risque du point de vue de la circulation routière. C'est pourquoi les gestionnaires locaux ont commandité ce travail, afin d'établir des bases de gestion solides qui tiennent compte des différents intérêts en jeu et des potentialités de développement des effectifs de cerfs.

Nos premiers objectifs ont consisté à décrire l'utilisation actuelle de l'espace par le cerf et à construire des cartes de répartition de l'habitat potentiel. Nous avons effectué des analyses de sélection de l'habitat hiérarchisées. Nos résultats montrent que les populations de cerfs s'établissent dans les forêts ouvertes les plus tranquilles (à distance des habitations et des routes carrossables), aussi bien dans le massif jurassien que dans le bassin genevois. A l'intérieur des zones de présence, les reposées (endroits où les cerfs se couchent la journée pour ruminer) sont également établies dans les forêts les plus ouvertes et les moins perturbées, qui sont caractérisées, en été, par un couvert herbacé dense (graminées, *Festuca altissima* et framboisiers). De plus, nous avons montré l'importance de la thermorégulation comme composante de l'habitat, principalement durant les matinées hivernales. Nos résultats sur les exigences écologiques du cerf au niveau de l'habitat pourront être intégrés dans les futurs plans de gestion de la forêt, du public et du territoire. Nous avons également construit des cartes saisonnières de répartition de l'habitat potentiel à partir de variables de l'habitat dérivées de systèmes d'information géographique (SIG). Ces cartes montrent que des régions évaluées comme favorables ne sont actuellement pas occupées par les cerfs.

Est-ce que les cerfs pourront coloniser ces régions favorables et par où passeront-ils pour les atteindre? Nos derniers objectifs consistaient à répondre à ces deux questions. Pour ce faire, nous avons comparé statistiquement l'habitat situé sur les passages à cerfs connus avec l'habitat moyen du Bassin genevois. Cette comparaison, basée sur un SIG, nous a permis d'élaborer un modèle des passages à cerfs (corridors), à l'aide duquel nous avons construit une carte des probabilités de présence de corridors. Les passages à cerfs sont caractérisés par une haute densité de végétaux ligneux (forêts, haies, arbre isolés) et sont distants des zones habitées. La carte des probabilités de présence de corridors montre aussi les corridors potentiels et les zones à risque du point de vue de la circulation routière. Nous avons ensuite développé *DeerDisperser*, un logiciel qui simule des déplacements de cerfs. Nous l'avons lié à la carte des potentialités de déplacements et calibré pour estimer les probabilités de passage entre patchs d'habitats favorables. Ainsi, nous pouvons déterminer si des régions favorables encore actuellement inoccupées peuvent être colonisées par les cerfs dans le futur et quels seront les chemins d'accès à ces régions. Ce logiciel sera également utile aux gestionnaires de la faune et du territoire, qui pourront tester l'effet de leurs scénarii de gestion sur la connectivité du paysage, par exemple en construisant virtuellement une route dans le SIG. Notre démarche est à notre connaissance la première qui n'est pas basée principalement sur des jugements et valeurs d'experts.

Nos résultats, ainsi que les outils développés, devraient assurer une gestion critique et efficace des populations de cerfs, tenant compte de la gestion forestière, du réseau routier et du public. Comme *DeerDisperser* doit être calibré, la méthode adoptée pourra être étendue à d'autres espèces animales.

## FOREWORD

This thesis was done simultaneously to a mandate and we intended to base thesis on red deer radiotracking. As we were not able to catch enough animals, radiotracking results were not used and presented in this thesis. Nevertheless mandate report (Patthey 2003) is available on line at :

<http://www.dse.vd.ch/forets/faune/infos/cerfs.html>,

<http://www.geneve.ch/nature/organisation/sfpnp/insp-faune/esp-prio/cerfs.html>,

[http://www.wild.unizh.ch/prog/wildman/rothirsch\\_d.html](http://www.wild.unizh.ch/prog/wildman/rothirsch_d.html)

## **CONTENTS**

<b>1. INTRODUCTION</b>	<b>7</b>
<b>1.1. General Introduction</b>	<b>7</b>
<b>1.2. Red deer</b>	<b>8</b>
<b>1.3. Study area</b>	<b>11</b>
1.3.1. Overview	11
1.3.2. Lowland and Geneva Bassin	11
1.3.3. Jura mountains	11
<b>1.4. Red deer in the study area: a historical perspective</b>	<b>13</b>
<b>1.5. Habitat selection</b>	<b>15</b>
1.5.1. Overview	15
1.5.2. Habitat selection levels and observation scale	15
<b>1.6. General methods</b>	<b>16</b>
1.6.1. Geographic information systems	16
1.6.2. Red deer indices	18
1.6.3. Modeling	18
1.6.4. Programming tools	21
<b>1.7. Aim, objectives and thesis contents</b>	<b>22</b>
<b>2. RED DEER POPULATION HABITAT IN WESTERN SWITZERLAND</b>	<b>25</b>
<b>2.1. Summary</b>	<b>25</b>
<b>2.2. Introduction</b>	<b>26</b>
<b>2.3. Methods</b>	<b>27</b>
2.3.1. Overview	27
2.3.2. Land use variables	27
2.3.3. Disturbance variables	29
2.3.4. Habitat selection analyses	29
<b>2.4. Results</b>	<b>31</b>
2.4.1. Winter	31
2.4.2. Summer	32
<b>2.5. Discussion</b>	<b>36</b>
2.5.1. ENFA GIS model performances	36
2.5.2. Habitat features	37

<b>3. SCALE-DEPENDENT SEASONAL HABITAT SELECTION OF AN EXPANDING RED DEER POPULATION IN THE SWISS JURA MOUTAINS</b>	<b>41</b>
<b>3.1. Summary</b>	<b>41</b>
<b>3.2. Introduction</b>	<b>42</b>
<b>3.3. Study area</b>	<b>43</b>
<b>3.4. Methods</b>	<b>43</b>
3.4.1. Overview	43
3.4.2. Red deer presence data	45
3.4.3. Local scale variables	45
3.4.4. Home range scale variables	45
3.4.5. Data analysis	46
<b>3.5. Results</b>	<b>47</b>
3.5.1. Model evaluation	47
3.5.2. Summer habitat	47
3.5.3. Winter habitat	49
<b>3.6. Discussion</b>	<b>53</b>
3.6.1. Model strength and weakness	53
3.6.2. Red deer habitat selection	53
<b>3.7. Management implications</b>	<b>56</b>
<b>4. HIERARCHICAL BED-SITE SELECTION FOR AN EXPANDING RED DEER POPULATION</b>	<b>57</b>
<b>4.1. Summary</b>	<b>57</b>
<b>4.2. Introduction</b>	<b>58</b>
<b>4.3. Methods</b>	<b>59</b>
4.3.1. Overview	59
4.3.2. Data	60
4.3.3. Statistical analysis	63
<b>4.4. Results</b>	<b>66</b>
4.4.1. Summer habitat selection	66
4.4.2. Winter habitat selection	67
4.4.3. Model evaluations	72
<b>4.5. Discussion</b>	<b>73</b>
4.5.1. ENFA strengths and weaknesses	73
4.5.2. Habitat selection overview	73
4.5.3. Hierarchical habitat selection	74
4.5.4. Yearly habitat selection	74
4.5.5. Seasonal habitat selection	74
4.5.6. Micro-climate selection	75
4.5.7. Sexual habitat selection	76
<b>4.6. Management implications</b>	<b>77</b>



<b>5. MODELLING CORRIDOR HABITAT QUALITY FOR RED DEER</b>	<b>79</b>
5.1. Summary	79
5.2. Introduction	80
5.3. Study area	82
5.4. Methods	83
5.4.1. Field data	83
5.4.2. Digital data	83
5.4.3. The Corridor habitat suitability model	84
5.4.4. Least-cost distance analyses	85
5.5. Results	85
5.5.1. Corridor habitat suitability model	85
5.5.2. Least-cost distance analyses	86
5.6. Discussion	91
5.6.1. Model strengths and limits	91
5.6.2. Corridor features	91
5.7. Management implications	92
5.8. Overview	93
<b>6. DEERDISPERSER, A SPATIALLY EXPLICIT INDIVIDUAL-BASED MODEL TO MEASURE CONNECTIVITY BETWEEN HABITAT PATCHES</b>	<b>95</b>
6.1. Summary	95
6.2. Introduction	96
6.3. Model description	97
6.3.1. Model overview	97
6.3.2. Model inputs	98
6.3.3. Movements rules	100
6.3.4. Model runs and outputs	101
6.3.5. Sensitivity analysis	102
6.4. Discussion	102
6.4.1. Random walk model assumptions	102
6.4.2. Random walk model results	105
6.4.3. Scenario tests	105
6.4.4. Links with population viability analysis	105
6.5. Conclusion	106

<b>7. PREDICTING HABITAT PATCH COLONIZATION PROBABILITIES FOR AN EXPANDING RED DEER SUBURBAN POPULATION</b>	<b>107</b>
<b>7.1. Summary</b>	<b>107</b>
<b>7.2. Introduction</b>	<b>108</b>
<b>7.3. Methods</b>	<b>109</b>
7.3.1. Model overview	109
7.3.2. Model inputs	109
7.3.3. Model parameters	110
7.3.4. Calibration/validation process	110
<b>7.4. Results</b>	<b>111</b>
7.4.1. Calibration	111
7.4.2. Tests on the second part of the study area	113
<b>7.5. Discussion</b>	<b>113</b>
7.5.1. Strengths and weaknesses of the model	113
7.5.2. Predicting inter-patch connectivity	114
<b>7.6. Management implications and future prospects</b>	<b>115</b>
<b>7.7. Conclusion</b>	<b>116</b>
<b>8. CONCLUSIONS AND PERSPECTIVES</b>	<b>117</b>
<b>8.1. Habitat selection and habitat suitability maps</b>	<b>117</b>
<b>8.2. Corridor selection and colonization probabilities</b>	<b>119</b>
<b>8.3. Management applications of modeling results: illusion or reality?</b>	<b>121</b>
<b>8.4. Towards spatial wildlife management modeling of red deer populations</b>	<b>122</b>
<b>8.5. General conclusion</b>	<b>124</b>
<b>9. BIBLIOGRAPHY</b>	<b>125</b>
<b>10. ACKNOWLEDGMENTS</b>	<b>136</b>
<b>11. GLOSSARY</b>	<b>138</b>
<b>12. ABBREVIATIONS</b>	<b>140</b>
<b>13. APPENDICES</b>	<b>141</b>



*A red deer habitat point of view*

# 1. INTRODUCTION

---

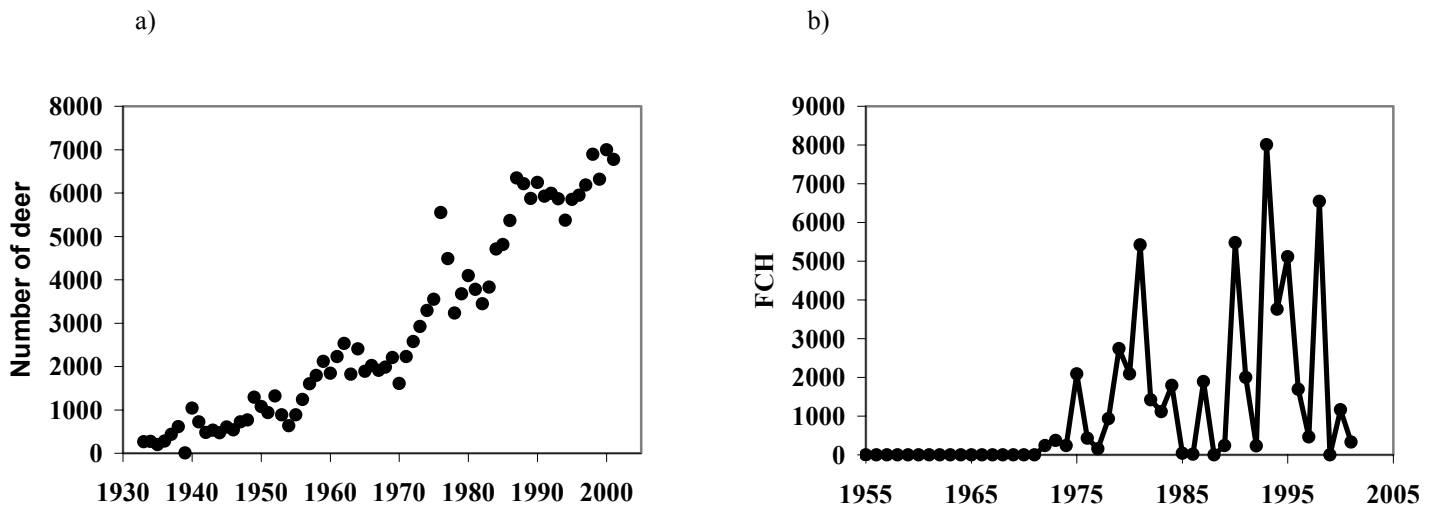
*Overview, background, concepts, thesis structure and goals*

## 1.1. General Introduction

Red deer (*Cervus elaphus*) management is an important challenge for resource managers as the species has considerable negative impact on forest structure and species diversity, both at local and landscape scales (Hobbs 1996, Reimoser and Gossow 1996, Putman and Moore 1998). The species can also cause serious deer-vehicle collisions and injuries to car drivers (Groot Bruinderink and Hazebroek 1996). On the other hand, red deer are popular large mammals, in particular for hunters and conservationists as it is true for deer in general (DeCalesta and Stout 2000).

In Western Switzerland, red deer were been extirpated due to excessive hunting around 1850. By the end of the 19<sup>th</sup> century, the introduction of federal hunting regulations favored a comeback of the species (Righetti 1995), that is still expanding its range in Switzerland at the present time (Figure 1-1a). More recently, the species started recolonizing the Jura Mountains after a re-introduction of some individuals along the French border during late 1950. The current population level in this area is considered as low. A minimum of 220 animals was estimated based on spotlight counting (Patthey 2003). However, over the last five years, wildlife authorities have recorded clear indications of a local population growth and expansion. As a consequence, and in order to prevent human-wildlife conflicts associated with the impact of the species on forested habitats (Figure 1-1b) and motorways, wildlife managers are currently required to set management options that consider spatial and temporal colonization possibilities of red deer populations. Regional deer recovery needs to be understood in a spatially explicit manner to improve future red deer population management.

Recent, spatially-explicit habitat, population viability and management analyzes have shown usefulness of computer-based simulations that integrate demographic and detailed landscape information (Mace and Waller 1996, Mladenoff et al. 1996, Van Apeldoorn et al. 1998, Rushton et al. 2000). Such simulations allow identification of key areas to protect, detection of wildlife corridors to preserve or optimization of landscape management effects. They may, for example, help to optimize a road plan that minimizes impacts on the focal species by comparing simulated effects of each potential planning (Lathrop and Bogner 1998).



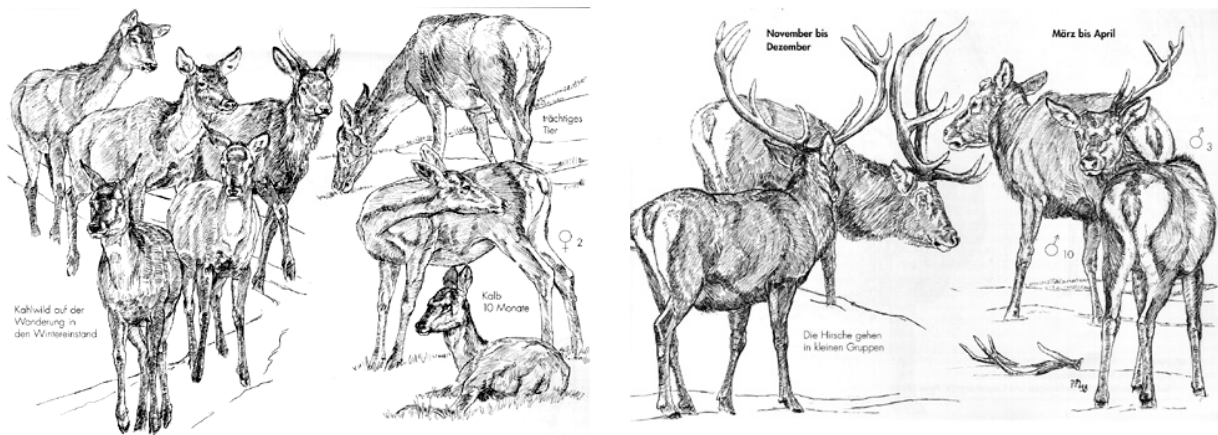
**Figure 1-1:** a) Number of red deer hunted in Switzerland between 1933 and 2001 (from SAEFL, [http://www.umwelt-schweiz.ch/buwal/fr/fachgebiete/fg\\_wild/dienstleistungen/jagdstatistik/index.](http://www.umwelt-schweiz.ch/buwal/fr/fachgebiete/fg_wild/dienstleistungen/jagdstatistik/index.)) and b) evolution of red deer annual damage compensations (FCH) for the Vaud state (from SFFN, [http://www.dse.vd.ch/forets/faune/pdf/chasse\\_stat.pdf](http://www.dse.vd.ch/forets/faune/pdf/chasse_stat.pdf)).

## 1.2. Red deer

The Red deer is the largest ungulate of central Europe and is a highly dimorphic species (Figure 1-2). Adult males weigh between 170 to 220 kilograms whilst females weigh between 90 and 120 kilograms (SFFN, *unpublished*). Unlike females, males have antlers. Body length varies from 170 cm to 220 cm, and height at withers varies from one to 1.4 meters.

*Cervus elaphus* has been subdivided into several subspecies from North America and Asia (wapiti group) and Europe (red deer group). These species subdivisions were mainly based on morphological and behavioral traits but are currently under review based on genetic analyses (e.g. Emerson and Tate 1993, Polziehen et al. 2000).

Information on red deer ecology comes essentially from well-established populations. The most famous long-term study of population dynamics and behavioral and social ecology is the Island of Rhum (Scotland) (e.g. Clutton-brock et al. 1982, Coulson et al. 1999). In North America, researchers mainly studied wapiti habitat selection (e.g. Edge et al 1987). More recently, several studies in central Europe investigated space use (Szemethy et al. 1999, Hamann and Klein 1999) or food consumption (e.g. Picard et al. 1991, Gebert and Verheyden-Tixier 2001) and north European studies (e.g. Mysterud et al. 2000, Mysterud et al. 2002, Yoccoz 2002) brought up new results on red deer population dynamics.



**Figure 1-2:** Females with young (left) and males (right) red deer. Courtesy of Dr P. Meile, Jagd- und Fischereiinspektorat Graubünden.

Before human landscape transformations, the red deer was an open habitat animal (Clutton-Brock et al. 1982), however, the species is ubiquitous and may live in various types of habitat, from the Mediterranean to Scandinavia. In Switzerland, its presence is mainly associated to forested areas although they can live in open undisturbed areas (Haller 2002).

The Red deer is classified as an intermediate feeder (Hoffmann 1985, Gebert and Verheyden-Tixier 2001) although red deer can eat up to near 15 kilograms of fresh plants per day. Diet is composed of a mix of grass, sedges and concentrate food items (browse and plant items rich in soluble cell contents such as forbs, seeds, fruits and cultivated forbs (Hofmann 1985). Diet is large and its main variation depends on habitat (Gebert and Verheyden-Tixier 2001).

The Red deer is a gregarious species. Except during the rut, males and hinds seldom associate with each other, and live in groups of same sex (excluding calves and first year animals). The main annual rut begins in mid September and ends mid October. Stags generally disperse from their mother at the age of two and join stags groups. Meanwhile, hinds keep near their birth place. For a temperate climate forest, Hamann and Klein reported male natal dispersal length up to 60 kilometers while females disperse less than 10 kilometers (*unpublished data*). The social structure is matriarchal, based on the familial trio: hind-calve-first year young. Hinds in the same group are generally genetically related. The size of group depends on time of year and on density of population and varies between one to more than 200 (e.g. Haller 2002). When they give birth, females leave their young from the previous year and thereafter

spend the summer in small matriarchal groups. During rut and hard winters, hinds may form bigger groups. Annual population growth depends mainly on density. The proportion of females with one-year old young may vary mostly between 0.4 and 0.7 (Clutton-Brock et al. 1982). Females may give birth to one calf (very rarely two) each year from their second year of life, up to 14 years old (Clutton-Brock et al. 1982).

Annual home range of stags may be very large (up to 6000 hectares, Georgii and Schroeder 1983, Koubek and Hrabe 1996, Klein and Hamman 1999, Szemethy et al. 1999, Patthey 2003) whereas hind annual home range is generally smaller than of adult males. Adults seasonally use small patches within their annual home range (Table 1) and may move from their summer to their winter ranges over large distances (e.g. Blankenhorn 1978). Activity is centered on diurnal bedding sites (Hamann et al. 1997, Hamann and Klein 1999). During daytime, deer are mainly present in dense forests where they find shelter and food. During the night, they frequently move to open forests or surrounding arable areas (Catt and Staines 1987).

**Tableau 1-1:** Overview of a sample published mean red deer home-range sizes reported in Europe according to the following methods: MCP= minimum convex polygon; core area: 1=Kernel 50% utilization, 2= Cluster 90% utilization, 3= grid cells).

Reference	Region	Animals		Mean yearly home range size	
		Sex	N	MCP Km <sup>2</sup>	Core area Km <sup>2</sup>
Patthey 2003	Jura mountains (CH, F)	M	2	26-43	4.1-5.2 <sup>1</sup>
Patthey 2003	Jura mountains (CH, F)	F	1	35	5.5 <sup>1</sup>
Klein & Hamman 1999	Vosges (F)	M	6	23 (12-39)	0.66-3.2 <sup>2</sup>
Hamann et al 1997	Vosges (F)	F	9	8.6± 5.2	1.4± 4.0 <sup>2</sup>
Szemethy et al 1999	Babat (H)	F	3	4.9± 2.1	3.25 ±2.0 <sup>3</sup>
Szemethy et al 1999	Hajos (H)	M	3	78± 35	6.3± 0.8 <sup>3</sup>
Szemethy et al 1999	Babat (H)	F	5	36± 16	6.5± 1.0 <sup>3</sup>
Georgii & Schröder 1983	Bavaria (DDA)	M	11	3.9± 1.1*	2.1± 0.6*

\* spring to autumn



## 1.3. Study area

### 1.3.1. Overview

The study area is situated in western Switzerland and France (Figure 1-3) and includes lowlands and mountains. It is bordered to the West and the South by the Jura Mountains, to the North by the administrative limit of the Vaud state and to the East by the Highway N1 on the Swiss Plateau. Elevation ranges from 360 (Swiss Plateau lowest point) to 1720 meters in the Jura Mountains.

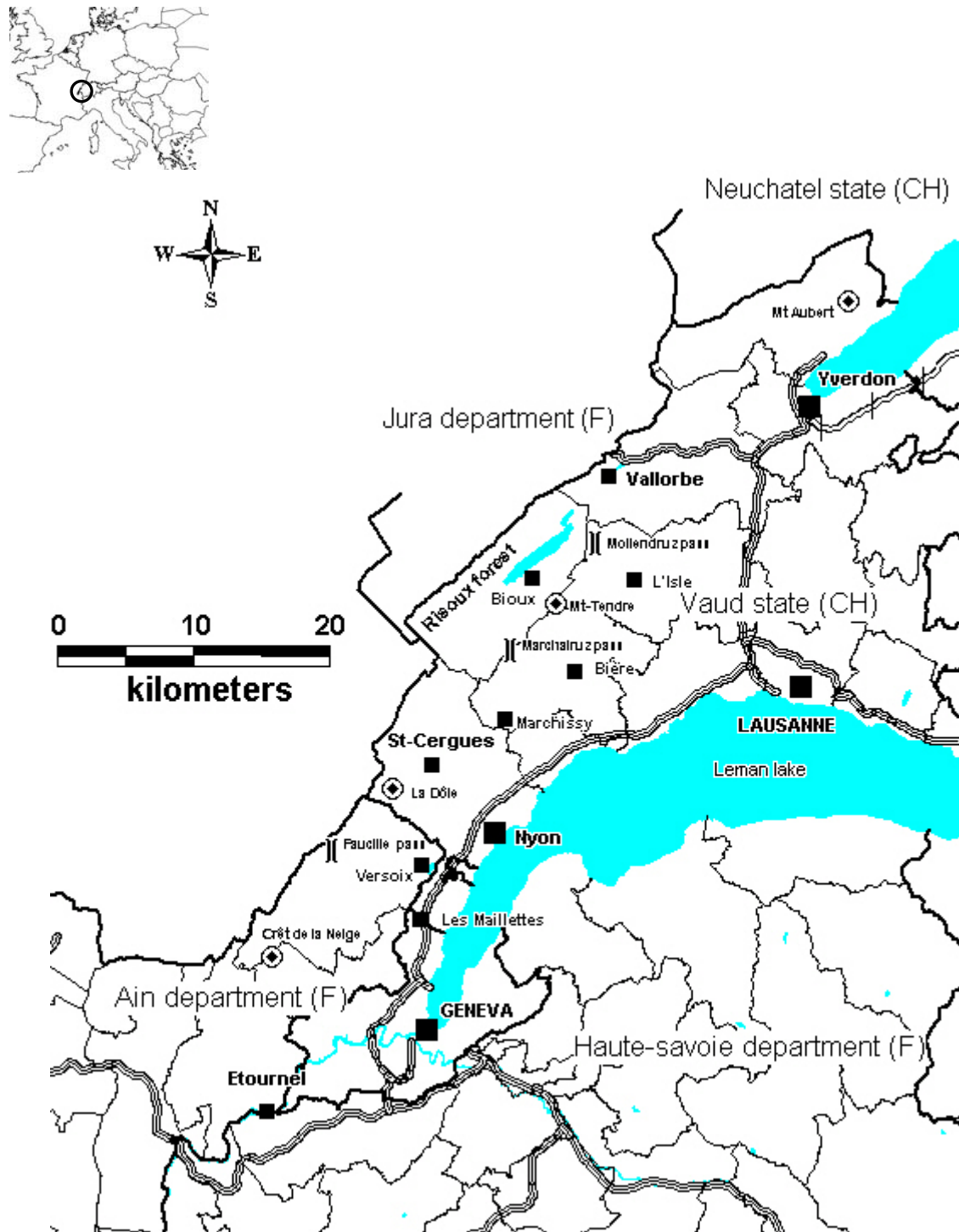
### 1.3.2. Lowland and Geneva Bassin

In the lowlands, arable lands are used for vineyards, orchards, and cereal production. Grazing occurs occasionally in hilly areas. Natural forests are small in size and deciduous but due to timber harvest, forests are managed as small units from pure plantation to natural regeneration.

The Geneva Bassin is situated at the extreme West end of the Swiss Plateau where it surrounds the city of Geneva. Landscape is highly fragmented by roads, villages and agriculture.

### 1.3.3. Jura mountains

The Jura Mountains consist of a long ridge forming the Western limit of the Swiss Plateau, and their main features are generally rolling shape, a hard climate, a limestone substratum and an intermixed landscape of grass and woodlands, due to cattle farming and agriculture. The natural vegetation of the Jura Mountains belongs to the Fagion (Vittoz 1998). The vegetation begins at lowland to 600 meters with oak forests (*Carpinion betuli*), then beech forest up to 1000 meters (*Fagenion*). Forest associations are dominated at higher altitude by spruce in combination with beech and fir (*Abieti-Fagenion*). The tree line is about 1500 meters high. Timber harvest pressure is higher at lower altitudes and grazing pressure is more important at upper elevation (Ribben 1957).



**Figure 1-3:** The study area in Switzerland and nearby France. For a precise definition of the study perimeters see figures 2-1, 3-1, 4-1 and 5-1).

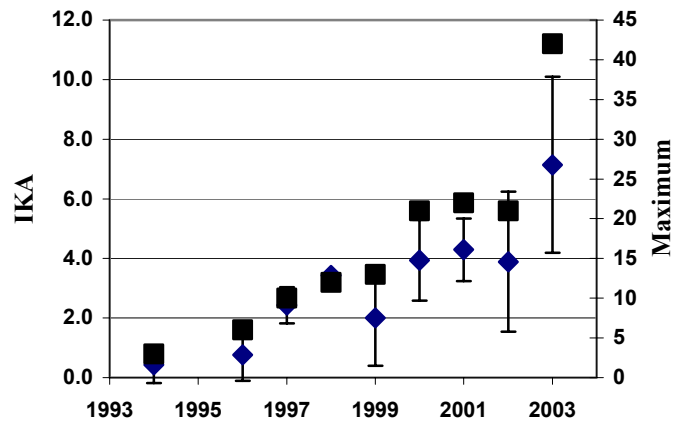
#### 1.4. Red deer in the study area: a historical perspective

As a consequence of an uncontrolled and excessive hunting pressure, red deer disappeared from Western Switzerland and nearby France at the end of the 19th century (Rhigetti 1995).

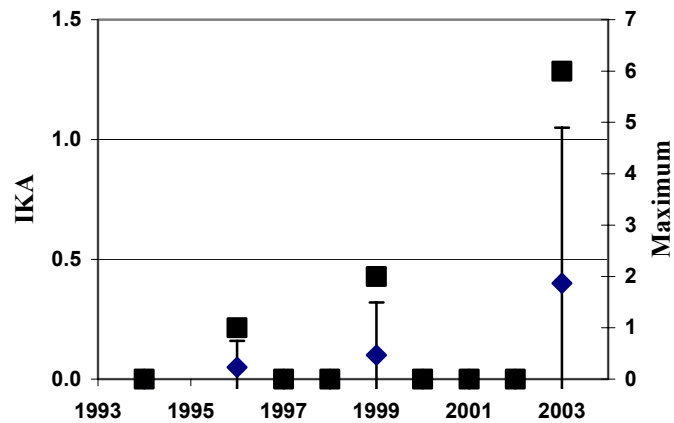
In order to allow red deer to colonize its lost range, re-introductions were undertaken in the Versoix area (Figure 1-3) by French hunting associations in 1955 and 1956 with 5 and 6 animals respectively (Fournier 1997). Illegal reintroductions were also reported at the beginning of 1980's in Creux du Van (Neuchâtel) and subsequent prohibited introductions are not excluded (Blant 2001). After introductions, the Versoix population rapidly increased in size (Figure 1-4) followed by an expansion into the nearby Jura Mountains and the Etournel, a hunting reserve situated 20 kilometers to the south (Fournier 1997), resulting in two distinct populations of a minimum of 80 animals each (Patthey 2003). The Creux du Van introduction has not been successful as only a few individuals are now present (Patthey 2003). A third population is located between Marchairuz and Vallorbe and currently consists of a minimum of 50 individuals (Figure 1-4). This population may be a result of natural colonization by individuals from the Versoix populations and was first found at the beginning of 1980's (B. Reymond, *comm. pers.*). Illegal culls are likely to have considerably limited red deer expansion as a high hunting pressure (Fournier 1997). Between the three populations mentioned above, almost every year a few red deer indices were found. In recent years, red deer presence was also reported in the Marchissy and Bioux regions, which indicates that the population is expanding.

In this area, the only known red deer predators are hunters. Lynx (*Lynx lynx*) predation on red deer is not excluded (Okarma et al. 1997) although the species has been extensively surveyed (Jobin et al. 2000). Red deer are hunted in France and in Vaud state, but in Geneva state hunting has been forbidden since 1974. Hunting is allowed outside wildlife reserves, in France from September to January and in Switzerland generally from December to January. Overall annual hunting bags were always less than 25.

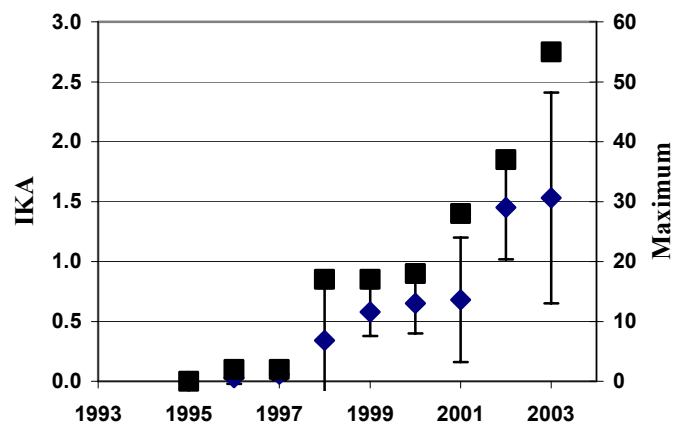
a)



b)



c)



**Figure 1-4:** Evolution of spring spotlight count indices from 1994 to 2003 in a) Versoix area, b) Marchissy region and c) Mt-Tendre region. Mean number of deer observed per spotlight kilometer (IKA: diamonds) (and its standard deviation) and the number of animals seen during the best count (maxima: squares) are indicated (from Patthey 2003).

## 1.5. Habitat selection

### 1.5.1. Overview

Animal populations need adequate quantity and quality of available resources for their survival. It is often assumed that a species will select resources that are necessary to fit its life requirements. Habitat choice is the result of animal decisions that balance the trade-off between predation risk (human disturbances), foraging (resource richness) and climatic factors. Theoretically, animals should select habitats that minimize the ratio of mortality risk to net energy intake (Lima and Dill 1990). Such decisions (i.e. leaving a rich place to go to a safer place) may be linked with the range for which animals can perceive key landscape elements (Lima and Zollner 1996). Therefore, a way to analyze habitat selection is to compare used resources to available or non-used resources (e.g. Manly et al. 1993).

### 1.5.2. Habitat selection levels and observation scale

Habitat selection can be envisaged as a hierarchical spatial series of decisions that an organism makes to settle in a particular location (Hilden 1965, Senft et al. 1987). Johnson (1980) proposed the use of habitat selection levels as follows (Figure 1-5):

1. Selection of a geographic range of a species (1<sup>st</sup> selection level)
2. Choice of an individual or a social group home range within a geographical range (2<sup>nd</sup> selection level)
3. Choice of general features (i.e. foraging site) within the home range (3<sup>rd</sup> selection level)
4. Selection of particular elements (i.e. food items) from those available (4<sup>th</sup> selection level).

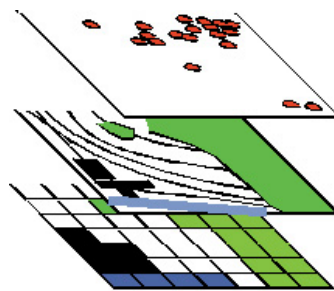
Animals can perceive their environment over a wide range of scales that may affect their final choice within a focus selection level (Rettie and Messier 2000) (Figure 1-5). The term “level” is used to indicate “the level of organization revealed by observation at the scale under consideration” (Morrisson and Hall 2002). Observation scale is the resolution at which patterns are perceived (by the species) or measured (by the observer) and can be divided into grain, extent and period. Thus, the scale of selection and the scale of observation are not synonymous (King 1997). In this work, to avoid confusions (George and Zack 2001), we used the term *selection level* as reference to level of organization and the term *scale* as a reference

to scale of observation. Thus we named the 2<sup>nd</sup> selection level, the *population selection level*, the 3<sup>rd</sup> selection level, the *home range selection level* and used as *population scale variables*, variables that are estimated within an area equivalent to a population range, *home range scale variables*, variables that have a home range extent, as *local scale variables*, variables measured in the vicinity of the location and as *micro-scale variables*, variables measured at a very fine scale (<1-2 m) (Figure 1-5).

## 1.6. General methods

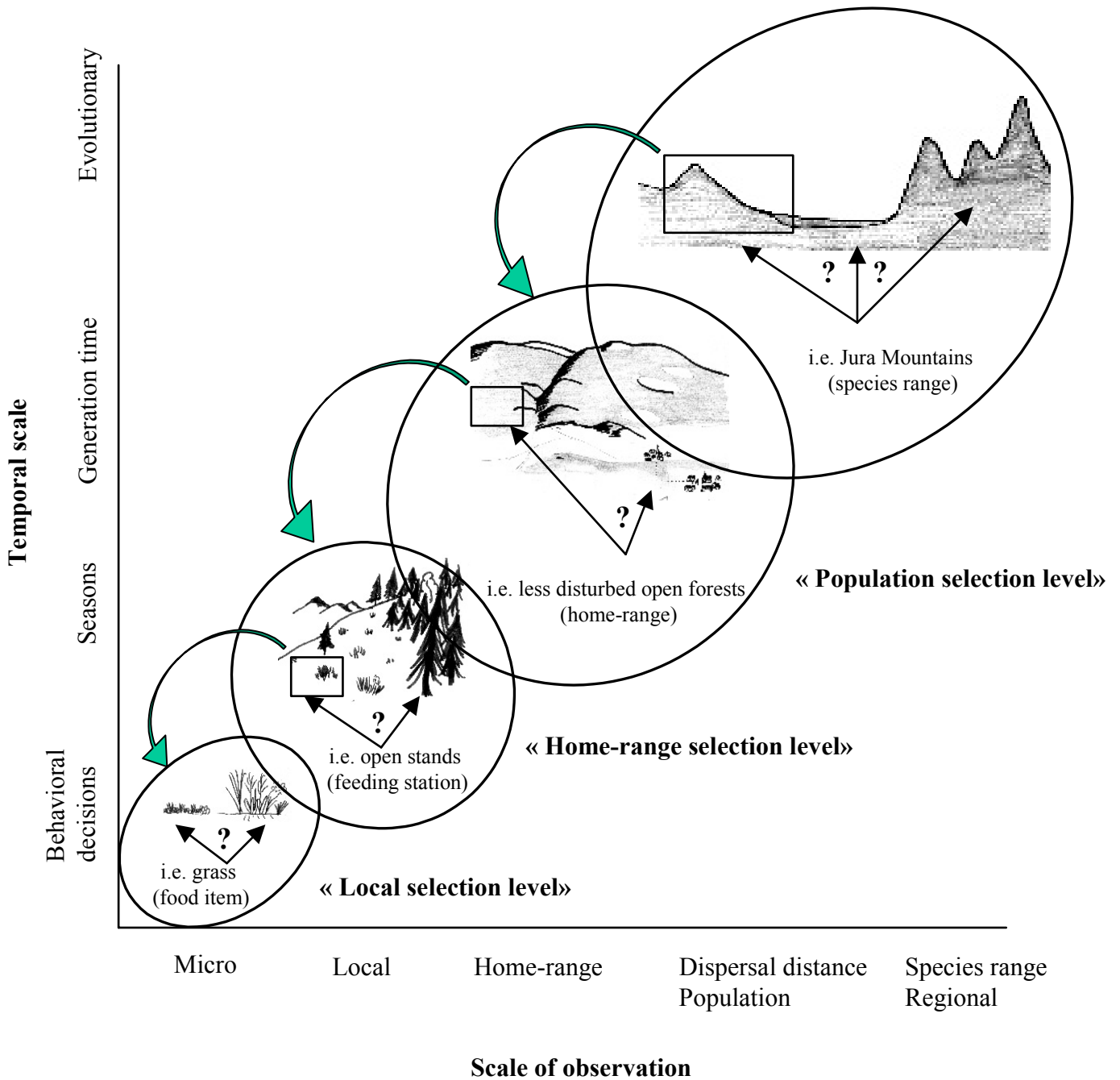
### 1.6.1. Geographic information systems

Geographic information systems (GIS) are powerful and complex computer-based tools for landscape modeling. The most important feature of GIS's is that they link spatial data models to a database management system and therefore relate descriptive information to space. Data are stored in different layers within GIS (Figure 1-6). For example, one layer may hold land cover data and another, a species distribution. GIS enable data to be overlaid and combined by any mathematical function. Data are most often stored in a grid cell network named raster maps, but vector formats can also be used (i.e. state boundaries). The resolution at which landscape data are stored within a GIS will therefore depend on the specific objectives of the study and the spatial extent of the area being considered like unfortunately on the availability of data at the specify grain and on computer performances (storage and calculation).



**Figure 1-6:** Raster and vectorial data layers in a Geographic Information System (GIS). From top to bottom: vectorial point map, vectorial habitat type map and its associated raster map.

GIS analyses were performed with IDRISI32.2 (Clarks Lab), MAPINFO 6.0 (MapInfo Corp.), Biomapper (Hirzel et al. 2002), ValueExtractor (Patthey 2002), StratSampler (Patthey 2002).



**Figure 1-5:** Relationship between temporal, spatial scales of observation and levels of a habitat selection, with red deer theoretical examples in the Jura Mountains. The four selection levels (Johnson 1980) are: 1) Selection of a geographic range of a species (regional selection level), 2) Choice of an individual or a social group home ranges within a geographical range (population selection level), 3) Choice of general features within the home range (home range selection level), 4) Selection of particular elements from those available (local selection level). Adapted from Senft 1997, Bissonnette 1997 and George and Luca 2001.

### **1.6.2. Red deer indices**

From November 1999 to January 2000, the southern slope of the Jura Mountains was investigated from Col de la Faucille to Vallorbe, at two elevations (800-900 and 1200-1300 meters) in order to locate winter red deer range in the study area. Total length of transects was about 300 km. During summer 2000, all kilometers squares were investigated to find at least one red deer presence indices and to identify red deer summer range. Investigation time was limited to one hour per kilometer square. All the 680 red deer indices encountered in the field were recorded with a 10 meters precision (with GPS, compass and altimeter) and then registered into a GIS. Indices were sexed when possible.

Rangers perform spot-light counts every spring. Counts of rutting red deer were also carried out in the two main populations of the Jura Mountains. All these visual and audible observations were registered, totalizing 592 records.

All indices encountered during specific investigations during subsequent years, such as the 265 bed sites or during other fieldwork, were registered in the same way.

The whole data set of these presence indices (total end 2001: 1545), was incorporated in a GIS database that was completed by all valuable information coming from rangers, foresters, hunters and naturalists. Spatial accuracy and confidence level were also recorded.

We constructed a red deer *winter distribution map* with observations from 15 January to 28 February, and a *summer distribution map*, with observation from 1 July to 31 August. Extreme presence points were bonded to form polygonal presence maps representing red deer population ranges. We considered two groups of indices to be disjointed if more than one kilometer (home-range radius size) separated them and thus constructed two different presence range polygons.

### **1.6.3. Modeling**

#### *Overview*

Models are simplifications of reality and are widely used to help us understand complex systems. They are any formal representation of the real world. A model may be conceptual, diagrammatic, mathematical, or computational. Models can be used to test our ideas and



generate new hypotheses by performing ‘experiments’ that would not normally be possible in the field. For example, we may investigate how habitat manipulation would influence a species distribution, which is obviously impossible at a large-scale.

#### *Model construction framework*

First a conceptual model is formulated on the basis of an ecological concept. Secondly the model is formulated in a statistical way. Then the model passes through the calibration-validation process, which tests the ad equation of the model in a larger range of situations in order to define its range of application (Guisan and Zimmermann 2000).

#### *Predicting species occurrences and ENFA*

A lot of predictive species occurrence models have been developed and are currently used in ecology in order to characterize habitat-species relationships (i.e. logistic regression). Formulation of this relationship allows improving or setting-up of management and conservation options (i.e. Corsi et al. 2000) as well as testing habitat change scenarios (Rushton et al. 2000, Whitfield et al. 2001). Each model has it’s own assumptions, limits and strengths including the trade-off between accuracy and generality, compared to others models (See Manly (1993), Boone and Krohn 2000, Guisan and Zimmermann (2000) for an overview of current methods and guideline to construct predictive habitat models). A possible output of these models, when used in conjunction with GIS, are habitat suitability (HS) maps. These maps are static models in contrast to potential distribution maps, that integrate the probability that the species may access these suitable areas (Hausser 1995).

Here we present the Ecological Niche Factor Analysis (ENFA) in more detail, as this recent model has been a main tool of this study. ENFA differs from previous analyses in the regard that it only needs presence data (Hirzel et al. 2002). This particularity leads to an intuitively more appropriate analysis in the case of spreading and cryptic species for which we can not assess absence in a reliable way (Zaniewski et al. 2002). Furthermore ENFA was revealed to be more robust in such cases (Hirzel et al. 2001). In the modeling process, ENFA compares ecological characteristics of species’ presence points to ecological characteristics of all study area points. A factorial analysis, similar to a Principal Component Analysis, is first performed on ecological variables to extract the same number of independent axes or factors. The scores give a weight (contribution) of each variable to each factor. A particularity of ENFA compared to classical factorial analyses is that factors have an ecological meaning in the sense

of Niche (Hutchinson 1957). The first axis represents the species' *marginality*. Marginality is defined as the difference between the mean value of species' points and mean value of study area points in the  $n$  ecological variables space. The global marginality value varies from zero to one (though the value can exceed one). A marginality value close to zero means that there is no difference in mean between the species habitat and available habitat. The other remaining axes represent the species' *specialization*, which results in a linear combination of the ecological variables that maximize the variance of the study area point distribution compared to the species' one. The global specialization value varies from one to infinity. More compliant is the tolerance value – the inverse of specialization - that varies from zero to one. A species showing a tolerance value close to zero occupies a thinner niche than a species with a tolerance value close to one. From the first axis, which retain most of the system variance, we can calculate predicted habitat suitability (HS) values ranging from 0% (unsuitable) to 100% (suitable).

In the *cross-validation* analysis, the species locations are randomly divided into  $k$  equal size and mutually exclusive partitions.  $k-1$  data sets are used to compute a habitat suitability map (HS) model and the left-out partition are used to validate it. This process is repeated  $k$  times, each time leaving out a different partition. On each cross-validation HS map, the following statistics are computed:

- The fraction of validation cells in the left out partition that have a HS value greater than 50. This statistic gives an absolute assessment of the model quality.
- The fraction of validation cells in the left out partition that have a HS value greater than 50 with deduction of those cells that achieve this result by chance. This statistic assesses the *contrast* of the model by comparing whole validation cells to whole study area.
- The confidence error maps (5% and 95%) on HS values.

Boyce et al. (2002) published a method for evaluating presence/availability model predictions that are based on the  $k$ -fold cross validation (Fielding and Bell 1997). This method is similar to those used in Vos 1999 and Storch 2002. It's principle is to divide the data set into  $k$ -fold partitions. The model is trained with  $k-1$  partitions and validated with the remaining set in order to find predicted HS values. The strength of this method is to calculate a HS selection

index, the *area-adjusted frequency*. HS values are grouped into categories. The index value is equal to the proportion of “cross-validated used locations” within a HS category divided by the proportion of the corresponding HS category, available in the landscape. An index value of one corresponds to a random use of the focal HS category. The assumption of the method is that if the model is robust, high HS categories will be used more frequently than expected according to their availability, low HS categories will be used at lower frequencies than expected. Finally, the relationship between HS categories and area-adjusted frequencies is tested with a rank correlation analysis for each k-fold partition and its average.

We used the BIOMAPPER2.0 (Hirzel et al. 2002) software to perform ENFA on our data sets.

#### **1.6.4. Programming tools**

Programming allows development of tools to gain time for recurrent operations, to transform files into adequate formats or to develop self-adapted tools. During this work, we conceived and created several softwares in an object-oriented programming language (Delphi 4).

- ValueExtractor is an indispensable tool that allows exporting selected values from IDRISI raster maps into any statistical program. The output format is a text file with x, y coordinates and z values corresponding to the pixel values.
- StratSampler performs, in a user-friendly manner, random stratified samplings based on Idrisi32 maps.
- IdrisiPlus is linked to Idrisi32. It allows performance of the same operation on a group of maps when Idrisi32.2 does not provide that possibility and has time-saving and reduced mouse click operations.
- DeerDisperser is the central tool of this work and will be precisely described in chapter 6.

These tools (included in the CD appendix) have been used in different projects such as Randin and RickeBusch 2001, Hirzel and Guisan 2002, Jaquiéry and Brändli 2003, Sachot et al. 2003, Morard 2003, Pellet et al. (*submitted*).

## **1.7. Aim, objectives and thesis contents**

The aim of this work is first to describe and identify suitable habitats for red deer, and secondly to estimate, the probability that red deer will colonize predicted suitable habitats. Another objective is to test landscape management scenario effects on habitat suitability maps and connectivity networks. To reach our objectives we need to improve the description of red deer habitat use and dispersal habitat use in our study area. This knowledge is essential to managers as species management or conservation efficiency closely depends on the quality of our understanding of its habitat requirements (Mooty et al. 1987).

In summary, we pursue 4 specific objectives:

1. To describe habitat use
2. To construct habitat suitability maps
3. To describe dispersal habitat use, i.e. corridor selection (see glossary for a definition)
4. To estimate between-habitat patch colonization probabilities

This work is structured into two main parts, corresponding to the two main steps, divided each into three chapters (Figure 1-7).

The first part concerns static habitat use and corresponds to the first two objectives. The first step to achieve is to construct habitat suitability models in order (1) to map suitable areas for red deer future spreading and (2) to characterize suitable habitat in order to derive management actions. Several studies on established *Cervus elaphus* populations have shown red deer sensitivity to human disturbance (Pettrak 1996, Hodgetts et al. 1998, Milsspaugh et al. 2000, Philipps and Alldredge 2000, Conner et al. 2001, Sibbald et al. 2001) and habitat composition (Catt and Staines 1987, Morellet et al. 1996). However, habitat selection by colonizing populations of red deer is poorly understood in contrast to established populations. Swiss red deer habitat use was already analyzed with a one square kilometer resolution (Hausser 1995). Nevertheless, the habitat characterization was based mainly on Swiss Alps presence data. This relationship may therefore not be applied to our study area characterized by a different landscape (Osborne and Suarez 2002, Boyce et al. 2002, Zimmermann et al. *in prep*). Recent studies on habitat selection have shown the importance of analyzing several

spatial scales in order to improve ecological understanding (Didier and Porter 1999). Habitat use was therefore investigated from population to home range selection levels with different spatial and temporal scales (Figure 1-5). In chapter 2 and 3, red deer habitat selection is analyzed at the population selection level, with population, home range and local scale factors over two seasons to find habitat requirements. In chapter 4, we analyze winter and summer bedding site selection at the population and home range selection level, with home range, local and micro-scale variables, in order to describe individual requirement on a local scale basis.

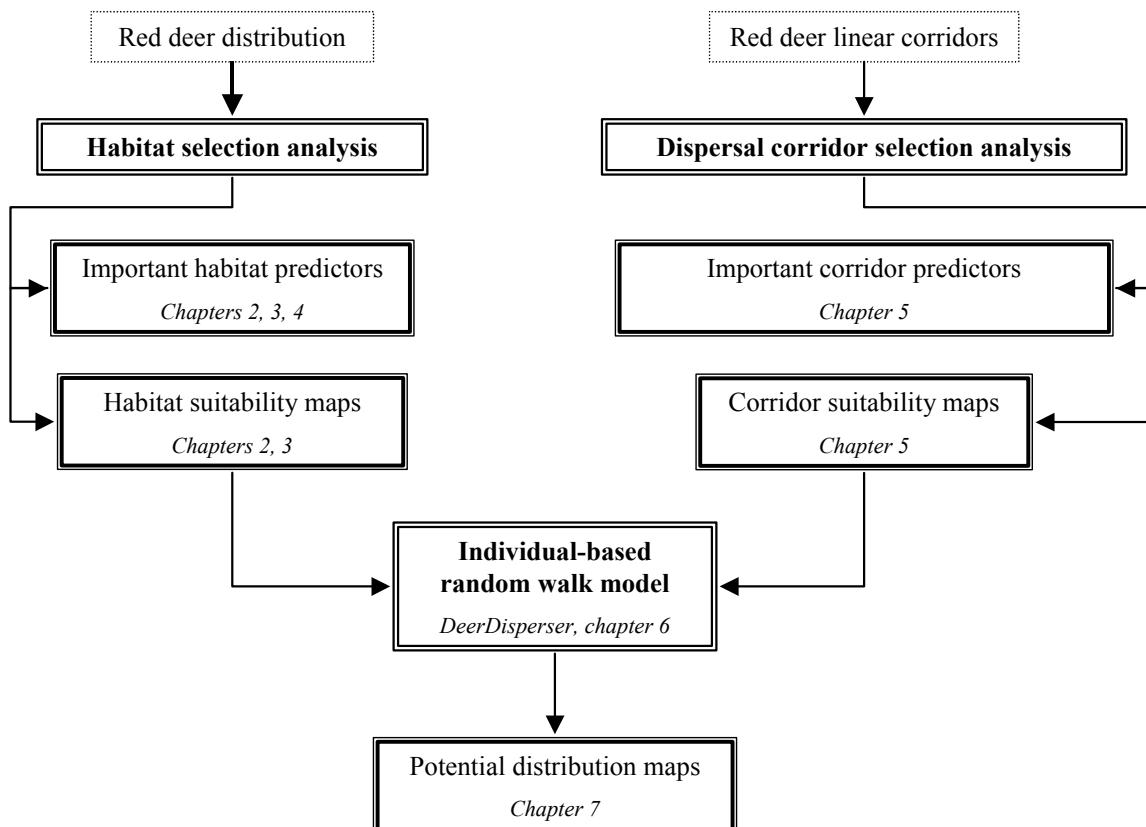


Figure 1-7: Thesis organization.

The second part deals with dispersal habitat use (or corridor selection). In chapter 6 we developed and described a spatially-explicit random walk individual based model. In chapter 5 we constructed a corridor suitability map for red deer that we next incorporated into our random walk model to estimate habitat patch connectivity for the Geneva suburban area (Chapter 7). Combination of habitat suitability maps with between-habitat patches connectivity estimations resulted in red deer potential distribution maps.

All chapters consider potential issues for red deer management that are summarized in the last chapter. Special attention was paid to forest management, human disturbance and landscape fragmentation management. Modeling utility, limits and strengths are also discussed.

We submitted some of the chapters to international journals as follows:

Patthey, P., Neet, C.R., and F. Klein. Scale-dependent seasonal habitat selection of an expanding red deer population in the Swiss Jura Mountains, *submitted*.

Patthey, P. Neet, C.R. and F. Klein. Modelling of red deer corridors in a suburban area, *to be submitted*.

Patthey, P. Neet, C.R. and F. Klein. Predicting habitat patch colonization probabilities for an expanding red deer suburban population, *to be submitted*.

Patthey, P., Gawronski, E., Dunand, I., Neet, C.R., and F. Klein. Hierarchical bed-site selection for a red deer expanding population: applications to its management, *to be submitted*.

## 2. RED DEER POPULATION HABITAT IN WESTERN SWITZERLAND

---

*Landscape selection level at population and home range scales*

### 2.1. Summary

- 1) In western Switzerland, red deer are colonizing new areas after re-introduction. As a consequence of conflicts between forestry, traffic and hunters, there is an urgent need to understand the species habitat use in order to improve its management.
- 2) Winter and summer red deer habitat use at the population level and at several habitat scales was analyzed for the Jura Mountains and the lowlands. Habitat parameters were derived from GIS databases in order to reflect land-use and human disturbances. Important habitat features were defined and habitat suitability (HS) maps constructed.
- 3) Overall quality of HS models was good. ENFA analysis 1) revealed that red deer select the quieter (distant to inhabited areas and open roads, lower frequency of buildings) and larger forested areas, and 2) predicted that some presently unoccupied areas are suitable for red deer. This result reinforces the importance of recreation management for red deer management.
- 4) As population and home range scale variables are both important depending on season, we suggested that the combination of multi-scale variables can efficiently predict red deer land use in a global landscape, and therefore that resulting models are useful habitat suitability predictors. We are confident that our models can be used for management purposes i.e. to test management scenarios in the study area. Nevertheless, models should be improved by integrating more detailed variables such as forest typology.

## **2.2. Introduction**

Since their re-introduction to the Divonne area in the 1950's on the border between Switzerland and France in the Jura Moutains, *Cervus elaphus* increased in numbers and expanded its range. This borderline area includes two ecological regions; the Jura Mountains and the lower lands named Plateau. The Jura Mountains are characterized by a woody and rolling landscape (Figure 1-3) whereas the Plateau is characterized by a mixed of agriculture, urbanization and a few small forests. Highways and roads are densely distributed on the Plateau. All these forests are increasingly used for recreation purposes.

Forest damage and risks associated with deer-vehicle collision on one hand and the great value of red deer as a game species, on the other hand, generate conflicts that require wildlife managers to improve their knowledge of red deer habitat use in this area.

Habitat use of *Cervus elaphus* is clearly related to human disturbance and habitat composition (Morellet et al. 1996). Human disturbance may affect behavior (Pollard and Littlejohn 1995, Whittington and Chamove 1995, Petrak 1996, Hodgetts et al. 1998), movements (Cole et al. 1997, Conner et al. 2001) and distribution (Rowland et al 2000, Milsspaugh et al. 2000) and may decrease reproductive output (Philips and Alldredge 2000) and survival rates of red deer (Cole et al. 1997). The effect of these two main parameters on red deer habitat choice may be different when considering the habitat selection level, spatial and temporal scales (Senft et al. 1987).

In this chapter, we analyzed habitat selection at the population level (section 1.5.2) using different spatial scales and seasons in order to (1) define important habitat features according to scale and seasons and (2) construct habitat suitability maps in order to improve future red deer management.



## 2.3. Methods

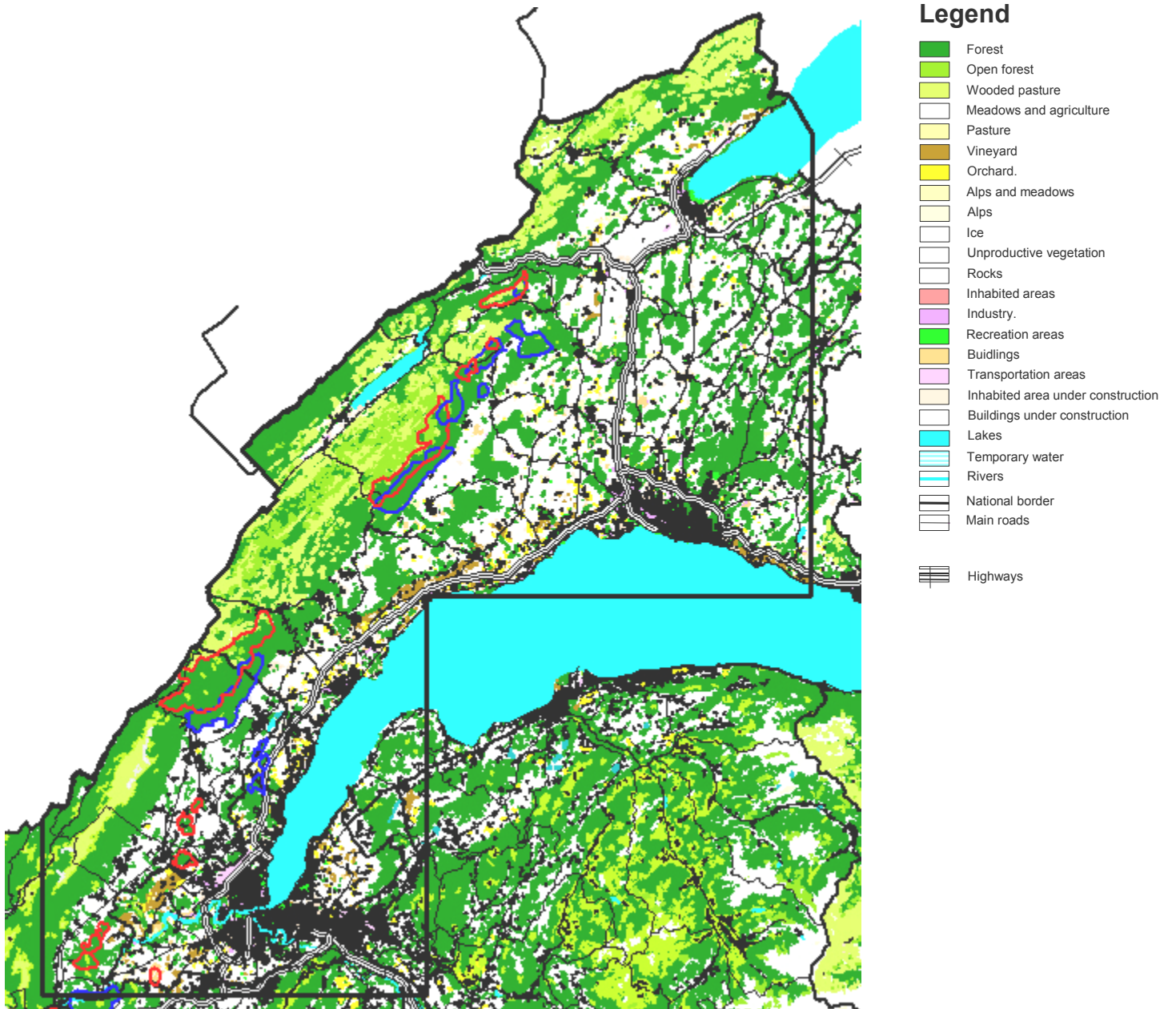
### 2.3.1. Overview

Habitat selection should be considered as a hierarchical process (Section 1.5.2). At the second level of selection, individuals choose their home range inside an area. Most habitat selection analyses are performed using radiotracking data on a sample of individuals. This sample is assumed to be representative of the population or of a part of the population, e.g. females. Thereafter, habitat inside the combination of all home ranges was compared to habitat inside study area (e.g. Millsaugh et al. 1998, McLoughlin et al. 2002). Due to the high acquisition costs of such data, other sampling methods that are not necessarily less adequate may be used (Manly et al. 1993). In this study, we considered an expert red deer presence map developed in chapter one as the population range that correspond to the combination of all individual home ranges. We analyzed habitat selection at the population level by comparing habitat inside the presence range with habitat in our study area.

Animals may perceive their environment at different scales (George and Zack 2001) and some authors have shown that habitat models that include more than one scale generally improved model performances (Didier and Porter 1999, Manel et al. 1999, Karl et al. 2000). Scale is composed of grain and extent. In this study we varied extent for different habitat parameters.

### 2.3.2. Land use variables

We used the Lemans Council database (1999) to derive potentially relevant habitat variables for red deer habitat selection (Table 2-1). This database contains habitat type maps stored in a vectorial format. We rasterized this information into one hectare grid cell maps and applied a circular moving window to obtain frequency maps. We varied radius of the moving window from 1 km (assuming that value corresponds approximately to a seasonal home range size in our study area, Georgii 1980, Georgii & Schroeder 1983, Kroubek & Hrabec 1996, Patthey 2003) to 5 km (corresponding to a population range size, Bonnet and Klein 1993). We also constructed habitat type distance maps in which each pixel of the map corresponds to the minimal distance to the habitat type.



**Figure 2-1:** Study area (bold polygon) and summer (red) and winter (blue) distribution of red deer.

### 2.3.3. *Disturbance variables*

Human-caused disturbance may be considered as a form of predation risk (Frid and Dill 2002). Open road avoidance by red deer has already been reported (Grover and Thompson 1986, Morellet et al. 1996, Cole et al. 1997, Rowland et al. 2000) especially in forests, as roads increase leisure activities and the human presence in any point of the landscape (Underhill and Angold 2000). We used the VECTOR25 database (OFT 2000) that contains vectorial information on 10 road types from walking ways to highways with a 5 meters precision (Table 2-1). However, it is impossible to perform analyses at that grain and at the extent of our study area due to current incompatible computer capacities. Therefore, we rasterized these data into 10 meter square pixel size maps and derived distance maps, which we transformed into one-hectare resolution maps. Thus each hectare sized pixel value was the mean of a hundred 10 meter size pixels. Consequently, the amount of information may be computed with a limited loss of source data accuracy. We also calculated the size of the polygons free of roads and attributed this value to each corresponding pixel. We calculated distance to and frequency of inhabited, transportation and recreation areas (from the Lemans council database) that are source of human perturbation.

### 2.3.4. *Habitat selection analyses*

Habitat model performance may decrease using an inappropriate extent, especially when landscape structure is not sufficiently homogeneous (Boyce et al. 2002, Osborne and Suarez-Seoane 2002). The Jura Mountains and the Plateau are both homogeneous even though their landscape characteristics differ (e.g. elevation and associated land-use) (Hegg et al. 1993). Therefore, we divided our analysis into two parts: Jura Mountains and Plateau. Without this distinction, these large-scale differences between the Jura Mountains and the Plateau would have masked slight differences that may be relevant at a finer scale and that may be essential for management purposes (Porter and Church 1987, Boyce 2002, Osborne and Suarez-Seoane 2002, Zimmermann et al. *in prep*, this study, *unpublished data*). We limited the Jura Mountains region to an area within 500 meters from the foot of mountains and, similarly, the Plateau is limited to the area that was not more distant than was within 500 meters from the start of the Jura Mountains. Consequently, there was a 500 m overlap between the ranges. This overlap was used to limit the loss of important habitat parameters.

**Table 2-1:** Codes of the ecogeographical variables used for ENFA analysis. (1: Leman Council (1999), 2: VECTOR25 (OFT, 2000); R: radius of frequency analysis).

<b>Description</b>	<b>Source</b>	<b>Distance to</b>	<b>Frequency analyses</b>	
			Home range scale Radius = 1km	Population scale Radius =5 km
<b><i>Habitat variables</i></b>				
Pasture	1	PastureDist	PastureHR	PasturePR
Forests	1	-	ForestHR	ForestPR
Open forest and alps	1	-	OpenForestHR	OpenForestPR
Meadows and agriculture	1	-	MeadowHR	MeadowPR
Orchards	1	OrchardDist	OrchardHR	OrchardPR
Vineyards	1	VineyardDist	VineyardHR	VineyardPR
<b><i>Disturbance variables</i></b>				
1st class roads	2	Road1Dist		
2nd class roads	2	Road2Dist	-	-
3rd class roads	2	Road3Dist	-	-
Forest roads	2	Road4Dist	-	-
Forest trails	2	Road5Dist	-	-
Walking ways	2	Road6Dist	-	-
All roads	2	RoadAllDist	-	-
Area free of roads	2	FreeRoadArea	-	-
Recreation areas	1	RecreationDist	RecreationHR	RecreationPR
Transportation areas	1	TransportDist	TransportHR	TransportPR
Inhabited area	1	InhabitedDist	InhabitedHR	InhabitedPR

Several studies have shown that a considerable distance may separate seasonal home ranges (e.g. Blankenhorn et al. 1978). Therefore seasons were analyzed separately (See section 1.6.2 for seasonal distribution) so that our analyses were separated into four parts: Jura Mountains and Plateau, both for summer and winter.

A multivariate analysis was applied on our variables in order to discriminate between habitat inside the red deer range and over the entire landscape. We may not obtain real absence data, as red deer may not yet have colonized all favorable areas. Therefore we used the ENFA multivariate analysis (see section 1.6.3 for a detailed description of ENFA analysis) that is robust in the case of a spreading species (Hirzel et al. 2001).

Non-normal variables were normalized before analyses. When we observed high correlations between one or more variables, one variable was selected according to its facility to reflect ecological meaning and the other removed. If a variable was not continuous enough, it was removed. Numbers of factors for habitat suitability computation were chosen according to the

broken-stick method (Hirzel et al. 2002). The calibration-validation modeling process was done using the Jack-knife cross-validation method (See section 1.6.3).

Jura Mountains and Plateau habitat suitability maps were overlaid to present them simultaneously, and the mean of the Jura Mountains and the Plateau pixel values was calculated when the two maps overlapped.

## 2.4. Results

### 2.4.1. Winter

Cross-validation procedures confirmed the quality of ENFA models, since the mean reclassified HS value varies from 57 to 70 and has low associated confidence intervals (Table 2-2). In addition, contrast values are high and the information explained by the models ranged from 73% to 99%.

Red deer winter habitat in the Jura Mountains is marginal by comparison to overall available habitat (Table 2-2, marginality 0.80). Marginality scores showed that forest densities (population scale:0.35, home range scale: 0.36), pastures (0.37) , distance to pasture (0.37), and recreation areas (0.21) predicted higher HS values according to their marginality scores (Table 2-3). In contrast, red deer presence habitat has lower open forest (-0.21. -0.20) and pasture (-0.39, -0.38) densities. Forest frequencies at home range scale, distance to meadows, agriculture, buildings and orchards have high specialization scores and so reveal sensitivity to any shift from their optimal values (Table 2-3).

According to ENFA, Plateau winter suitable habitat is marginal from overall habitat (Table 2-2: marginality = 0.91) and is characterized by high forest frequency (scores: 0.38, 0.34), a low inhabited area density (frequencies:-0.25, -0.20, distance to: 0.35), low pasture and meadows density and is distant from recreation areas (0.22) (Table. 2-4). Frequencies and distance to inhabited areas and orchard and frequency of forest at home range-scale showed a high sensitivity to shift away from their optimal values, according to their scores on specialization axes (Table 2-4).

**Table 2-2:** Cross validation process on red deer ENFA analyses for Jura Mountains. See section 1.6.3 for further details.

<b>Statistics</b>	<b>Winter</b>		<b>Summer</b>	
	<b>Jura Mountains</b>	<b>Plateau</b>	<b>Jura Mountains</b>	<b>Plateau</b>
Marginality	0.80	0.91	0.79	0.87
Tolerance	0.56	0.31	0.57	0.03
Explained Information	0.73	0.90	0.79	0.99
Validation: species HS>50	0.79 [0.75-0.85]	0.57 [0.45-0.69]	0.71[0.65-0.76]	0.63[0.51-0.72]
Validation: “Contrast”	0.53 [0.49-0.58]	0.45 [0.34-0.57]	0.44[0.38-0.50]	0.43[0.30-0.52]

### **2.4.2. Summer**

As for winter, summer cross-validations revealed good performances. Species and global HS values have a low overlap (Table 2-2).

For summer habitat selection in the Jura Mountains, marginality scores showed that forest frequency (0.35, 0.38), distance to buildings (0.29), 1<sup>st</sup> (0.22) to 4<sup>th</sup> (0.24) class roads and meadows (0.26) were positively correlated with habitat suitability values (Table 2-5). On the other hand, meadows frequency (-0.18, -0.25) was negatively correlated with HS values. The specialization scores revealed that red deer are sensitive to shifts away from their optimal values on forest and meadows frequencies at the population scale, and also to distance from orchards (Table 2-5).

According to the ENFA marginality scores, summer suitable habitats in the Plateau are surrounded by a high forest frequency (0.30, 0.34), are distant to 1<sup>st</sup> (0.35) to 4<sup>th</sup> class roads (0.32) and inhabited areas (0.26), and had low inhabited area frequencies (-0.29, -0.26) (Table 2-6). Distance to recreation areas (-0.68) and transportation areas (0.68) have high specialization scores showing sensitivity to any shift away from their optimal values (Table 2-6).

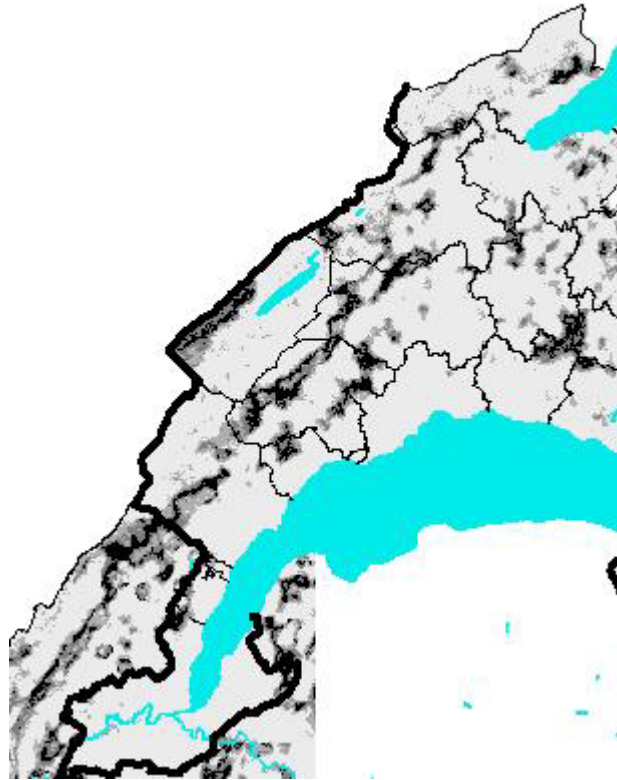
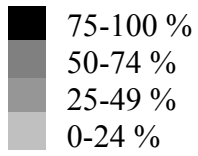
**Table 2-3:** Scores of the variables on the selected factorial axes (out of 33) from the ENFA winter analyses for red deer in the Jura Mountains. Percentages indicate the amount of variance explained by each factor. M= marginality, S1 to S2= specialization factors. The marginality scores indicate the correlation between each variables and the factor. The greater the absolute value of the coefficient, the higher this variable contributes to the marginality. Positives marginality scores values mean that Red deer prefers location with higher values than average location in study area, a negative value means that Red deer prefers the low values. The absolute values of specialization scores indicate the correlation of each variable to each specialization factor but here the sign has no meaning. The higher the value, the more restricted is the range of the red deer on the corresponding variable.

<b>Variables</b>	<b>M</b> 15%	<b>S1</b> 16%	<b>S2</b> 14%
<b>Habitat</b>			
PasturePR	<b>-0.39</b>	-0.03	0.01
PastureHR	<b>-0.38</b>	0.07	0.03
PastureDist	<b>0.37</b>	-0.01	0.00
ForestPR	<b>0.35</b>	<b>-0.20</b>	-0.08
ForestHR	<b>0.36</b>	<b>0.62</b>	<b>-0.96</b>
OpenForestPR	<b>-0.21</b>	-0.02	0.00
OpenForestHR	<b>-0.20</b>	-0.07	0.02
OrchardPR	-0.05	-0.05	0.02
OrchardHR	-0.05	0.14	0.04
OrchardDist	0.12	<b>-0.35</b>	-0.13
MeadowPR	0.06	<b>-0.28</b>	<b>-0.10</b>
MeadowHR	-0.08	0.07	0.02
MeadowowDist	0.11	<b>-0.33</b>	<b>-0.11</b>
<b>Disturbance variables</b>			
Road6Dis	-0.09	0.01	0.00
Road5Dist	-0.04	0.03	0.01
Road4Dis	-0.16	0.05	0.02
Road3Dist	-0.16	0.04	0.01
Road2Dist	0.04	0.17	-0.05
Road1Dist	-0.03	0.09	0.04
RoadAllDist	0.13	0.03	-0.01
FreeRoadArea	<b>-0.22</b>	-0.04	0.01
RecreationPR	-0.01	0.05	0.02
RecreationHR	-0.01	0.00	0.00
RecreationDist	<b>0.21</b>	-0.15	0.05
InhabitedPR	-0.06	-0.08	0.04
InhabitedHR	-0.11	-0.09	-0.04
InhabitedDist	0.05	<b>-0.37</b>	<b>0.13</b>

**Table 2-4:** Scores of the variables on the selected factorial axes (out of 31) from the ENFA winter analyses for red deer in the Plateau. For legends : see table 2-3.

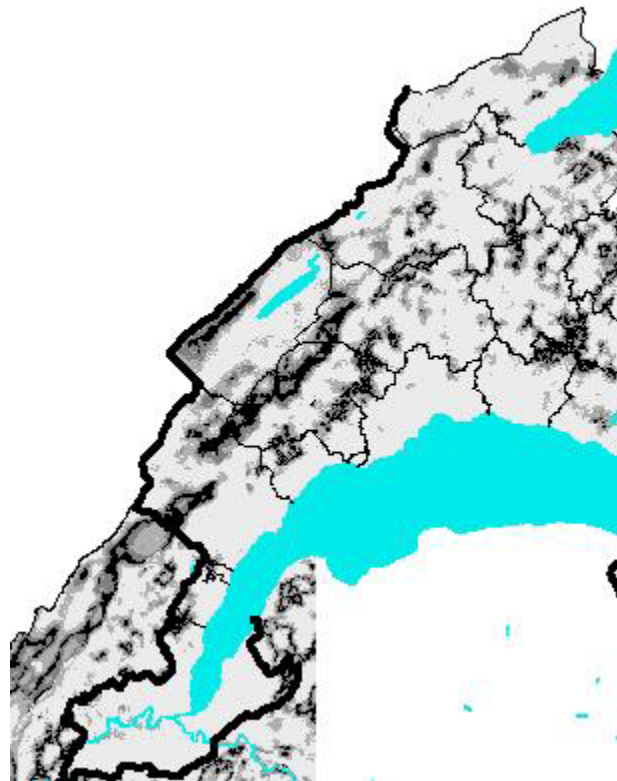
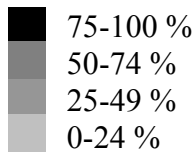
<b>Variables</b>	<b>M</b> 12%	<b>S1</b> 18%	<b>S2</b> 13%	<b>S3</b> 9%
<b>Habitat variables</b>				
PasturePR	<b>-0.22</b>	0.16	0.06	0.07
PastureHR	<b>-0.21</b>	<b>0.25</b>	0.06	0.11
PastureDist	<b>0.19</b>	0.18	0.08	-0.23
ForestPR	<b>0.38</b>	-0.02	0.08	-0.21
ForestHR	<b>0.34</b>	<b>-0.28</b>	<b>-0.18</b>	-0.06
OpenForestPR	0.05	-0.08	0.05	0.20
OrchardPR	-0.08	<b>-0.57</b>	<b>0.75</b>	<b>-0.40</b>
OrchardDist	<b>0.21</b>	-0.03	<b>-0.28</b>	<b>-0.49</b>
MeadowPR	<b>-0.29</b>	0.06	-0.02	-0.16
MeadowHR	<b>-0.26</b>	0.11	-0.02	0.04
MeadowowDist	<b>0.28</b>	0.05	-0.05	0.16
<b>Disturbance variables</b>				
Road6Dist	-0.12	-0.06	-0.09	0.08
Road5Dist	0.06	-0.03	-0.03	-0.06
Road4Dist	0.10	0.08	-0.06	-0.07
Road3Dist	-0.07	-0.03	0.03	-0.13
Road2Dist	0.13	-0.03	<b>0.19</b>	-0.04
Road1Dist	0.05	0.07	0.13	0.15
RecreationPR	-0.02	0.07	0.08	0.01
RecreationDist	<b>0.22</b>	-0.02	0.06	0.07
InhabitedPR	<b>-0.25</b>	<b>-0.22</b>	<b>-0.46</b>	<b>0.43</b>
InhabitedHR	<b>-0.20</b>	<b>-0.54</b>	0.07	<b>0.32</b>
InhabitedDist	<b>0.35</b>	<b>-0.30</b>	-0.02	0.20

**HS values**



**Figure 2- 2:** Summer habitat suitability map Forest red deer in east Switzerland, as computed from ENFA. France-Switzerland (large black line) and districts (fine black) borders are indicated.

**HS values**



**Figure 2-3:** Winter habitat suitability map Forest red deer in east Switzerland, as computed from ENFA. France-Switzerland (large black line) and districts (fine black) borders are indicated.



**Table 2-5:** Scores of the variables on the selected factorial axes (out of 26) from the ENFA summer analyses Forest red deer in the Jura Mountains. For legends : see table 2-3.

Variables	M 39%	S1 18%	S2 10%	S3 8%	S4 5%
<b>Habitat variables</b>					
PasturePR	-0.16	0.03	-0.03	-0.08	-0.08
PastureHR	-0.08	-0.02	-0.05	0.01	0.01
PastureDist	0.04	-0.03	-0.10	0.15	<b>0.19</b>
ForestPR	<b>0.35</b>	<b>0.74</b>	<b>0.40</b>	<b>-0.41</b>	<b>0.63</b>
ForestHR	<b>0.38</b>	<b>-0.48</b>	<b>-0.54</b>	<b>0.35</b>	<b>-0.57</b>
OpenForestPR	0.11	0.01	0.00	0.01	-0.02
OpenForestHR	0.06	0.01	0.01	-0.06	0.01
OrchardPR	-0.05	0.01	0.06	-0.09	-0.01
OrchardHR	0.04	0.00	-0.03	-0.02	0.01
OrchardDist	0.05	0.02	0.14	<b>-0.61</b>	<b>-0.16</b>
MeadowowPR	-0.18	<b>0.42</b>	0.11	0.01	<b>0.30</b>
MeadowowHR	<b>-0.25</b>	-0.15	-0.15	0.04	-0.25
MeadowowDist	<b>0.26</b>	-0.01	-0.02	-0.02	0.03
VineyardPR	-0.12	0.05	-0.07	-0.02	0.09
VineyardHR	-0.11	0.09	<b>-0.68</b>	-0.14	-0.01
<b>Disturbance variables</b>					
Road6Dist	-0.16	0.03	0.03	0.02	-0.03
Road5Dist	-0.13	0.00	0.05	0.01	0.00
Road4Dist	<b>0.24</b>	0.00	0.01	0.03	-0.01
Road3Dist	0.11	-0.01	0.01	-0.05	0.04
Road2Dist	0.14	0.00	0.01	0.03	-0.02
Road1Dist	<b>0.22</b>	-0.02	-0.04	-0.15	-0.01
RoadAllDist	0.08	0.01	-0.01	-0.01	0.00
FreeRoadArea	0.11	-0.02	-0.03	0.01	0.06
TransportPR	-0.08	0.02	0.00	0.08	-0.03
TransportHR	-0.07	-0.01	-0.01	0.03	0.01
RecreationPR	-0.13	-0.01	-0.04	-0.05	<b>0.20</b>
RecreationDist	0.02	0.01	-0.02	<b>0.46</b>	-0.03
InhabitedPR	<b>-0.30</b>	0.09	0.07	-0.05	0.08
InhabitedHR	<b>-0.28</b>	-0.01	0.02	0.04	-0.04
InhabitedDist	<b>0.29</b>	0.03	-0.01	0.14	0.01

**Table 2-6:** Scores of the variables on the selected factorial axes (out of 23) from the ENFA summer analyses Forest red deer in the Plateau. For legends : see table 2-3.

Variables	M 99%	S1 0%
<b>Habitat variables</b>		
ForestPR	<b>0.30</b>	<b>-0.14</b>
ForestHR	<b>0.34</b>	-0.06
OrchardPR	-0.16	-0.01
OrchardHR	-0.13	0.00
MeadowowPR	-0.12	-0.09
MeadowowDist	0.21	0.00
MeadowowHR	-0.20	0.00
VineyardPR	-0.07	0.00
VineyardHR	-0.12	<b>0.16</b>
<b>Disturbance variables</b>		
Road6Dist	-0.10	-0.01
Road5Dist	-0.05	-0.02
Road4Dist	<b>0.32</b>	0.01
Road3Dist	0.22	-0.02
Road2Dist	0.14	0.00
FreeRoadArea	<b>0.35</b>	-0.02
RoadAllDist	0.19	0.01
Road1Dist	0.18	-0.04
TransportDist	-0.12	<b>-0.68</b>
RecreationPR	-0.14	0.09
RecreationDist	0.00	<b>0.68</b>
InhabitedPR	<b>-0.29</b>	0.00
InhabitedDist	<b>0.26</b>	-0.01
InhabitedHR	<b>-0.26</b>	-0.07

## **2.5. Discussion**

### ***2.5.1. ENFA GIS model performances***

Models predicting habitat suitability are based on their specific assumptions and consequently have their own limitations. Among their restrictions, the most important are (see Guisan and Zimmermann 2000 for a review): accuracy and resolution of input maps, sampling design, biotic interactions (e.g. competition), causality, historical factors, spatial autocorrelation, response curves (statistical techniques), data set evaluation (vs. calibration data set) and spatially explicit uncertainty assessment (evaluation).

We chose to divide our study region according to its two well-defined ecosystems. Our choice to limit the spatial extent of the analysis was necessary to overcome the potential bias that may induce spatial heterogeneity (Porter and Church 1987, Osborne and Suarez-Seone 2002).

The spatial grain of HS analyzes is also of importance, since an inadequate grain may fail to detect habitat selection (Manel et al. 2000). Generally, spatial grain choice results in a trade-off between i) study area extent, ii) availability of data, iii) cost of obtaining data, iv) computer performances and v) perception scales of the species. Here we analyzed habitat selection of an ungulate species over a very large area at the population selection level. We use broad habitat classes registered at 1 ha resolution. This grain is sufficient to construct habitat maps for a red deer population, as we use habitat type frequencies corresponding at least at the home range extent (see section 1.2). However, our models perform well according to the cross-validation results. Future habitat suitability analyses should use more detailed habitat typology such as forest stand composition or structure, to improve model performances. For example, the Grand Risoux forest (Figures 1-3 and 2-3) will probably no longer be predicted as suitable for red deer wintering, which is unexpected for forests that experience high snowfall. Over such a large study area, an alternative would be to construct forest typology maps using satellite images (Franklin et al. 2001).

### 2.5.2. *Habitat features*

Our results are consistent with the literature on red deer inhabiting in an area with forested mountains and high levels of urbanization. During both seasons, our results confirmed the close association of red deer with quieter and larger forested areas (Gonzales and Pépin 1996 for a review).

Main winter habitat features are slightly different for the Jura Mountains and the Plateau, as revealed by their scores on factorial axes and seasonal distributions of suitable habitats. Favorable winter areas are situated at the foot of the Jura Mountains and in largest forest patches of the Plateau (Figure 2-2). During summer, suitable habitat distribution occurs over a large area, especially in the Jura Mountains (Figure 2-3).

In our study area, red deer clearly select forests and not the open habitats such as pastured alps or open forests, their original habitat. Forests are obviously selected for their low level of human disturbance (Gonzales and Pépin 1996).

Red deer distribution is negatively correlated with presence of buildings (frequency and distance to) as assessed from their high marginality scores. Consequently these variables reveal their pertinence as habitat predictors. Surprisingly, these human disturbance factors were not used in previous studies, expect for Morellet et al. (1996), perhaps because most research was conducted in uninhabited areas such as parks or scientific reserves (Edge et al. 1987, Cole et al. 1997, Millspauch et al. 1998, Rowland et al. 2000).

Our results confirm that open road avoidance by red deer is a widespread phenomenon and that a spatially explicit road component is required for red deer habitat models (Edge et al. 1987, Morellet et al. 1996, Cole and al. 1997, Rowland et al. 2000). As closing roads may be costly and unpopular while maintaining open roads may be expensive and controversial, the road - red deer relationship and its effects need better understanding. Roads are avoided from first class roads to simple forest roads, as long as car access is possible. Walking ways and forest trails used by pedestrians that penetrate inside forests seem to have only a slight (even positive) relationship to red deer distribution. Moreover during summer, red deer were located in larger areas free from roads. Therefore, inside our study areas a lower density of open roads appears to be more important than a smaller density of pedestrian ways. We also found that forests near inhabited areas, such as villages, are less suitable than forest away from public areas. We suggest that a travel cost distance from the source of perturbation (towns, recreation

areas) or a map of human landscape frequentation may give a better spatial explanation to our results. For instance, Wang and Manning (1999) successfully simulated public frequentation indices based on field measurements of public road use and distances to perturbation sources (parking, town) for recreation management. Unfortunately, this type of road use information is currently not available in our study area.

Wintering areas in the Jura Mountains have smaller road-free areas (Table 2-3, marginality score:-0.22). This unexpected result may be explained by the fact that the largest road-free areas are situated at higher altitude (open forests and alps), where snow depth is excessively important for red deer wintering. Therefore, ENFA gave a spurious result with no ecological meaning, a case where correlations do not assess causality (Guisan and Zimmermann 2000). Further winter HS analyses should therefore be performed with an extent limited to the available landscape, which should provide better results (Osborne and Suarez-Seone 2002). In this new scale extent, it is likely that red deer will be located in the larger areas free of roads.

The multi-scale analysis offers additional insight into red deer ecology and requirements in the Jura Mountains and the Plateau. Our models showed that two main habitat features, forest frequency and inhabited areas frequencies, are both important at the home range and population scales. Therefore, managers need to consider not only home range scale variables but also population scale variables, such as meadow or forest frequencies.

Managers may use GIS models for at least three purposes. Firstly, main red deer habitat preferences revealed by ENFA analysis (see next chapter) are useful information regarding red deer management (Mooty et al. 1987). Secondly, habitat suitability maps point out favorable regions that are actually free of deer. This type of information is essential for managers and may be considered directly, i.e. to define future potential conflicts areas (Lathrop et al. 1998, Sanderson et al. 2002). Thirdly, habitat models may be used to test quantitative and spatial effects of landscape management scenarios (Van Apeldoorn et al. 1998, Rushton et al. 2000, Whitfield et al. 2001). Scenarios may, for example, be to diminish forested areas or to modify arable land use in order to visualize effects on habitat, both in quality and size.

In conclusion, managers must account for the entire combination of habitat features that vary by scale and season in order to incorporate them into their land-use plans. Management of road access and related human disturbances remains important for red deer management. They should be vigilant of the fact that due to an increased use of some forests by the public and the general decrease of forest size, red deer may move to other suitable habitats or unfortunately, to less suitable areas in which they may cause damage. Moreover, as habitat selection is not static in time, analyses should be repeated in a few years, to adequately fit with a potential red deer adaptation shift to its environment. For instance, over the last decades, roe deer *Capreolus capreolus* has over the last decades, shown a rapid colonization of open arable lands that are not the original habitat of this forest species (Cargnelutti et al. 2002).

*A red deer habitat point of view*

### 3. SCALE-DEPENDENT SEASONAL HABITAT SELECTION OF AN EXPANDING RED DEER POPULATION IN THE SWISS JURA MOUNTAINS

---

*Landscape selection level at home-range and local scales*

#### 3.1. Summary

- 1) Red deer (*Cervus elaphus*) are currently recolonizing the Jura Mountains. To assess the consequences of their expansion, wildlife managers plan to develop management options complying with possible colonization scenarios for this problematic species, a task requiring spatially-explicit understanding of red deer dynamics.
- 2) Habitat-suitability (HS) models, based on Ecological-Niche Factor Analysis (ENFA) were built in order to describe red deer present distribution and analyze the factors determining it. ENFA was preferred among alternative statistical approaches, as it relies on presence data only, which is particularly appropriate in the case of a spreading species.
- 3) The home range scale ecogeographical predictors used to compute the HS model were calculated within a 1 km radius, in the form of percentage cover of various land-use units, distance to roads, length of forest-pasture edges and indices of hunting pressure. At the local scale, variables such as plant cover indices were measured within a 50 m diameter plot. Presence/absence of red deer was determined in each cell according to an expert survey.
- 4) We found that current red deer distribution is adequately modeled using mainly land-use variables measured at home range scale (e.g. forest density). Human disturbance also plays an important role and may be modeled with derived variables such as distance to roads or buildings. Forests with *Festuca altissima* are selected in both seasons and reveal their importance for red deer ecology and management. The model predictions outside the current range are of interest for management decisions but will have to be validated in the future, according to red deer range expansion.

## **3.2. Introduction**

Red deer were extirpated around 1850 in Western Switzerland due to excessive hunting. Presently, the species is recolonizing the Jura Mountains after a re-introduction of some individuals along the French border during late 1950s. In this area, population size has remained small and is currently estimated at 50 to 100 animals. However, over the last five years, wildlife authorities have recorded clear indications of a local population growth and expansion (Figure 1-4). As a consequence, and in order to prevent human-wildlife conflicts associated with the impact of the species on forested habitats and motorways, wildlife managers currently require to set wildlife management options that consider spatial and temporal colonization possibilities of red deer populations. Regional deer recovery needs to be understood in a spatially explicit manner to improve future red deer population management.

Several studies on established *Cervus elaphus* populations have shown the importance of two main factors: human disturbance (Petрак 1996) and habitat composition (Morellet et al. 1996). Human disturbances (e.g. noise, hunting, etc) seriously impact behavior (Whittington and Chamove 1995, Pollar and Littlejohn 1995, Petрак 1996, Hodgetts et al. 1998) and, consequently affects movements (Conner et al. 2001), distribution (Millspaugh et al. 2000) and reproduction (Phillips and Alldredge 2000). Red deer need quiet places with sufficient food resources (Roloff et al. 2001) mainly herbaceous plants (Gebert and Verheyden-Tixier 2001). However, habitat selection by colonizing populations of red deer is poorly understood relative to established populations.

Our objectives are (1) to characterize important red deer habitat components by comparing habitat inside red deer distribution maps with available habitat in our study area in order to derive management actions and (2) to construct a habitat suitability model to map areas that red deer might colonize in the future.



### 3.3. Study area

Surveys of vegetation structure and red deer presence were conducted in the Jura Mountains in the state of (Canton de Vaud, approximately 500 km<sup>2</sup>, 46°30'/6°20'). The Jura range is in the west limit of Switzerland at the end of Swiss Plateau, and its main features is generally rolling shape (Figures 2-1, 3-1). The range is situated on a southwest to northeast axis. The study area is bordered to the South and the West by the French border, to the North by the canton of Neuchâtel and to the East by the lower limit of the Jura Mountains (550 meter elevation isocline) and the Plateau area. Climate varies according to elevation and local characteristics may occur at a given elevation due to the topographic effects. As elevation increases, vegetation changes from oak forest (550 m) to beech forest, fir forest and sub alpine vegetation types (1670 m). At higher altitude, pasture and woodlands are still intermixed with one another over a very large area, due to cattle farming and agriculture. Below 550m of altitude agriculture dominates the landscape.

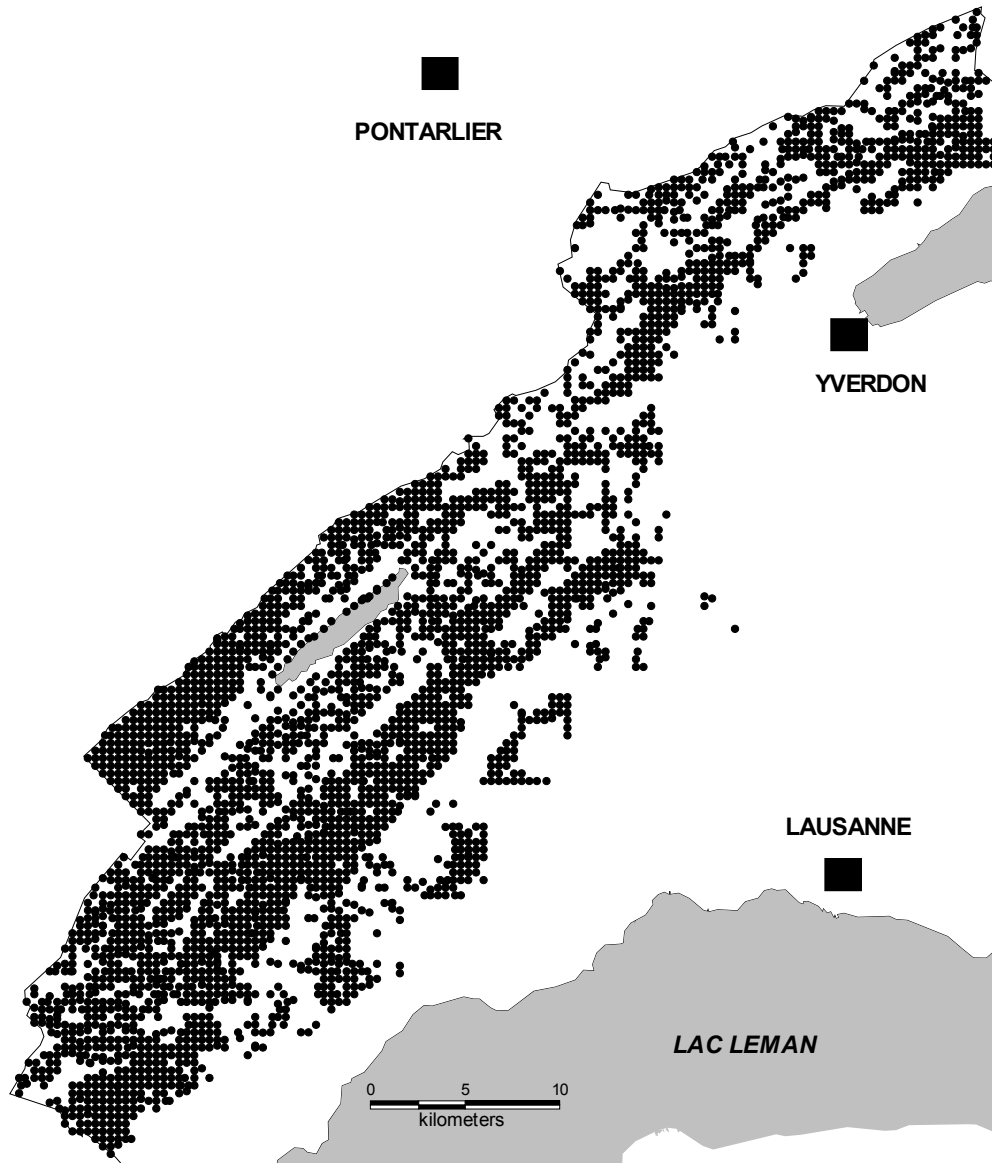
### 3.4. Methods

#### 3.4.1. Overview

The Red deer is a large herbivore that is likely to interact with its environment at different spatial and temporal scales (Senft et al. 1987). Recent studies on habitat selection have shown the importance of analyzing several spatial scales in order to improve ecological understanding (Didier and Porter 1999). We analyzed red deer habitat selection at two spatial scales. We defined home range scale variables measured over an area corresponding to a home range extent, and local scale variables that measure habitat features close to the sampling point (Figure 1-5). Winter and summer seasons have been analyzed separately as red deer habitat use differs seasonally (Hamann et al.1997, Klein and Hamann 1999).

In our study area, red deer were exclusively observed inside forests. Thus, we limited our habitat selection analyzes to forested areas. We applied a regular sampling over the whole study area and compared forest plots inside red deer distribution maps to the complete set of forest plots, hereafter referred to as available forest plots. This comparison is conformed to the 2nd level of selection defined by Johnson (1980), with inferences at the population level.

For each forest plot we measured local variables in the field or derived home range scale variables with the help of geographic information systems (GIS) that might be relevant for red deer, including topographical, food, forest stand structure and potential disturbance source variables.



**Figure 3-1:** Forest sample plots used for red deer habitat selection analyses in the Swiss Jura Mountains. For a land-use view see figure 2-1.

### **3.4.2. Red deer presence data**

After its reintroduction near the French border, red deer rapidly colonized the Southern part of the study area. Two decades later, the species was found in the center of our study area. During the last 15 years, red deer indices were found over almost the whole study range, but most red deer observations were made in two main areas located in the south and in the center of the study area (Figure 3-4).

We combined information collected by 35 rangers and covering the whole study area with systematic transects totalizing 294 km to define areas with red deer indices. We then performed two intensive surveys during winter 1999 and summer 2000 into these areas and in a 2 km large buffer corresponding to 1.8 km length survey per square kilometer. For both seasons, nearly 680 presence indices were found, localized with ten meter precision GPS and reported on maps. Extreme presence points were bonded to form polygonal presence maps representing red deer population ranges. We considered two groups of indices to be disjointed if more than one kilometer (home range radius size) separated them and thus constructed two different presence range polygons. We did not take into account sex difference (Clutton-brock et al. 1987, Conradt et al. 2000, Weckerly et al. 2001) as our field survey did not enable differentiating between male and female distribution in a reliable way.

### **3.4.3. Local scale variables**

Meier (2000) conducted a summer survey for all Vaud state forest on a 400x400 meter grid based on the Swiss Coordinate System. For each node of the grid, 31 vegetation variables were measured on a 50 m diameter plot: canopy, understory and grass percent cover, cover for 14 species using Braun-Blanquet (1964) indices, slope and elevation (Table 3-2, Table 3-3). For this study, we used the data of all the sampling plots (3246) inside our study area.

### **3.4.4. Home range scale variables**

We used a Geographic Information System (GIS) to derive several variables that we expected to be relevant to broader scale (Table 3-2, Table 3-3). We calculated distances to six types of roads, from walking ways to 1st class roads, included at a 10 m resolution in the VECTOR 25 Swiss database (OFT, 2000). 1<sup>st</sup> class roads are the road type just below highways. The GEOSTAT database (OFS, 2000) was used to calculate densities of some habitat types within a 2 km diameter - corresponding approximatively to a mean seasonal home ranges (Georgii

1980, Georgii & Schroeder 1983, Kroubek & Hrabe 1996, Patthey 2003)) - moving window and distances to each habitat types. This database consisted in a grid with a 100m-cell size, with a habitat type attributed to each cell. As high hunting pressure affects red deer habitat use (Millspaugh et al. 2000, Conner et al. 2001), we derived a wild boar (*Sus scrofa*) and a roe deer (*Capreolus capreolus*) hunting index. As both species are abundant and hunted all over our study area, hunting bags were used for this purpose. Wild boar hunt is allowed from October to January. However, in practice, the main hunting period is from December to January (Conservation de la Faune, *unpublished data*) when snow cover helps for game tracking. Roe deer are hunted predominating with dogs and in October only. Vaud state is divided into small hunting regions defined by main roads. Mean annual hunting bags from 1986 to 2000 were calculated per hectare of forest for these regions and attributed to each corresponding forest hectare grid of the GIS map. We calculated a gaussian average using a 1 km moving window for each forest hectare. We did not take red deer hunting data into account as only very few animals have been culled over the last decades (less than 10 animals per year). We used the wild boar hunting index for winter analysis and the roe deer hunting index for summer analysis.

### **3.4.5. Data analysis**

Forest sample points inside the seasonal species ranges (summer: n=148, winter: n=166) were assessed as equivalent to presence points.

Since *C. elaphus* is actually colonizing new regions, we can not assess the absence of the species with certainty and we therefore used the Ecological Niche Factor Analyses (ENFA) (Section 1.6.3, Hirzel et al. 2002) to calculate habitat suitability values, based on presence data only.

One of any pair of variables with an  $r >$  of 0.9 was eliminated to control for multicollinearity. We retained the variables we assessed to be easier to interpret ecologically or to be measured more accurately (Guisan and Zimmermann 2000). In order to build HS maps, the number of factors were kept according to the Broken-Stick method (Hirzel et al. 2002).

The K-fold cross-validation method developed by Boyce et al. (2002) (Section 1.6.3) was used for evaluating our predictions. We used 8 k-folded sets as recommended by Huberty's (1994) rule of thumb for nearly 50 variables. HS values were classified into 10 equal-interval

categories from zero to one insuring a consistent sample of reclassified points into each category.

ENFA was also performed with the disturbance and the vegetation groups of variables separately in order to better understand their spatial effect on red deer distribution.

GIS analyses and ENFA were computed with the programs BIOMAPPER 2.0 (Hirzel et al. 2002) and IDRISI 32 (Eastman 2001).

## 3.5. Results

### 3.5.1. Model evaluation

Winter and summer area-adjusted frequencies are positively and significantly correlated with HS categories (Table 3-1), indicating that the model predicts cross-validated used locations quite well. Moreover, all seasonal k-folded sets revealed significant positive correlations, indicating overall good model performances. The summer model is more significantly correlated but has larger uncertainties, especially for high HS values (Figure 3-2, Figure 3-3).

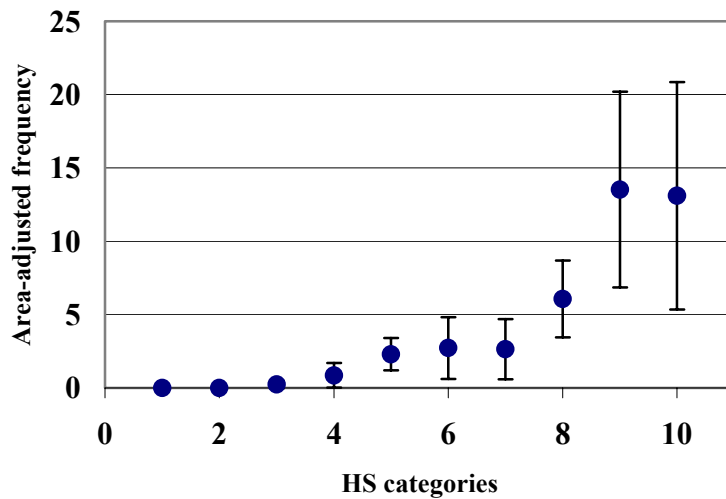
### 3.5.2. Summer habitat

Elevation, slope and edges were excluded from analyses due to high correlations with other variables. ENFA revealed that forest plots inside summer red deer distribution are marginal as compared to the reference data set (Table 3-2, marginality = 1.57). Marginality scores showed that summer distribution is correlated with forests with high fescue (*Festuca altissima*)(0.43), red raspberry (0.16) and maple (*Acer sp.*) (0.22) covers, and are at high distances from buildings (0.31). In contrast, summer red deer forest plots have less English ivy cover (*Hedera helix*) (-0.15), meadow, grass land (-0.30) and pasture (-0.20) density. Distances to orchards and roads, density of meadows, roe deer hunting pressure index and alpage-forest edges have high scores on specialization axes, showing sensitivity to any shift away from their optimal values.

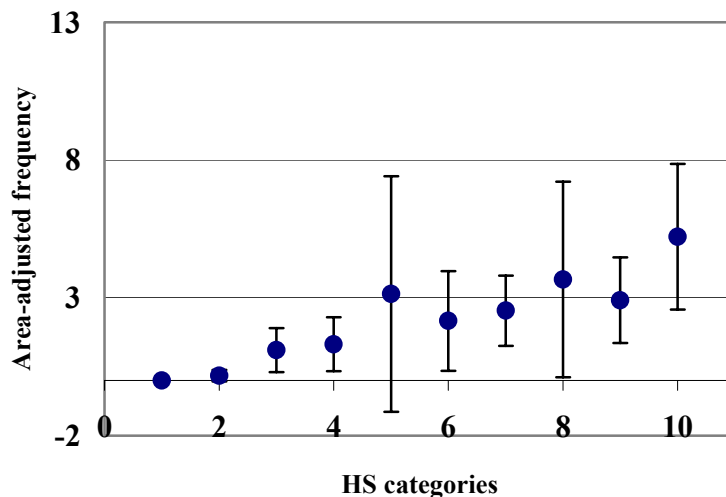
We built a summer HS maps with four factors that explained 84% of the system information. This map shows that only a small number of forest plots seem to be very suitable in the north

of our study area (Figure 3-4). Some other predicted favorable areas are localized between the current red deer ranges.

The red deer summer habitat is clearly more restricted due to vegetation requirements than to disturbance factors (Figure 3-4).



**Figure 3-2:** Mean ( $\pm$  S.D.) area-adjusted frequency of HS categories for summer red deer ENFA models in the Swiss Jura Mountains. Spearman-rank correlation ( $r_s = 0.973$ ,  $p < 0.001$ ) indicates that model predicted cross-validated locations well.



**Figure 3-3:** Mean ( $\pm$  S.D.) area-adjusted frequency of HS categories for winter red deer ENFA models in the Swiss Jura Mountains. Spearman-rank correlation ( $r_s = 0.903$ ,  $p < 0.001$ ) indicates that model predicted cross-validated locations well.

**Table 3-1:** Cross-validated Spearman-rank correlations ( $r_s$ ) between HS categories and area-adjusted frequencies for each partitions and average red deer ENFA HS model sets in the Swiss Jura Mountains. Results are presented for summer and winter.

Set	Summer		Winter	
	$r_s$	P	$r_s$	P
1	0.791	<0.01	0.819	<0.01
2	0.939	<0.001	0.713	<0.05
3	0.957	<0.001	0.706	<0.05
4	0.816	<0.01	0.620	<0.05
5	0.954	<0.001	0.584	<0.05
6	0.853	<0.01	0.607	<0.05
7	0.853	<0.01	0.790	<0.01
8	0.794	<0.01	0.794	<0.01
Average	0.973	<0.001	0.903	<0.001

### 3.5.3. Winter habitat

We built a winter habitat model using ENFA from all variables but excluded elevation, slope and edges as a consequence of high correlations. Red deer winter habitat was marginal (Table 3-3, marginality=1.36). According to the marginality axis, favorable forest plots were surrounded with a higher density of forests (score: 0.33), had a higher fescue (0.28) and Dog's mercury (*Mercurialis perennis*) (0.29) covers as well as a higher wild boar hunting index (0.22). Alpage density (-0.28), bilberry (*Vaccinium myrtillus*) (-0.22) and wood rush (*Luzula sylvatica*) (-0.21) covers, and distance to orchards (-0.23) were lower in the winter presence range than in the whole study area. Density of forest, distance to secondary roads, orchards and parking showed a high sensitivity to shifts away from their optimal values, according to their scores on specialization axes.

To build a winter habitat suitability map, we used the first seven factors, which represented 81% of the explained information. The HS map reveals other suitable forest plots along the bottom of the Swiss Jura Mountains on a Southwest to Northeast axis (Figure 3-4).

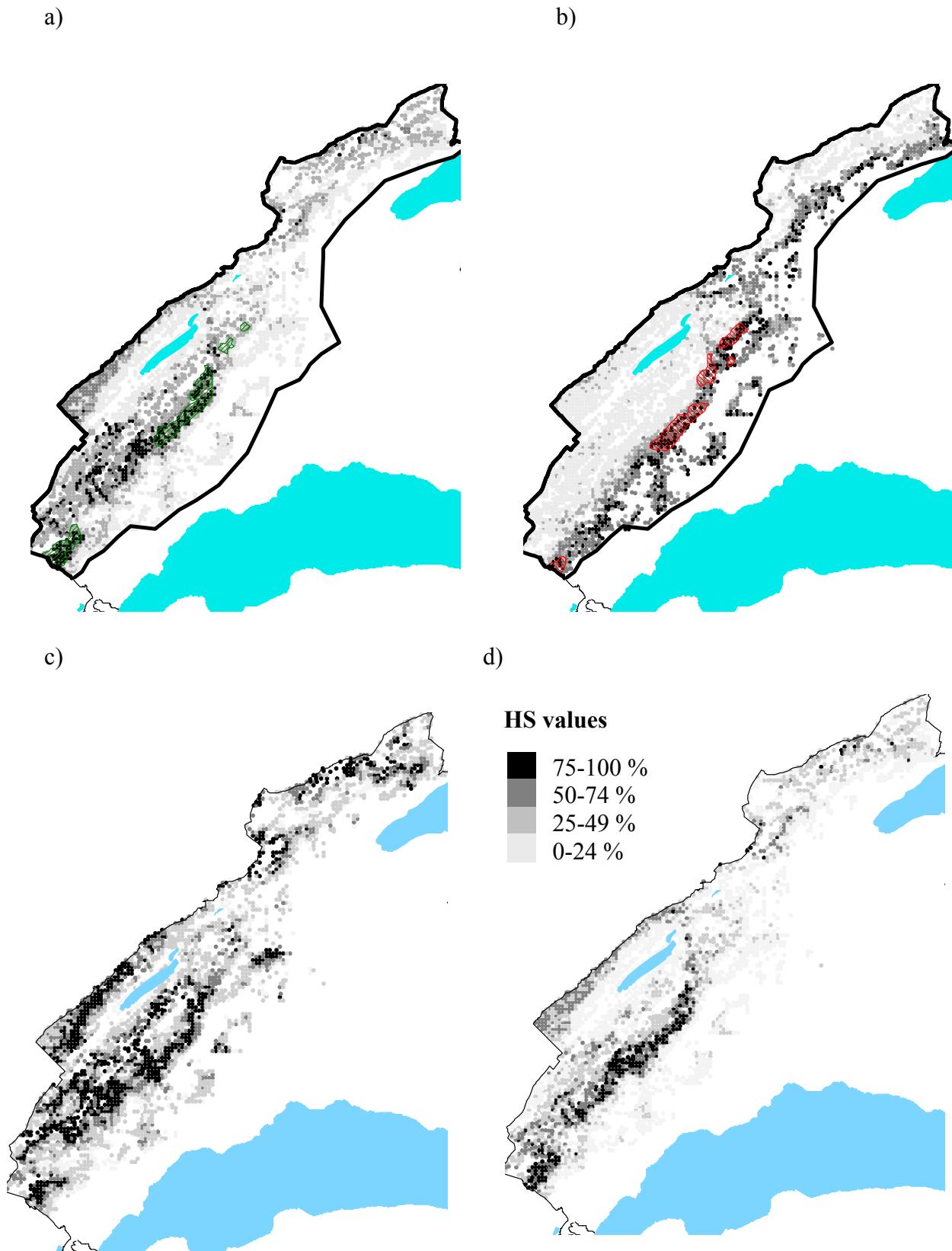
**Table 3-2:** Scores of the variables on the first four selected factorial axes (out of 46) from the summer ENFA for red deer in the Jura Mountains. Percentages indicate the amount of variance explained by each factor. M= marginality, S1 to S3= specialization factors, Explained information 84 %. The coefficients of the scores related to the marginality factor indicate the correlation between each variables and the factor. The greater the absolute value of the coefficient, the higher this variable contributes to the marginality. Positives marginality scores values mean that Red deer prefers location with higher values than average location in study area, a negative value means that Red deer prefers the low values. The absolute values of specialization scores indicate the correlation of each variable to each specialization factor but here the sign has no meaning. The higher the value, the more restricted is the range of the red deer on the corresponding variable.

<i>Marginality : 1.57</i>	<b>M</b>	<b>S1</b>	<b>S2</b>	<b>S3</b>
<i>Tolerance : 0.40</i>	40%	31%	15%	11%
<b>Local scale variables</b>				
Fir Abies alba (Canopy cover)	<b>0.16</b>	0.03	-0.04	0.01
Fir (Bush cover)	0.15	0.03	-0.01	-0.04
Fir (Grass cover)	<b>0.18</b>	0.01	0.02	-0.04
Sycomore Apple (Canopy cover) <i>Acer pseudoplatanus</i>	<b>0.22</b>	-0.02	0.00	-0.02
Sycomore Apple (Bush cover)	0.13	0.02	-0.02	0.00
Sycomore Apple (Grass cover)	<b>0.17</b>	0.01	0.02	-0.01
Canopy cover	-0.09	-0.04	-0.08	-0.01
Bitter grass cover <i>Cardamina heptaphylla</i>	0.11	0.02	-0.01	0.00
Subcanopy cover	0.08	-0.05	-0.03	0.00
Bush cover	0.10	-0.01	-0.01	-0.02
Grass cover	0.06	-0.01	0.00	0.03
Beech (Canopy cover) <i>Fagus sylvatica</i>	0.08	0.02	0.09	0.03
Beech (Bush cover)	<b>0.20</b>	-0.01	-0.04	0.01
Beech (Grass cover)	<b>0.16</b>	-0.01	-0.02	0.01
Shade fescue <i>Festuca altissima</i>	<b>0.43</b>	-0.01	-0.01	0.01
Ash (Canopy cover) <i>Fraxinus excelsior</i>	-0.07	-0.02	0.00	-0.07
Ash (Bush cover)	-0.03	-0.01	0.02	-0.03
Ash (Grass cover)	-0.06	-0.02	0.02	0.01
English evy (Grass cover) <i>Hedera helix</i>	<b>-0.15</b>	0.00	<b>-0.51</b>	<b>0.35</b>
Wood rush cover <i>Luzula sylvatica</i>	0.04	-0.01	0.05	0.00
Dog's mercury cover <i>Mercurialis perrenis</i>	-0.02	-0.01	-0.07	0.03
Millet grass cover <i>Milium effusum</i>	0.02	0.00	-0.01	0.02
Spruce (Canopy cover) <i>Picea excelsia</i>	0.02	0.00	-0.02	0.01
Spruce (Bush cover)	0.05	0.00	-0.02	0.01
Spruce (Grass cover)	0.06	-0.02	-0.02	0.02
Blackberry <i>Rubus fruticosus</i>	-0.05	-0.04	-0.08	-0.01
Red raspberry (Bush cover) <i>Rubus ideaus</i>	<b>0.16</b>	0.01	0.04	-0.04
Red raspberry (Grass cover)	0.14	-0.02	-0.07	0.03
Bilberry <i>Vaccinium myrtillus</i>	0.05	0.00	-0.07	0.01
<b>Land-use home-range scale variables</b>				
Forest (Density)	<b>0.27</b>	<b>-0.19</b>	<b>0.18</b>	0.01
Open forest (Density)	0.21	0.01	-0.04	0.07
Alpage (Density)	-0.05	0.02	<b>0.28</b>	0.00
Orchard (Distance)	-0.03	<b>-0.88</b>	0.12	0.07
Meadow and agriculture (Density)	<b>-0.30</b>	0.03	<b>0.34</b>	<b>-0.62</b>
Pasture (Density)	<b>-0.20</b>	-0.02	<b>-0.19</b>	<b>0.53</b>
Edge Forest-Pasture	-0.08	<b>-0.30</b>	-0.02	0.01
<b>Disturbance home-range scale variables</b>				
Parkings (Distance)	0.12	0.05	<b>0.15</b>	0.02
Buildings (Distance)	<b>0.31</b>	-0.07	0.07	-0.01
Roads (Distance)	0.04	0.00	0.03	0.01
1 Class roads (Distance)	0.08	0.15	0.05	0.03
2 Class roads (Distance)	0.15	0.11	-0.05	-0.09
3 Class roads (Distance)	0.00	0.03	0.01	-0.05
4 Class roads (Distance)	0.01	0.02	-0.02	-0.02
Forest layers (Distance)	0.15	-0.01	-0.03	0.02
Walking ways (Distance)	-0.08	0.00	-0.04	-0.05
Roe deer hunting index	-0.10	<b>0.19</b>	<b>0.61</b>	<b>0.41</b>



**Table 3-3:** Scores of the variables on the first seven selected factorial axes (out of 46) from the winter ENFA for red deer in the Jura Mountains. For legends : See Table 2-3.

<i>Marginality : 1.36</i>	<b>M</b>	<b>S1</b>	<b>S2</b>	<b>S3</b>	<b>S4</b>	<b>S5</b>	<b>S6</b>
<i>Tolerance : 0.59</i>	24%	10%	8%	7%	6%	4%	4%
<b>Local scale variables</b>							
Fir <i>Abies alba</i> (Canopy cover)	0.17	-0.02	0.00	0.01	0.02	-0.16	0.12
Fir (Bush cover)	0.12	0.01	0.00	0.05	0.10	-0.03	0.01
Fir (Grass cover)	0.18	0.01	0.10	-0.01	0.08	0.00	0.10
Sycamore Apple (Canopy cover) <i>Acer pseudoplatanus</i>	0.10	0.02	-0.05	0.00	-0.03	-0.05	-0.02
Sycamore Apple (Bush cover)	-0.06	0.06	0.02	-0.04	0.00	0.04	-0.04
Sycamore Apple (Grass cover)	0.05	-0.04	0.01	0.04	0.09	0.07	-0.01
Canopy cover	0.02	0.02	-0.02	-0.04	-0.06	0.16	-0.15
Bitter grass cover <i>Cardamina heptaphylla</i>	-0.01	0.02	-0.02	0.10	0.03	-0.12	0.13
Subcanopy cover	0.11	0.02	-0.01	-0.03	-0.03	0.18	-0.07
Bush cover	0.06	0.00	0.05	-0.01	-0.12	0.07	-0.03
Grass cover	-0.15	-0.02	-0.02	0.09	-0.03	-0.07	0.07
Beech (Canopy cover) <i>Fagus sylvatica</i>	0.19	-0.01	0.09	0.04	0.05	-0.06	0.02
Beech (Bush cover)	0.16	-0.07	-0.07	0.05	0.00	-0.10	-0.07
Beech (Grass cover)	<b>0.21</b>	0.08	-0.11	-0.07	0.11	-0.03	-0.01
Shade fescue <i>Festuca altissima</i>	<b>0.28</b>	0.05	-0.01	-0.05	0.05	0.06	-0.06
Ash (Canopy cover) <i>Fraxinus excelsior</i>	0.04	0.03	0.01	0.02	0.06	-0.10	0.03
Ash (Bush cover)	0.03	0.01	-0.02	-0.03	-0.01	0.01	0.05
Ash (Grass cover)	0.08	0.03	-0.02	-0.02	0.00	0.13	-0.11
English ivy (Grass cover) <i>Hedera helix</i>	0.18	0.00	-0.01	-0.01	-0.05	0.01	0.16
Wood rush cover <i>Luzula sylvatica</i>	<b>-0.21</b>	0.16	<b>0.39</b>	0.03	<b>0.41</b>	<b>0.48</b>	0.02
Dog's mercury cover <i>Mercurialis perennis</i>	<b>0.29</b>	0.01	0.07	0.00	0.02	0.05	0.01
Millet grass cover <i>Milium effusum</i>	0.01	-0.02	-0.03	-0.01	0.00	0.04	-0.02
Spruce (Canopy cover) <i>Picea excelsia</i>	-0.17	-0.03	0.03	-0.04	0.07	-0.15	0.16
Spruce (Bush cover)	-0.10	0.04	0.05	-0.01	0.06	0.06	-0.04
Spruce (Grass cover)	-0.07	-0.02	0.01	0.03	-0.02	0.01	0.01
Blackberry <i>Rubus fruticosus</i>	0.15	0.00	0.00	-0.06	0.03	-0.04	0.06
Red raspberry (Bush cover) <i>Rubus ideaus</i>	0.01	0.02	0.02	0.03	0.08	0.03	-0.02
Red raspberry (Grass cover)	0.03	-0.02	0.06	-0.03	0.00	-0.01	-0.01
Bilberry <i>Vaccinium myrtillus</i>	<b>-0.22</b>	-0.05	0.06	-0.03	-0.08	0.04	-0.04
<b>Land-use home-range scale variables</b>							
Forest (Density)	<b>0.33</b>	<b>-0.68</b>	<b>0.22</b>	<b>0.46</b>	0.00	0.07	-0.07
Open forest (Density)	-0.15	-0.02	-0.30	0.17	0.16	0.02	-0.29
Alpage (Density)	<b>-0.28</b>	<b>-0.25</b>	-0.10	<b>0.43</b>	0.05	-0.16	<b>0.36</b>
Orchard (Distance)	<b>-0.23</b>	<b>-0.39</b>	0.11	<b>-0.47</b>	<b>0.29</b>	-0.13	-0.20
Meadow and agriculture (Density)	0.01	<b>-0.25</b>	<b>0.23</b>	<b>0.33</b>	<b>0.21</b>	-0.15	<b>-0.27</b>
Pasture (Density)	0.01	0.02	-0.01	-0.02	0.06	-0.05	0.11
Edge Forest-Pasture	0.06	-0.03	0.01	<b>-0.35</b>	0.08	0.00	0.04
<b>Disturbance home-range scale variables</b>							
Parkings (Distance)	-0.03	0.03	<b>-0.42</b>	-0.04	<b>0.44</b>	0.05	<b>0.35</b>
Buildings (Distance)	0.06	-0.02	-0.09	-0.19	<b>-0.38</b>	<b>0.34</b>	<b>0.54</b>
Roads (Distance)	-0.07	0.00	-0.02	0.03	0.08	0.00	-0.05
1 Class roads (Distance)	-0.12	0.02	0.31	0.04	-0.19	-0.15	-0.01
2 Class roads (Distance)	0.06	0.39	0.53	-0.03	-0.04	-0.59	-0.23
3 Class roads (Distance)	-0.13	0.06	0.03	0.02	-0.04	-0.01	0.01
4 Class roads (Distance)	-0.16	-0.06	0.03	0.05	-0.15	0.01	0.01
Forest layers (Distance)	0.05	0.02	0.02	-0.01	-0.02	0.01	0.05
Walking ways (Distance)	-0.06	-0.03	0.05	0.04	-0.10	0.03	0.09
Wild boar hunting index	<b>0.22</b>	0.18	-0.11	-0.16	<b>0.40</b>	-0.05	0.12



**Figure 3-4:** a) Summer and b) winter red deer habitat suitability maps in the Swiss Jura mountains, as computed by ENFA. Summer and winter distribution maps used to construct the HS model are indicated with diagonal polygons. Summer habitat suitability maps based only on c) disturbance variables and d) vegetation variables.

## 3.6. Discussion

### 3.6.1. *Model strength and weakness*

Models that predict species occurrence are based on specific assumptions. Consequently they have their own limitations and should be used according to the study objectives (Guisan and Zimmermann 2000).

Our first objective was to characterize current red deer habitat use. In the case of a spreading species, we are unable to assess absence data (i.e. not yet visited) and therefore, analyzes based on absence data cannot be used. We chose ENFA because it avoids this bias (Hirzel et al. 2002, Zaniewski et al. 2002) and because Hirzel et al. (2001) showed that ENFA is robust in the case of an expanding species. Our second objective was to construct a model that predicts areas that red deer will colonize in the future. We used presence data from a limited part of our study area to construct a HS model that was used to extrapolate the expected distribution on the other part. At present, we cannot validate the model with an independent data set, as we do not have further data on the recolonization of the region by red deer. Nevertheless, we suggest that our model reliably predicts suitable areas beyond the current species range for two reasons. First, the actual distribution is not the result of a colonization process limited by barriers. The whole study area is available to red deer, a fact supported by presence indices found outside the present distribution. Secondly, landscape beyond the actual range is similar to the landscape actually colonized (Hegg et al. 1993) and, consequently, no landscape heterogeneity is expected to bias model results or limit model performances (Osborne and Suarez-Seoane 2002). We therefore suggest that the red deer population simply needs more time to settle down in new areas. Assuming that landscape and red deer habitat use will not change, we will be able to verify this assessment in the future.

### 3.6.2. *Red deer habitat selection*

We hypothesized that red deer distribution may be related to vegetation, topography and human disturbance factors at both local and home range scales. Our analysis successfully predicted the correlation between these factors and the current distribution in the Swiss Jura Mountains.

Several home range scale variables, among those describing land-use had high scores on marginality and specialization axes, while only a few local variables had high scores that are essentially correlated to the marginality axis. This indicates that home range scale variables mainly characterize red deer population habitat choices and that habitat choice is less sensitive to local variables. Our results offer additional insight into red deer ecology and requirements in the Swiss Jura Mountains. We therefore suggest that red deer may be considered to perceive their environment at different scales to establish their populations. In this way, our results are consistent with Manel et al. (1999) and Karl et al. (2000) who predicted that habitat selection models might be enhanced using several analysis scales.

During both seasons, but particularly in winter, we found a negative correlation with human disturbance variables. Forest plots with deer were situated at higher distances from human disturbance factors such as roads, buildings and parking, than forest plots without deer. These results are consistent with previous findings on established populations in different countries. Several authors have shown (Edge et al. 1987, Cole et al. 1997, Morellet et al. 1996, Rowland et al. 2000) that roads are avoided by elk (*Cervus elaphus nelsonii*) in United States and red deer in France, suggesting that road avoidance by *Cervus elaphus* is a widespread phenomenon. Surprisingly, no previous work incorporated the distance to the source of disturbance (e.g. building areas) as an indicator of human perturbation. Further analysis should possibly consider cost distances from the source of perturbations to deer locations, with travel cost values per habitat types. For instance, Wang and Manning (1999) simulated a disturbance index for recreation management purposes. Unfortunately much basic information on roads, such as frequency of use, is usually not available in current databases and therefore had to be measured in the field.

Fewer roe deer were culled in the red deer summer range than in the whole study area. We believe that this result is due to an effective lower hunting pressure in these areas, because roe deer counting revealed no difference in density between the two areas (Centre de Conservation de la Faune, *unpublished data*). According to our results, a high wild boar hunting index predicts a high winter suitability value for red deer. We suggest that the wild boar hunting index is likely to give a better indication of similar habitat requirements between wild boar and red deer than a hunting pressure index. During wintertime, hunters use snow tracks to encircle wild boars whereas in summer, hunters surround forests where they only

expect to find roe deer. Therefore, red deer may be less disturbed during winter than during summer.

We used several plant covers as local variables. We chose consumed plant species (e.g. Fescue, Red raspberry, see Gebert and Verheyden-Tixier 2001) or factors that reflect forest structure such as canopy cover. Presence of red deer in our study area is clearly associated to forests with *Festuca altissima*, red raspberry or fir. Other local variables were also important and some of them, although known to be consumed, appear to be negatively correlated with red deer occurrence. In these cases, we can not exclude that some local variables are indirect predictors of such habitat types rather than direct (resource consumed) predictors. As an example, we found that in summer, red deer forest plots have a low cover of English ivy (summer marginality score: -0.15), a species fed upon wintertime. Red deer certainly do not avoid these English ivy forests but select other forest types at higher altitude where this plant does not grow. Although it is a drawback of modeling approaches (Guisan and Zimmermann 2000), we do not need to infer causality for habitat relationships of a red deer to reach our objectives.

Analyses with two temporal scales were obviously needed as confirmed by our results that reveal a different habitat selection pattern between seasons. According to our model, suitable winter habitats are situated in beech forest at lower altitudes, probably as snow depth constrains use at higher elevations. A low level of disturbance is also of importance. In summer, suitable areas were located in the less disturbed open forests and at higher elevation.

### **3.7. Management implications**

Human disturbance is a factor that limits distribution of red deer in the Swiss Jura Mountains. Distance to roads or building areas and probably roe deer hunting index may spatially measure human disturbance. In this way, sources of human disturbance may be integrated into management decisions. However, despite the importance of this factor, managers must account for the combination of other relevant habitat features that vary by scale and season.

Our separate analysis with different kind of variables, such as disturbance or habitat variables provides useful tools for managers. This may help to discriminate spatially why the habitat in a focus area is suitable or unsuitable.

Although our models reveal good performances, their predictions beyond current deer range are subject to caution. At present, only a few modeling approaches have been adequately validated outside their calibration range (Roloff et al. 2001, Guisan et al. 2002). ENFA seems to overestimate HS values (Zaniewski et al. 2002), which is probably preferable than underestimating the potential range of a problematic species. On the other hand, one should be aware of the negative consequences on the level of politics confidence. Winter and summer analyses have revealed important spatial differences regarding suitable habitats. This information is important for managers, e.g. as a geographical combination of wide suitable summer ranges with limited suitable winter ranges may lead to deer overabundance and high level of forest, meadow and grassland damage during winter time. Such a combination of maps should allow managers to anticipate such problems.

## 4. HIERARCHICAL BED-SITE SELECTION FOR AN EXPANDING RED DEER POPULATION

---

*Landscape and home range selection level / population to fine scale*

### 4.1. Summary

- 1) Red deer (*Cervus elaphus*) are currently recolonizing the Jura Mountains. Wildlife managers require management options that consider spatial and temporal colonization possibilities to handle the risks associated with an expanding red deer population.
- 2) During two years, winter and summer habitat selection were assessed at two selection levels in order to describe the species actual distribution and analyze the factors determining it. Second-order selection level (landscape-population) was measured by comparing random plots inside presence range with random plots over the study area. Third-order selection level (population-individual) was evaluated by comparing bedding sites with random plots inside presence range.
- 3) An overall hierarchical habitat selection pattern was observed. We found that habitat variables measured at home range scale, e.g. frequency of open forests or distance to main roads, were the most relevant at the second order selection level. At the third-order selection level, microhabitat features were important, i.e. low visibility, high herbaceous cover in summer and high solar radiation during winter mornings.
- 4) We suggest favoring mixed open forests in the less disturbed area to improve red deer management and limit potential red deer forest conflicts.
- 5) Our results suggest that red deer establish their populations according to home range scale variables, but locate them, within their distribution range, on a local scale basis. This result reinforces the importance of multi-scale analysis of hierarchical habitat selection processes to improve red deer management measures.

## **4.2. Introduction**

Red deer (*Cervus elaphus*) are currently recolonizing the Jura Mountains. This picturesque icon of wildlife provides recreational opportunities for hunters, artists and a large section of the public (DeCalesta and Stout 2000) but on the other hand red deer may seriously negatively impact forests and meadows (Gill 1992, Putman and Moore 1998). It may be also a threat to human safety (e.g. vehicle collisions) (Groot Bruinderink and Hazebroek 1996). Local managers require wildlife management options that consider spatial and temporal colonization possibilities to handle the risks associated with an expanding red deer population.

Several studies on established *Cervus elaphus* populations have shown the importance of two main factors: human disturbance (Petraik 1996) and habitat composition (Morellet et al. 1996). Human disturbances (i.e. noise, hunting, ..) seriously modify behavior (Hodgetts et al. 1998, Sibbald et al. 2001) and consequently, movements (Conner et al. 2001), distribution (Millspaugh, et al. 2000) and reproduction (Phillips and Alldredge 2000). Red deer need quiet place with food supply (Roloff et al. 2001) mainly of herbaceous plants (Gebert and Verheyden-Tixier 2001). At a finer scale, red deer location may be influenced by micro-climate (Mysterud and Ostbye 1999) such as thermal cover (Millspaugh et al.1998, Chen et al.1999) that is closely linked with energy budget. However, habitat selection by colonizing populations of red deer is poorly documented in contrast to established populations. Therefore, red deer habitat use needs to be better described in our study area. This knowledge is essential to guide managers and improve efficiency of species management or conservation plans that depend closely on the quality of our understanding of its habitat requirement (Mooty et al. 1987).

Our goal is to assess winter and summer habitat requirements at two selection levels in order to describe the species actual distribution and analyze the factors determining it. We performed our analysis during two consecutive years, and discuss results regarding management implications.



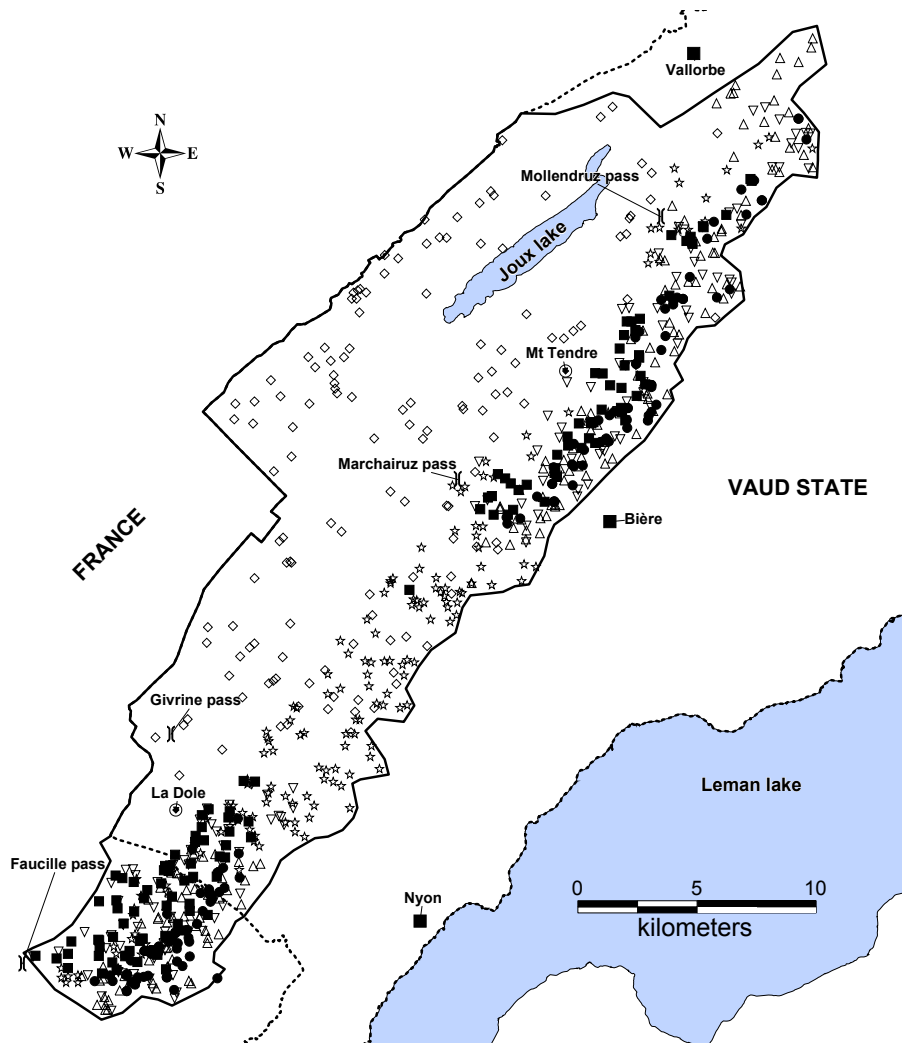
## 4.3. Methods

### 4.3.1. Overview

We limited our study area to the Jura Mountains in Vaud state (Switzerland) and nearby France, between the Faucille pass (F, Ain) and Vallorbe (CH, Vaud). This area includes two well-defined distinct population ranges (see Chapter 2 and 3).

Our sampling design is based on summer and winter hierarchical habitat selection (Section 1.5.2). Failure to consider habitat selection as a hierarchical process may possibly result in misleading notion of habitat selection patterns (McLoughin et al. 2002). In the presence ranges (PR) and in absence regions (AR), forest stand plots were randomly selected. In the presence range, one bedding site (BS) was sampled per km<sup>2</sup>. For each forest stand or bedding site, several habitat variables were measured in the field or derived from geographic information systems (GIS). Johnson's (1980) second-order selection level (*landscape selection level*) was measured by comparing AR and PR. Third-order selection level (*home range selection level*) was evaluated by comparing PR and BS. To test for bedding site selection, we used univariate and multivariate analyses. We performed the same sampling (described in the next section) over two consecutive years.

Because large herbivores interact with their environment at a variety of spatial and temporal scales (Senft et al. 1987, Turner et al. 1997), recent works have emphasized the importance of scale-dependent habitat selection processes and recommend use of more than one spatial and temporal scale (Edge et al. 1987, Storch 1997, Apps et al. 2001, Jaberg and Guisan 2001). In many cases, multi-scale studies improved the model result (Wiens 1989, Karl et al. 2000, Rotenburry et al. 2002). We therefore analyzed red deer habitat use for two seasons and used micro to population scales ecological descriptors.



**Figure 4-1:** Study area and sample plots for red deer hierarchical habitat selection in the Jura Mountains (1999-2001). Summer (black squares) and winter (black circles) bed sites, summer (inverse triangles) and winter (triangles) random points inside red deer range, summer (diamonds) and winter (stars) random plots outside red deer range.

#### 4.3.2. Data

##### *Sampling design*

Previous fieldwork allowed construction of two precise expert distribution maps for summer and winter (Chapter 2, 3). During the last ten years, red deer indices were found over all the study area (Patthey 2003). However, during winter, no indices were found in the western part, where snowfall is probably too high for red deer wintering. Moreover, previous analyses (Chapter 3) reveal that only the eastern slopes of the Jura Mountains are suitable for wintering. Consequently, we excluded the western part as available winter forest in order to limit broad scale landscape heterogeneity and

improve our model performance (Osborne and Suarez-Seoane 2002). A stratified random sampling was performed to select AR and PR plots. As no bedding sites were found outside forested areas, the random sampling was applied only on forests. Elevation classes of 100 meters were used as strata to have a good representation of all the forested landscape. We checked for absence of species indices at all sample points.

Red deer presence ranges were divided into 1 km<sup>2</sup> squares (KS) according to the Swiss federal topography office grid. We chose a KS size equivalent to a seasonal red deer home range (Hamann et al. 1997, Klein and Hamann 1999) in order to limit potential pseudo-replication and spatial autocorrelation effects. For the same reason, contiguous KS were sampled in the shorter practicable time (generally 0-1 day) limiting pseudo-replication (two bedding sites from the same individual). Searching time per KS was limited to two hours to standardize sampling effort. We attempted to find one male and one female bedding site per KS.

In winter, during day time red deer feed near bed sites, although at night they frequently move far away to a selected main feeding station, generally at lower altitude (This study, unpublished data). To locate winter bed sites, we began our search after snowfall by walking along the lower isoclines of the KS to find a red deer trail that we next backtracked. If we did not find a track, other isoclines were followed at up to 4 isoclines per KS (which took approximatively two hours). We believed that we found mainly diurnal bed sites. During summer, we assigned a bed site if at least one red deer indice (i.e. feces, evidence of browsing, hair) was found in the vicinity. Whenever possible, we sexed indices. Within a bedding site, beds were marked and numbered, and measurements were taken later. One bed per bedding site was chosen randomly. We used a GPS, a compass and an altimeter to find bedding site coordinates and location of random plots with a precision of about 10 meters. Bedding site search was performed from mid-January to the end of February in 2000 and 2001, and during July and August months in 2000 and 2001. During these periods, female and male red deer home ranges are generally stable (Hamann et al. 1997, Klein and Hamann 1999, Patthey 2003). We found respectively 60 and 62 summer bed sites over 116 KS prospected, and 51 and 52 winter bedding sites over 116 KS sampled. We sampled 60-100 AR and PR sites were sampled per year, but because of some

missing data, fewer random sites were used in particular analyzes. More random sites were sampled than bedding sites because a larger sample was required to adequately describe the available forested landscape of our study area.

We tried, but failed, to find one male and one female bedding site per KS. Not enough males were present during the study period and in winter they formed small groups, reducing sample size.

### *Habitat factors*

On each plot, we measured *micro* and *local scale variables* (Figure 1-5) in the field or derived several broader scale variables with the help of GIS that might be relevant for red deer including topographical, food, microclimate, forest stand structure and potential human disturbance variables.

Altitude, aspect and slope were measured with altimeter, GPS and compass. Aspect was transformed into two continuous (0 to 1) variables depicting North to South and East to West aspects. Amount and arrangement of cover provides food and protection against adverse weather and predators. Percent canopy cover, ground cover under 1m, understory between 1-2 m and 2-5 meters and cover for 14 plant species were estimated within a 10 meter radius centered on the plot. We estimated percentage covers by eye with a 5% precision with the help of a conversion table. Plant species or groups of plant species were chosen according to their potential use as food (i.e. understory maple, grass), thermal cover (i.e. coniferous species) or key species for forest typology (Delarze et al. 1998). Deer probably choose a bedding site taking also into account fine microclimate features. Vegetation cover just over the bedding site (<2m) in a one-meter radius circle was also estimated. In order to have an estimate of potential solar energy on the bedding site during daytime, we used a solar compass (Appendix 13-1) which principle is based on the spherical densiometer (Higgins et al. 1996). The solar compass uses a curved, semi-transparent, mirror that reflects the overstory and canopy. Under the mirror, a daytime /month table is used to estimate when the sun arrives (> 50% exposure of each grid) on the sample point at the day hour and month in consideration. The grid contains squares for each hour (i.e. 8h-9h) of the day and for each month of the year. We next evaluated the proportion of the square that is covered by sun. Five cover classes from 0 (shaded) to 1 (sunny) were

used and the solar compass was employed only in summer and winter 2000. Visual obstruction caused by vegetation may be functionally important to wildlife, both as hiding cover (i.e. to allow a safe escape) and as thermal cover (i.e. barrier to wind). We estimated visual obstruction from a deer point of view. In this case, visibility was measured in four orthogonal directions (isoclines and slope). Visibility is defined as the maximum distance at which a dog or a human can be seen moving through a 1 meter precision distance binocular (Bushnell Yardage-Pro 400). The measure was performed at one-meter height. Mean visibility distance and its standard error, which indicates habitat heterogeneity, were calculated. For each plot, we evaluated a homogeneity value (subjective value from 1 to 3, homogeneous to heterogeneous) that reflects plot consistency against surrounding forest (Morellet et al. 1996). We also assessed a subjective penetrability value from 1 to 5, impenetrable to penetrable (Morellet et al. 1996).

We used a GIS to derive several *broad scale variables* (Figure 1-5) including *home range scale variables* such as density of habitat types inside 1 km (seasonal home range size) radius circles and several *population scale variables* in 5 km (approximation of a population home range) radius circles. We used the Leman Council database to define five potentially relevant habitat types with a one-hectare grain. Human disturbance factors influenced red deer distribution as they may be considered as a predation risk (Frid and Dill 2002). Roads are stored as vectors into the VECTOR25 GIS database. Distances to six specified types of roads and all roads were calculated with a 10 meter precision via a rasterization. We also calculated the size of the polygon free of roads around each plot and distance to building areas.

#### 4.3.3. *Statistical analysis*

We performed t-tests for unequal variance on some individual variables to test for difference in means between groups after square root transformation of distance variables and arsine transformation of frequencies variables. We used a more conservative value of  $P < 0.01$  to determine statistical differences. In our case an even smaller  $P$  value would be justified. Using the Bonferroni adjustment method to reduce the chance of type I errors (Sokal and Rolf 1996), the  $P$  value might be equal to 0.0021 for 50 variables. Such a conservative probability value would virtually preclude inferring that any observed differences were statistically significant (Meyer

et al. 1998); we therefore chose a priori a low error probability of 0.01, accepting the consequence of having lower power. We compared difference, homogeneity and penetrability between random plots and bedding sites with  $\chi^2$  tests (Sokal and Rolf 1996). We used a t-test on arcsine transformed sun exposure cover with unequal variance to examine difference between bed sites and random plots.

Univariate analyses do not take into account the multivariate structure of data. Therefore we used the ENFA analysis to identify the combination of variables that best separated bedding sites from random sites (Chapter 1.6.3). Before analyses, we normalized all of our variables if they were not. When we observed high correlations between one or more variables, one variable was selected according to its facility to reflect ecological meaning and the other removed. If variables were not sufficiently continuous, the variable was removed. Numbers of factors for habitat suitability computation were chosen according to the broken-stick method (Hirzel et al. 2002). The calibration-validation modeling process was done using the Jack-knife cross-validation method (See section 1.6.3).

To compare habitats inside and outside red deer areas, we pooled data over years, as we found no bedding site in the second survey on a random plot of the first survey. Bedding sites from the 2 years were considered as independent samples, although some bias may result from different bedding sites used by the same individuals.

We assumed that micro-scale variables did not affect population level habitat selection, as habitat diversity is high enough to provide microhabitat features. We therefore included micro-scale variables only in the home range selection level analyses.

The stratified random samplings were performed with StratSampler (Patthey 2002), data rasterization and distance calculation with Idrisi32 (Eastmann 2001), data extraction with ValueExtractor (Patthey 2002), circular analysis and ENFA computations with the BioMapper package (Hirzel et al. 2002).

**Table 4-1** : Description of the variables recorded at red deer bed site and random plots in the Jura Mountains, 1999-2001

<b>Variable</b>	<b>Description</b>	<b>Variable</b>	<b>Description</b>
<b>Local scale variables (in 10m radius circle)</b>		<b>Topographical variables</b>	
Canopy	Canopy cover (%)	Elev	Elevation (m)
SubCanopy	Subcanopy cover (%)	Asp.N	North to South aspect (0 to 1)
UnStory1	Bush (1-2m) cover (%)	Asp.E	East to West aspect (0 to 1)
UnStory2	Bush cover (2-5) cover (%)	Slope	Slope (°)
Grass	Grass cover (%)	<b>Disturbance variables</b>	
FirCan	Fir canopy cover (%)	Road1	Distance to 1 class road (m)
SpruCan	Spruce canopy cover (%)	Road2	Distance to 2 class road (m)
DecCan	Deciduous canopy cover (%)	Road3	Distance to 3 class road (m)
FirSCan	Fir subcanopy cover (%)	Road4	Distance to 4 class road (m)
SpruSCan	Spruce subcanopy cover (%)	Road5	Distance to forest layers (m)
DecSCan	Deciduous subcanopy cover (%)	Road6	Distance to walking ways (m)
ConBush	Coniferous bush cover (%)	RoadAll	Distance to all class roads (m)
FirBush	Fir bush cover (%)	RoadFree	Area free of roads (ha)
SpruBush	Spruce bush cover (%)	BuiltDist	Distance to building areas (m)
BeeBush	Beech bush cover (%)	Built10	Proportion of buildings inside a 1 km radius (%)
MappBush	Mapple bush cover (%)	Built50	Proportion of buildings inside a 5 km radius (%)
FirGrass	Fir grass cover (%)	<b>Broad scale variables</b>	
SpruGrass	Spruce grass cover (%)	Mead10	Proportion of meadow-agriculture inside a 1 km radius (%)
BeeGrass	Beech grass cover (%)	For10	Proportion of forests inside a 1 km radius (%)
MappGrass	Mapple grass cover (%)	OpFor10	Proportion of open forest inside a 1 km radius (%)
BilGrass	Bilberry grass cover (%)	Past10	Proportion of pasture inside a 1 km radius (%)
BBerGrass	Blackberry grass cover (%)	Mead50	Proportion of meadow-agriculture inside a 5 km radius (%)
HeigGrass	Height grass cover (cm)	For50	Proportion of forests inside a 5 km radius (%)
RRasGrass	Red raspberry grass cover (%)	OpFor50	Proportion of open forest inside a 5 km radius (%)
VisMean	Visibility mean (m)	Past50	Proportion of pasture inside a 5 km radius (%)
VisSdev	Visibility standard deviation (m)		
<b>Micro-scales variables (in 1m radius circle)</b>			
BushO	Bush cover (%)		
ConO	Coniferous cover (%)		
DecO	Deciduous cover (%)		
Homo	Homogeneity (1-3)		
Pene	Penetrability (1-5)		

## **4.4. Results**

### ***4.4.1. Summer habitat selection***

#### *Population selection level*

Broad scale variables are the main factors that differ between habitat inside red deer summer presence range and habitats outside presence range (Table 4-2). Inside presence range, random plots have a significantly higher grass cover, a higher density of pastures and a lower density of agriculture.

ENFA revealed that forest plots inside red deer summer presence range are marginal compared to the study area (Appendix 13-2, marginality = 0.82). Marginality scores showed that winter distribution is correlated positively with disturbance factors and broad scales such as forest (0.25), and meadow density (0.41). In contrast, winter habitat have a lower density of pastures (-0.30,-0.39), lower spruce cover (-0.22), and are distant from walkways (-0.28). Disturbance factors, broad scale factors and some local scale variables such as spruce cover have high scores on specialization axes, showing sensitivity to any shift away from their optimal values.

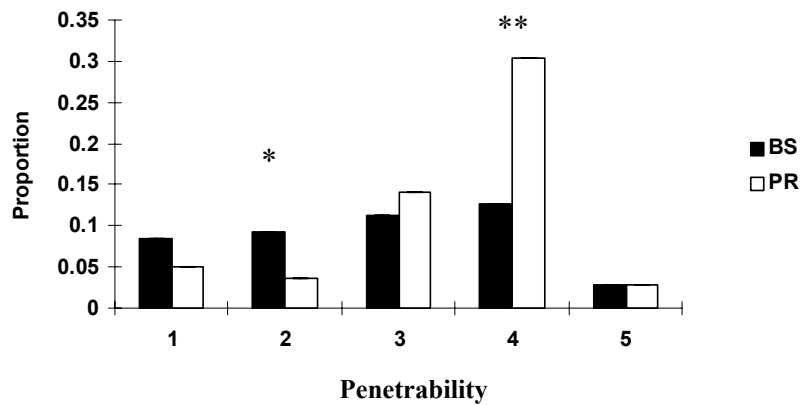
#### *Home range selection level during summers 2000 and 2001*

In summer, bedding sites are located at a higher elevation, have a higher cover of red raspberry, a higher amount (height and cover) of herbaceous plants, lower visibility, are more distant to disturbance factors (roads and buildings) and are localized inside areas free of roads with high surfaces and open forest (Table 4-4). They also have a lower cover of agricultural land.

According to ENFA, bed site habitat is marginal from habitat inside red deer presence range (Appendix 13-2, marginality= 0.52 and 0.88). According to the marginality axis, favorable bed sites were situated at a higher elevation (scores 2000:0.28, 2001:0.24), have a higher grass height (0.30, 0.28) and red raspberry cover (0.19, 0.21) as well as lower agriculture density and visibility (-0.18, -0.22). Overall, disturbance factors were lower in the winter presence range than in the whole study area. Broad scale factors showed a high sensitivity to shifts away from their optimal values in both years, disturbance factors only in 2000 and local scales factors in 2001, according to their scores on specialization axes.



Bedding sites penetrability distribution is different overall from random plots, in both summers 2000 ( $\chi^2$ ,  $p < 0.01$ ) and 2001 ( $\chi^2$ ,  $p < 0.001$ ). Bedding sites are globally less penetrable than AR plots (Figure 4-2). No differences in solar radiation exposure were observed.



**Figure 4-2** : Penetrability pattern on summer red deer bedding site (BS) and on random plots (PR) in the Jura Mountains, 2001. Penetrability varies from 1 (impenetrable) to 5 (penetrable). Overall distribution differs ( $\chi^2$ ,  $p < 0.001$ ). Distribution differences were tests by  $\chi^2$  tests : \*  $p < 0.05$ , \*\*  $p < 0.01$ .

#### 4.4.2. Winter habitat selection

##### *Population selection level*

Broad scale variables and disturbance factors are the factors that differ the greatest between habitats inside red deer presence range and habitats outside red deer presence range (Table 4-3). Inside presence range, random plots have a lower density of buildings and pastures, and are more distant to second-class roads and high densities of agricultural lands and forests.

ENFA revealed that forest plots inside winter red deer presence range are marginal compared to the study area (Appendix 13-2 A, marginality = 0.48). Marginality scores showed that winter distribution is positively correlated with disturbance factors and broad scales variables such as distance from second-class road (0.25) and density of meadows and agriculture (0.53). In contrast, winter habitats have a lower density of buildings (-0.21,-0.22), forest (-0.29) and pasture (-0.31,-0.27). Disturbance factors, broad scale factors and some local scale variables such as visibility, spruce and maple cover have high scores on specialization axes, showing sensitivity to any shift away from their optimal values.

**Table 4-2:** Environmental variables (untransformed) recorded at random points inside red deer absence range and at random points inside red deer presence range during summer in the Jura Mountains (2000-2001) with means independently significant. Differences were examined with t-tests. Significant level are indicated as \*p<0.01, significances with Bonferonni adjustments were indicated as \*\* P<0.05, \*\*\* P<0.01, \*\*\*\*P<0.001. For complete results, see appendix 13-3.

Variables	T-test		Absence range		Presence range	
	t	P	Mean	SD	Mean	SD
<b>Local scale variables</b>						
Grass	-3.31	0.00107 **	36.96	34.91	51.18	37.74
DecCan	2.19	0.02959	16.83	21.12	11.94	16.18
<b>Disturbance variables</b>						
Road2	-2.29	0.02256	1808.71	1125.47	2132.04	1182.11
<b>Broad scale variables</b>						
For10	2.17	0.03093	74.01	23.16	65.97	27.84
OpFor10	-2.26	0.02444	5.05	10.39	8.43	13.88
Past10	-3.11	0.00209 *	12.57	14.39	18.75	18.30
Mead50	2.92	0.00376 *	19.01	11.26	15.16	10.32
Past50	-2.74	0.00651 *	17.02	7.78	19.80	8.88

**Table 4-3:** Environmental variables (untransformed) recorded at random points inside red deer absence range and at random points inside red deer presence range during winter in the Jura Mountains (1999-2000) with means independently significant. Differences were examined with t-tests. Significant level are indicated as \*p<0.01, significances with Bonferonni adjustments were indicated as \*\* P<0.05, \*\*\* P<0.01, \*\*\*\*P<0.001. For complete results, see appendix 13-3.

Variables	T-test		Absence range		Presence range	
	t	P	Mean	SD	Mean	SD
<b>Local scale variables</b>						
SpruBush	2.00	0.04653	0.84	2.63	0.40	0.97
MappBush	2.54	0.01206	0.38	1.29	0.11	0.39
<b>Topographical variables</b>						
Slope	-2.04	0.04231	14.99	11.96	17.65	11.62
<b>Disturbance variables</b>						
Road2	-3.88	0.00013 ***	1470.70	1143.98	1945.09	1211.82
Road5	-2.01	0.04552	147.40	107.13	179.78	137.59
Built10	4.61	0.00001 ****	3.56	6.48	1.02	2.53
Built50	5.62	0.00000 ****	4.67	2.83	3.28	1.36
<b>Broad scale variables</b>						
Mead10	-2.62	0.00912	7.66	12.84	11.74	15.01
For10	-2.21	0.02784	74.72	21.06	79.42	18.87
Past10	4.42	0.00001 ****	11.23	13.46	5.40	9.36
Mead50	-8.73	0.00000 ****	20.35	8.68	28.03	7.04
For50	5.46	0.00000 ****	56.08	7.09	50.95	9.44
Past50	4.68	0.00000 ****	14.52	5.95	11.59	5.37

**Table 4-4:** Environmental variables (untransformed) recorded at red deer bed sites and at random points inside red deer range during summer 2000 and 2001 in the Jura Mountains with means independently significant. Differences were examined with t-tests. Significant level are indicated as \* $p < 0.01$ , significances with Bonferonni adjustments were indicated as \*\*  $P < 0.05$ , \*\*\*  $P < 0.01$ , \*\*\*\* $P < 0.001$ . For complete results, see appendix 13-3.

Variables	SUMMER 2000						SUMMER 2001							
	T-test		Bed site		Presence range		T-test		Bed site		Presence range			
	t	P	Mean	SD	Mean	SD	t	P	Mean	SD	Mean	SD		
<b>Local scale variables</b>														
Canopy	-0.15	0.87971	36.83	24.40	37.61	25.45	-3.02	0.00297	*	26.49	19.31	37.61	26.40	
FirCan	-0.85	0.39618	6.75	11.88	8.91	15.60	-1.99	0.04868		3.19	6.03	6.18	11.62	
DecCan	0.06	0.94969	15.23	19.29	15.15	18.48	-2.27	0.02449		14.95	15.96	22.39	23.18	
MappBush	-0.12	0.90783	0.93	2.19	0.98	2.19	3.15	0.00234	*	2.94	5.23	0.73	2.09	
GrassGrass	a						3.65	0.00045	**	3.32	4.21	1.22	1.96	
RRasGrass	2.09	0.04072	3.48	8.84	0.98	2.53	2.43	0.01788		4.60	11.78	0.82	3.08	
HeigGrass	3.29	0.00133	*	0.44	0.25	0.29	0.22	3.35	0.00108	*	0.52	0.50	0.24	0.43
ConO	3.28	0.00153	*	24.25	39.84	5.46	18.69	2.52	0.01360		10.86	16.66	4.94	9.22
DecO	1.66	0.09897	16.32	32.23	6.85	23.07	-3.44	0.00080	**	3.27	4.97	7.95	10.74	
VisMean	-2.09	0.03916	17.45	12.78	28.85	26.01	-4.56	0.00001	****	13.84	7.21	22.41	12.63	
VisSdev	-2.85	0.00584	*	7.82	8.05	17.04	22.51	-1.52	0.13201		8.21	5.56	10.14	7.47
<b>Topographical variables</b>														
Elev	3.22	0.00176	*	1262.50	157.69	1139.39	237.47	4.94	0.00000	****	1264.35	136.83	1118.38	220.76
Slope	-1.07	0.28625		16.17	12.78	18.72	12.65	-2.81	0.00577	*	23.02	7.91	26.84	8.25
<b>Disturbance variables</b>														
Road1	2.41	0.01773	2262.93	1346.80	1673.59	1130.69	0.19	0.84962		2072.57	1397.77	1995.59	1323.65	
Road2	0.78	0.43776	2411.33	1136.92	2266.00	1300.52	2.68	0.00824	*	2244.38	1113.87	1733.11	1176.54	
Road4	0.83	0.40936	401.87	366.96	368.94	410.59	3.71	0.00030	**	411.97	408.06	228.66	298.11	
RoadAll	2.73	0.00747	*	88.67	58.88	62.33	74.01	3.07	0.00258	*	69.48	42.07	50.32	54.55
RoadFree	-3.37	0.00130	*	20874.67	25230.12	13440.81	24248.72	2.25	0.02599		22938.65	27460.00	15278.18	22775.39
BuiltDist	3.00	0.00353	*	2029.55	619.07	1662.61	872.76	3.55	0.00052	**	1967.75	666.33	1549.59	762.01
Built10	-2.32	0.02397	0.03	0.26	0.48	1.40	-2.46	0.01586		0.10	0.35	0.58	1.71	
Built50	-1.14	0.25761	2.62	1.30	2.96	1.86	-2.41	0.01736		2.60	1.36	3.24	1.79	
<b>Broad scale variables</b>														
Mead10	-3.64	0.00059	**	1.40	2.60	8.83	14.65	-5.09	0.00000	****	1.25	1.91	8.43	12.27
Mead50	-2.14	0.03448	20.25	7.15	23.57	9.32	-3.99	0.00010	***	19.71	6.75	24.95	9.01	
Past50	1.05	0.29805	14.17	5.92	12.91	6.74	2.09	0.03806		14.97	5.25	13.09	5.40	

**Table 4-5:** Environmental variables (untransformed) recorded at red deer bed sites and at random points inside red deer range during winter 1999 and 2000 in the Jura Mountains with means independently significant. Differences were examined with t-tests. Significant level are indicated as \*p<0.01, significances with Bonferonni adjustments were indicated as \*\* P<0.05, \*\*\* P<0.01, \*\*\*\*P<0.001. For complete results, see appendix 13-3.

Variables	WINTER 1999						WINTER 2000					
	T-test		Bed site		Presence range		T-test		Bed site		Presence range	
	t	P	Mean	SD	Mean	SD	t	P	Mean	SD	Mean	SD
<b>Local scale variables</b>												
SubCanopy	3.47	0.00091 **	24.59	28.78	8.30	16.59	0.93	0.35141	6.38	7.27	5.16	7.55
FirCan	3.47	0.00109 **	11.67	21.35	0.36	1.18	1.90	0.05959	8.00	14.22	4.23	8.28
DecCan	-2.23	0.02738	6.86	16.62	14.71	20.11	1.37	0.17388	2.26	2.11	1.79	1.91
FirSCan	2.60	0.01216	9.04	23.48	0.15	0.68	1.31	0.19228	7.79	22.49	3.90	13.76
DecSCan	-2.44	0.01612	3.57	10.41	9.36	16.26	-1.32	0.19038	0.25	0.80	0.61	2.31
ConBush	3.24	0.00215 *	14.53	28.76	0.41	1.32	0.53	0.59531	3.19	5.17	2.70	5.19
FirBush	2.62	0.01175	10.27	25.06	0.30	1.11	-1.41	0.16170	1.13	1.54	1.97	5.11
SpruBush	1.68	0.09896	4.25	16.78	0.11	0.58	2.16	0.03336	2.08	5.24	0.74	1.20
MappBush	2.04	0.04626	0.27	0.92	0.01	0.10	-1.06	0.29292	0.16	0.40	0.23	0.54
BushO	a						2.47	0.01549	9.64	21.57	3.26	7.50
ConO	5.51	0.00000 ****	50.49	47.26	16.51	15.81	1.29	0.20033	10.99	20.73	6.43	18.42
DecO	-9.40	0.00000 ****	0.18	0.79	19.55	25.11	-1.93	0.05596	0.56	0.99	0.90	1.23
<b>Topographical variables</b>												
Asp.N	2.66	0.00895 *	0.70	0.22	0.58	0.29	0.56	0.57802	0.66	0.23	0.63	0.25
Slope	a						-4.13	0.00006 ***	13.19	7.03	18.87	10.52
<b>Disturbance variables</b>												
Road3	2.19	0.03072	287.14	196.96	230.91	213.78	-0.29	0.77288	287.77	229.29	298.39	233.77
RoadAll	4.21	0.00005 ***	76.80	45.27	48.34	40.34	1.77	0.07920	70.64	39.88	61.32	44.46
RoadFree	2.29	0.02435	22516.61	31275.95	11894.85	20411.76	0.84	0.40123	12270.09	19878.25	9736.70	15832.34
Built10	-0.51	0.60816	0.80	1.80	0.97	1.85	-2.30	0.02399	0.23	0.69	1.08	3.16
<b>Broad scale variables</b>												
For10	1.05	0.29702	80.71	21.99	77.47	20.43	3.72	0.00028 **	90.27	12.55	80.71	18.96
OpFor10	0.33	0.74247	1.98	4.46	1.68	5.64	-1.25	0.21407	1.05	3.55	1.79	3.97
Mead50	0.56	0.57928	30.00	8.05	29.33	6.23	2.74	0.00691 **	29.40	5.09	26.12	8.20
Past50	-0.33	0.74410	11.22	5.95	11.54	5.01	-2.55	0.01166	9.34	5.38	11.64	5.80

a, not recorded or missing values

*Home range selection level in winter 1999*

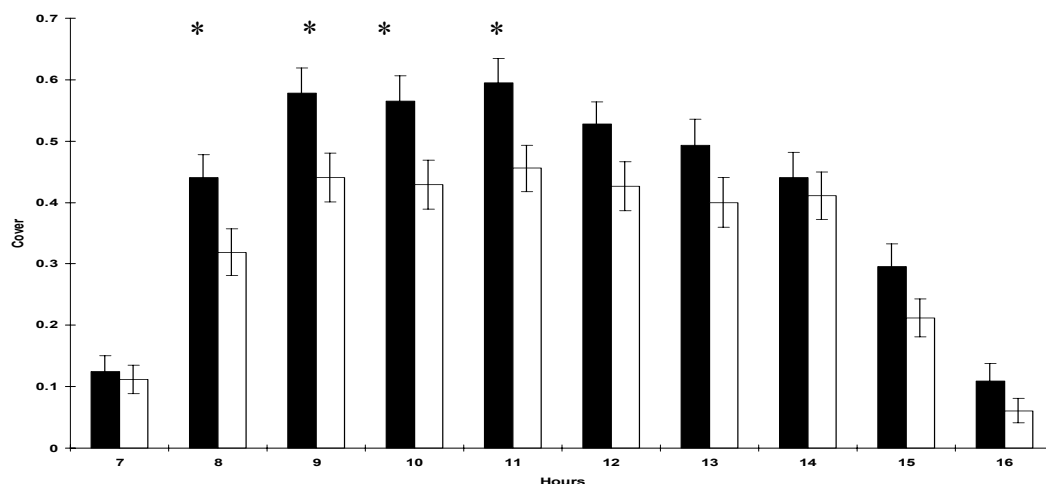
In the results for winter 1999, bed sites are more distant from all road-types, have a higher coniferous cover just over the bed, and a higher subcanopy, bush and Fir canopy cover than random points inside red deer range (Table 4-5). They are also more frequently exposed to south. Penetrability does not differ between PR and bedding sites ( $p>0.06$ ).

We excluded some variables as a consequence of high correlations. Red deer winter habitat was highly marginal (Appendix 13-2, marginality = 1.16). According to the marginality axis, favorable bed sites differ from random plots predominantly on local scale variables. Bed sites were surrounded with an overall higher cover of coniferous bushes, with a higher subcanopy cover (0.23) but with a lower spruce subcanopy cover. Both local scale variables and disturbance factors such as distance to buildings and density of buildings and broad scale variables showed a high sensitivity (tolerance=0.21) shift away from their optimal values, according to their scores on specialization axes.

*Home range selection level in winter 2000*

Univariate comparisons revealed that winter bed sites have a lower slope, a higher forest cover and higher agriculture density than random points (Table 4-5). Bed sites potentially received more solar radiation during winter mornings (Figure 4-6). Penetrability does not differ between PR and bedding sites ( $p>0.16$ ).

According to ENFA, winter bed site habitat is marginal (Appendix 13-2, marginality: 0.52) from habitat in random points inside red deer range. Marginality scores indicated that bed site distribution is positively correlated with a higher coniferous cover just over the bed (0.30), a higher forest (0.30) and agriculture density (0.28) and a higher heterogeneity (0.30). In contrast, bed sites have a lower slope (-0.31) and pasture density (-0.29).



**Figure 4-3:** Mean ( $\pm$ SE) sun exposure cover per daytime on red deer winter bed sites (black) and on random plots (white) inside red deer range in the Jura Mountains. Difference between means was tested on arcsine transformed values with t-test for unequal variance: \* $p < 0.05$ , \*\* $p < 0.01$ .

#### 4.4.3. Model evaluations

The ENFA models cross-validations revealed good performances (Table 4-6). Mean proportion of validation cells with a HS value greater than 50% is high (0.61-0.83) and significantly differs ( $p < 0.0001$ , bootstrap tests) from mean HS values expected if cells were randomly chose from the global distribution. Moreover, confidence intervals are relatively small.

**Table 4-6:** Results of ENFA models cross-validations (with seven k-fold partitions) for red deer in the Jura Mountains. On each jack-knife HS map, the following statistics are computed: a) the fraction of validation cells in the left out partition that have a HS value greater than 50, b) the fraction of validation cells in the left out partition that have a HS value greater than 50 with deduction of those cells that achieve this result by chance. This statistic assesses the *contrast* of the model by comparing whole validation cells to whole study area.

	Population selection level		Home range selection level			
	winter	summer	winter 1999	winter 2000	summer 2000	summer 2001
<b>Proportion of validation cells HS&gt; 50%</b>						
Mean	0.63	0.61	0.73	0.63	0.77	0.83
SD	0.06	0.11	0.19	0.13	0.12	0.10
90% confidence interval	[0.55, 0.71]	[0.45, 0.76]	[0.45, 0.96]	[0.45, 0.81]	[0.59, 0.89]	[0.70, 0.96]
<b>Probability of validation cells HS&gt;50% (bootstrap test)</b>						
Proportion	0.64	0.63	0.75	0.63	0.77	0.86
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
<b>Contrast</b>						
Mean	0.19	0.22	0.44	0.25	0.23	0.38
SD	0.06	0.09	0.18	0.12	0.09	0.09
90% confidence interval	[0.11, 0.26]	[0.09, 0.35]	[0.18, 0.64]	[0.08, 0.41]	[0.08, 0.32]	[0.26, 0.50]

## 4.5. Discussion

### 4.5.1. ENFA strengths and weaknesses

Choice of a multivariate presence/available modeling approach was guided by the necessity to cope with an expanding population in which we cannot assess absence data with certainty (Hirzel et al. 2002, Zaniwski et al. 2002). ENFA was preferred among other statistical approaches because of its robustness in the case of a spreading species (Hirzel et al. 2001). ENFA has another advantage; all variables included in the analysis are weighted, while in stepwise statistical approaches (i.e. GLM, GAM), the final model is a result of an “expert opinion” (Austin et al. 1984) where many trials are needed to find the “best” model. Some causal variables may be lost in the modeling process (Guisan and Zimmerman 2000, Zack 2001).

ENFA models provide fair to high model performances depending on season, year and level of selection (Table 4-6). We based our analysis only on a few presence sample points per year to avoid pseudo-replication and because population level is low. Model quality is sensitive to sample size (Hirzel and Guisan 2002) and robust models are difficult to construct with limited data. Moreover, validation of models with data from an expanding population, that are collected at a specific time, are difficult as some other sites are expected to be suitable.

### 4.5.2. Habitat selection overview

Habitat choice is the result of animal decisions that balance the trade-off between predation risk (human disturbances), foraging (resource richness) and climatic factors (reviewed by Myrnerud and Ostbye 1999). Theoretically, animals should select habitats that minimize the ratio of mortality risk to net energy intake (Lima and Dill 1990). Such decisions (i.e. leaving a rich place to a safer place) may be linked with the range for which animals can perceive key landscape elements (Lima and Zollner 1996). Moreover, individual red deer responses may be dependent on sex (Conradt et al. 2001), rank order (Clutton-brock et al. 1994), genotype (Coulson 1998) or resource distribution (Birtles 1998). Consequently, in our case, several factors may operate on red deer habitat selection. Thus we divide the discussion into several topics to make it more comprehensible, and summarize the topics in the section 4.6 “management applications”

#### **4.5.3. Hierarchical habitat selection**

At the population selection level (population range vs. study range), principally home range and population range scales variables have particularly high scores on marginality and specialization axes. At the home range selection level (bedding site vs. population range), micro, local, home range and population scale variables have high scores. Our results offer additional insight into red deer ecology and requirements in the Swiss Jura Mountains. We therefore suggest that Red deer may be considered: 1) to perceive their environment at different scales, 2) to establish their population ranges mainly on the basis of broad scales factors, and 3) inside the presence range, to select bedding sites according to several scales.

#### **4.5.4. Yearly habitat selection**

ENFA models at the home range selection level (bedding site vs. population range) differ between years. Some studies have already revealed that habitat use for a focus species may change with respect to time (Jonhson and Krohn 2002, Boyce et al. 2002). We suggest in our case that the contrasting weathers between the two annual surveys may have an impact on habitat choice. Ungulates may have different strategies to deal with the trade-off between foraging, predation risk and exposure to thermal extremes. Habitat choice for red deer may depend on weather (Merril 1991, Conradt et al. 2000). During high snowfall as in winter 1999 or cold and wet summers as in 2000, they may favor climate protection over predation risk. Although we have calibrated field measurements and bed site search, we may not completely exclude an observer effect.

#### **4.5.5. Seasonal habitat selection**

Our analyses clearly show a different seasonal habitat selection. This result is consistent with previous findings with ungulates in mountain areas (Georgii and Schroeder 1983, Koubek and Krabe 1996, Apps et al. 2001). In the Jura Mountains, snow cover may constrain use of higher altitudes, where lower temperatures, higher wind speeds and higher wind frequency occurrences may increase red deer energy expense. Changes in red deer habitat selection may reflect different strategies to meet habitat requirement.

We observed different habitat selection patterns among years (sections 4.4.1 and 4.4.2). Nevertheless, some variables are relevant for both years and thus reveal their particular importance (Johnson et al. 2002).



In summer, the higher density of open habitats (open forests, pasture) around bedding sites was probably the result of *Cervus elaphus* nutritional requirements. Open habitat components can be expected to have higher quantity and quality of forage, such as red raspberry and herbaceous plants. Our results are consistent with those of previous researches. Edge et al. (1987) differences observed between summer months in habitat use, and one of the main variables was the amount of foraging within 200m of each location. This also suggests that red deer eat during the daytime in the vicinity of the bedding-site (Hamann and Klein, unpublished data).

We also found an overall avoidance of disturbance factors such as roads and buildings during both seasons, but particularly during winter. Several authors have shown (Edge et al. 1987, Cole et al. 1997, Morellet et al. 1996, Rowland et al. 2000) that roads are avoided by elk (*Cervus elaphus nelsonnii*) in the United States, and red deer in France, supporting the view that road avoidance by *Cervus elaphus* is a widespread phenomenon. Although not mentioned in other studies, areas with a high density of buildings also have a negative impact on red deer distribution.

#### **4.5.6. Micro-climate selection**

Our results are consistent with previous findings and provide new insight into the role of habitat features in thermoregulation.

In temperate climates, Red deer survive cold winters with low food availability. Their body size combined with excellent fur insulation minimizes relative heat loss and energy requirements. Arnold et al. (*in prep*) have recently observed red deer hypometabolism associated with peripheral cooling during the coldest part of the day, a physiological mechanism of energy conservation. Deer may also reduce their activity to limit energy lost (Arnold et al. *in prep*). Lowering heat loss during winter seems to be essential for red deer. Since height, canopy closure, stem density modified temperature, wind speed, precipitations and solar radiations within stands (Cook et al. 1998), bedding sites might be also chosen for their quality in energy conservation. Chen et al. (1999) had found that red deer use more frequently denser coniferous shelter. All these result have been explained as thermoregulation-linked behaviors. A high and dense coniferous cover (protection against precipitation, reduction of radiant heat loss) is not necessarily always an advantage for ungulates. Cook et al. (1998) found no positive effect of high coniferous cover on domestic

elk-cows. Elk mass loss and winter mortality was higher in enclosures with high cover. The authors explained this by the lower level of solar radiation flux under dense cover. Our results suggest that Cook's explanation is correct, as we observed a greater influx of morning solar radiation at the bed site associated with a higher cover over the bed. Receiving warmth via solar radiation during the morning, may facilitate thermoregulation after cold winter nights.

For the summer period, Millspaugh et al. (1998) and Edge et al. (1987) have suggested that elk (*Cervus elaphus*) use bed sites characterized by a high coniferous cover to limit heat stress. We observed no difference in solar radiation between bedding site and random plots but coniferous cover just over the bed is also higher than in available plots. Our results do not validate or invalidate this explanation.

#### **4.5.7. *Sexual habitat selection***

We did not take into account a potential sex effect in our analysis because of a low male sample size. Red deer sex segregation has been reported for a long time (e.g. Clutton-Brock et al. 1982) but only a few studies try to explain it. Conradt et al. (2000) hypothesized that males are more sensitive to weather than females and that this difference may explain segregation of sexes in winter. They found a stronger response of males to bad weather (strong wind, low temperature and heavy rain) that supported their hypotheses. Focusing on bedding site, males might choose winter sites with a higher thermal conservation value. It is also possible that male red deer are less sensitive than females to human disturbance (F. Klein, *comm. pers*) as is probably the case with grizzly bears (Gibeau et al. 2002). Unfortunately our data set did not allow testing this hypothesis.

## 4.6. Management implications

Our results reaffirm much of what is known about red deer habitat selection in established populations, offer new insights, and emphasize that habitat selection is a complex process within which a lot of factors interact with one another. We observed different patterns of habitat use between years, seasons and selection level. Similarly, Edge et al. (1987) have found that elk habitat use may also differ between summer months. Application of such models in natural resource management and conservation planning are consequently complex as they need to account for the entire combination of ecological factors which vary by scale and season, to offer the best combination of food and shelter in the Jura Mountains.

We found a clear hierarchical habitat selection pattern. At the population selection level, habitat use occurred on a large-scale basis in which available habitat around the location and distribution from sources of disturbance were best correlated with red deer presence. The most important variables we identified were derived from geographic information systems. Consequently management options at the population level will probably be adequately evaluated with GIS that provide habitat suitability maps.

At the individual selection level, site-specific to broad scale variables discriminated well between bed sites and available locations. Broad scale variables are measured with GIS and it should be possible to estimate forest age structure (Scarth et al. 2001), forest typology (Franklin et al. 2001), even individual tree cover or tree height within GIS (Gong et al. 2002) within a few months and with a sufficient accuracy for management purpose. Micro-site variables such as visibility had to be estimated in the field by ground surveys. Consequently, mapping suitable bedding sites was not possible. Nevertheless, local factors, such as cover variables, are related to forest management, on which we may act and thus probably limit red deer-forestry conflicts (Völk 1999). The landscape distributions and the quality of suitable bedding sites may influence the impact of red deer on vegetation (Morellet 1996, Völk 1999). For instance, an important herbaceous plant cover near a summer bed site may limit forest browsing by red deer.

The role of bed site in energy conservation seems to be important. Bed site with high thermoregulation value limits red deer energy loss. Red deer use sunnier bed sites with higher coniferous cover during winter mornings. This suggests that a more open forest stand than a dense coniferous stand is necessary to allow sun to penetrate the canopy. During summer, red deer need open stands with a well-developed herbaceous cover but also with coniferous trees that provide shelter.

Based on our results, we strongly suggest that mixed stratified forests should be preferential to monospecific and dense coniferous forest stands. This forest type satisfies red deer microclimate, shelter and seasonal food requirements, and may certainly limit the impact of red deer on forest (Völk 1999), as red deer energy needs will be lower. Red deer social behavior is complex, they can be gregarious during winter or live alone during summer. Therefore groups may need large areas of shelter (Staines 1976) that need to be managed at the population range level.

## 5. MODELLING CORRIDOR HABITAT QUALITY FOR RED DEER

---

### *Corridor suitability maps*

#### 5.1. Summary

- 1) Corridors increase landscape connectivity between habitat patches and therefore are valuable conservation tools. Unfortunately, most studies that model corridors are based on expert knowledge and judgment. Here we present a biometrical based habitat corridor model for red deer in a suburban area and consider its applications.
- 2) We constructed a GIS spatially-explicit corridor habitat suitability model that statistically relates any point of the landscape to a probability of belonging to a corridor, by comparing habitat features of observed corridors to average landscape habitat in the whole study area.
- 3) Suitable red deer corridor habitat is characterized by a higher amount of trees such as forest or thickets, that are more distant from building areas and vineyards than available habitat. Roads do not seem to be an important factor in our study area.
- 4) Corridor suitability values were transformed into travel cost values. The cost distance map between forest habitat patches was calculated. The resulting map may be used to visualize areas that favor movements and to detect conflict regions.
- 5) Moreover, effects of landscape modification on the network of corridors may be tested by virtual landscape alterations

## **5.2. Introduction**

Habitat destruction and fragmentation are cited as the major causes of species loss (e.g. Wiens 1997, Hanski 2001). One of the consequences of habitat loss and fragmentation for animals is lower dispersal or movement capabilities between habitat patches (Berrgen et al. 2002) and, as a consequence, increased risk of local extinction (Fahrig and Meriam 1985, Anderson and Danielson 1997). That corridors counteract such effects is supported from several well-designed studies (Beier and Noss 1998 for a review). However, there is little empirical evidence to support the importance of corridors in population dynamics or in conservation (Rosenberg *et al.* 1997). For this reason, and considering that habitat fragmentation increases in connection with human population growth, identifying and managing wildlife corridors are nowadays important tasks for wildlife managers and urban planners (Bennett 1999, Holzang et al. 2001, Vuillemier and Prélaz-Droux 2002).

Spatially-explicit movement or dispersal data are rarely available because they are notoriously difficult to acquire (e.g. Beier and Noss 1998). Consequently, correlations between landscape features and dispersal movements are poorly and only recently documented (Stapp and Horne 1997, Bright 1998, Sjörgen-Gulve 1998, Sieving et al. 2000), particularly for large species (Alexander and Waters 2000, Palomares 2001, Zimmermann and Breitenmoser 2002, Dyer et al. 2002). Usually, the choice of corridors placement and their characteristics is defined according to expert knowledge and their efficiency is tested backwards (Clevenger and Waltho 2000, Holzang et al. 2001). This point is illustrated by the placement of corridors, that along roads are often based on wildlife-vehicle collision information (Singer and Doherty 1985, Holzang et al. 2001) with the assumption that a high mortality will indicate high corridor use. These expert choices are generally the only alternative to the expensive field studies required to acquire data on animal movements, generally over a short period of time. Nevertheless, as a consequence of the central importance of connectivity in population viability (analysis), it is important to improve the definition of spatial corridors' characteristics by considering the species specificity (Baguette et al. 2001), in order to improve wildlife management (Hobbs 1992, Clevenger et al. 2002).

Corridors were historically considered as linear features of vegetation that differ from the surrounding vegetation and connect at least two habitat patches (Hobbs 1992, Simberloff et al. 1992). However, some authors consider that corridors may have various discontinuous

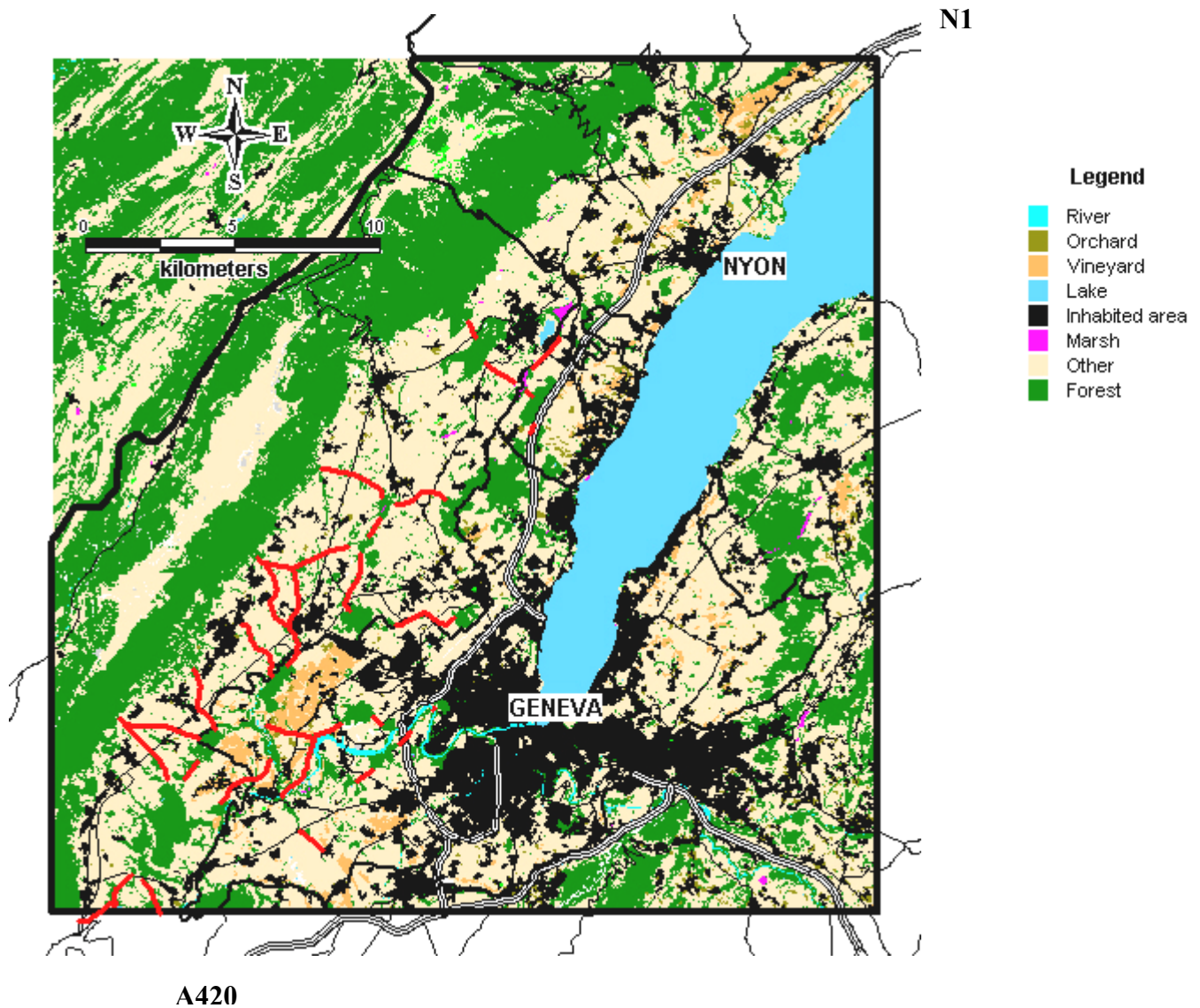
structural patterns in space and time, depending on the characteristics of the mover (Bennett 1999, Hess and Fischer 2001, Puth and Wilson 2001). For example, some birds and mammals species move non-linearly across the landscape utilising stepping-stones (Haig et al.1998). Therefore a corridor should be considered as a structure that canalizes and directs the flow of organisms, materials, or energy between patches (Puth and Wilson 2001).

In this chapter, the characteristics of known linear corridors used by red deer between forest habitat patches in the Geneva Bassin (Figure 5-1), a densely inhabited area, were examined.

In the Geneva Bassin, remnant forests are scattered across a landscape dominated by urban and agriculture structure. Red deer populations mainly occur in reserves and the mid-mountain forest surrounding the city of Geneva. A previous study (Chapter 2) revealed that several Geneva Bassin forests are suitable habitat for red deer and are currently partially occupied. Due to high level of fragmentation, we address some questions; do red deer colonize more suitable forests, where are the corridors located, where are the road traffic conflict areas and what will happen if forest fragmentation increases? To answer these questions, we compared landscape characteristics of observed corridors, to landscape characteristics of the whole study area in order to construct a spatially-explicit corridor habitat suitability model that statistically relates landscape features of a particular site to probability of fitting in a corridor. This model was applied on the Geneva Bassin landscape in order to visualize potential corridors. After transformation of corridor suitability values into travel cost values, a cost distance map (Vuillemier and Prélaz-droux 2002) was constructed to assess potential conflict areas for dispersal.

### 5.3. Study area

Our study area includes the western part of the Geneva Basin (Figure 5-1). Around the city of Geneva and its suburbs, the landscape is highly fragmented due to intensification of agriculture and urbanization. Crops, vineyards and pastures surround small woods, and many roads are present in this 450 km<sup>2</sup> flat area.



**Figure 5-1:** Land-use in the Geneva Basin. The border between Switzerland and France (large black line), red deer linear corridors (red lines), main roads (black lines) and highways (black and white lines).



## 5.4. Methods

### 5.4.1. *Field data*

In our study area, linear wildlife corridors have been mapped by expert assessment studies (ECOTEC 1999, Holzang et al. 2001). Rangers, foresters, hunters, naturalists, biologists and an official database (Centre Suisse de Cartographie de la Faune) have been consulted in combination with fieldwork, in order to adapt this map for red deer. We collected 13 vehicle-collision records, 20 sites of red deer path between two forested patches for the 1990-2001 period. All red deer information was collected in the western part of the Geneva Bassin that is bordered to the east and to the south by the highways N1 and A402, and to the west by the Jura Mountains (Figure 5-1).

### 5.4.2. *Digital data*

For all our GIS analyses, we used VECTOR25 (OFT 2000), a national vectorial database. We rasterized these data into a 10 meter squared cell raster map. This cell size was a compromise between the 5 meters grain of the database, landscape perception scale by the animal (see Puth and Wilson 2001) and limitations of computer performances.

From the database, we derived some ecological variables, which may be potentially relevant for red deer dispersal. We used information on 7 types of roads, from highways to footpaths, and on 8 habitat types from tree hedges to forest. For roads we separated highways into two parts: highways bridges and highways without bridges. Other roads were only considered outside build-up areas. As animals may perceive their environment at different scales (Johnson et al. 2002) and as habitat may have an influence radius, we calculated the frequency of some potentially important habitat features within circles of different radius using a circular moving window (Table 5-1). We limited the radius to 200 meters, because we rarely observed red deer at a distance greater than 200m from forest secondly due to computer performance limitations.

**Table 5-1:** Ecological variables used in the Ecological Niche Factor Analyses. Variables have been combined and/or transformed from VECTOR25 Swiss database (OFT 2000).

<i>Variable description</i>	<i>Original date code in VECTOR25</i>	<i>Code*</i> Without extension
Forest	Z_BaumS, Z_Gebue, Z_Wald, Z_WaldOf	Forest
Orchards	Z_ObstAn	Orchard
Isolated tree and thickets	BauReihe, Hecke, OBReihe, EinBaum, ObsBaum	Thicket
Marshes and wooded marshes	Z_SumGeb, Z_Sumpf, Z_SumWa, Z_SumpfWaO	Marsh
Vineyards	Z_Reben	Vine
Rivers	Z_Fluss	River
Other (agriculture mainly)	Z_Uebrig	Other
Highways bridges (outside inhabited areas)	AutRte, Rte2Chau, Rte3Voie, AutoBahn, AutoStr	HighWBridge
Highways without bridges (outside inhabited areas)	Same as before	HighWays
1st class roads (outside inhabited areas)	1_Klass, Rte2larg, Rte2Etr	Road1
2nd class roads (outside inhabited areas)	2_Klass, RteEtoi	Road2
3rd class roads (outside inhabited areas)	3_Klass, AutrRteA	Road3
Forest roads (outside inhabited areas)	4_Klass, AutrRteB	Road4
Forest trails (outside inhabited areas)	5_Klass, RteEtoi	Road5
Walking ways (outside inhabited areas)	6_Klass, Sentier	Road6
All roads (outside inhabited areas)	1 <sup>st</sup> to 6 <sup>th</sup> class roads	RoadAll
Inhabited area	Z_Siedl	Build

\* Extensions: “\_FQrX”, X corresponds to radius in meters

### **5.4.3. The Corridor habitat suitability model**

The linear corridors expert map (section 5.1.1) only contains corridors assumed to be frequently used and to connect two forest habitat patches. Therefore, as we cannot assess for real absence data, we used the Ecological Factor Analyses (ENFA) (See section 1.6.3) to construct a spatially-explicit corridor habitat suitability model.

The ecological variables have been normalized using the Box-Cox transformation if necessary before performing ENFA. If a variable was not continuous enough, it was removed. The number of factors retained was chosen on the basis of the broken-stick method (Hirzel et al. 2002). The K-fold cross-validation process was used to test model performances (see section 1.6.3). In the meantime corridor’s habitat suitability (CS) maps and their associated confidence maps were computed (see section 1.6.3).

#### 5.4.4. *Least-cost distance analyses*

The least-cost distances (Vuilleumier and Prélaz-droux 2002) between forest habitat patches was calculated using the IDRISI32 cost functions (Eastman 2001), which can integrate different permeability values from absolute barriers to no constraint to dispersal. The cost function generates a distance surface (also referred to as a cost surface) where distance is measured as the least cost (in terms of effort, expense, etc.) by moving over a friction surface. The unit of measurement in the output image are "grid cell equivalents". A grid cell equivalent of 1 indicates the cost of moving through a grid cell when the friction equals 1. A cost of 5 might arise from a movement through 5 cells with a friction of 1, or 1 cell with a friction of 5. Costs are determined radially from a set of source targets to the edges of the image.

To satisfy the IDRISI32.2 requirement, we transformed the resulting corridor suitability values (CV) into friction cost indices (F) using the following relationship:

$$F = -CV + 101$$

Therefore cost indices vary between 1 (corresponding to a CV of 0) and 101 (corresponding to a CV of 0).

## 5.5. Results

### 5.5.1. *Corridor habitat suitability model*

Frequency analyses were performed at 10, 50, 100, 150 and 200 meters radii. Preliminary correlation analyzes revealed that frequency in a radius of 150m was highly correlated with frequency values in a radius of 200m. We therefore removed the frequency of the 150m radius from the analyses. Some variables are not sufficiently continuous (less than 4 values per variable) and as a result final analyzes were performed on 49 variables.

The marginality factor has a high marginality value (0.65), showing that red deer corridor habitat is different from average habitat in the study area. The marginality factor explains 26 % of the specialization and indicates that sites suitable for corridors are localized mainly in forested area or near rivers and away from buildings (Table 5-2). Close to corridors the frequency of forest trails (marginality score:0.26) is higher than in study area. Habitat

tolerance was moderate (0.86) and mostly explained by inhabited areas, trees and forests frequencies (Table 5-2).

The corridor habitat suitability map (Figure 5-3) has been constructed using the first 3 factors (out of 49). 66% [confidence interval 64-69] of the validation cells in the left-out partition have a Corridor Suitability (CS) value greater than 50, which significantly differs (bootstrap test,  $p < 0.01$ ) from the 40 % expected if cells were randomly chosen from the global distribution. The “Contrast” value – comparison of the CS values whole study area with CS values on corridors - is 18% [0.16-0.21].

K-fold cross-validations and their resulting confidence maps (Figure 5-2) revealed that uncertainty of CS values is higher in the suburban area than in Jura Mountains, but are clearly small overall.

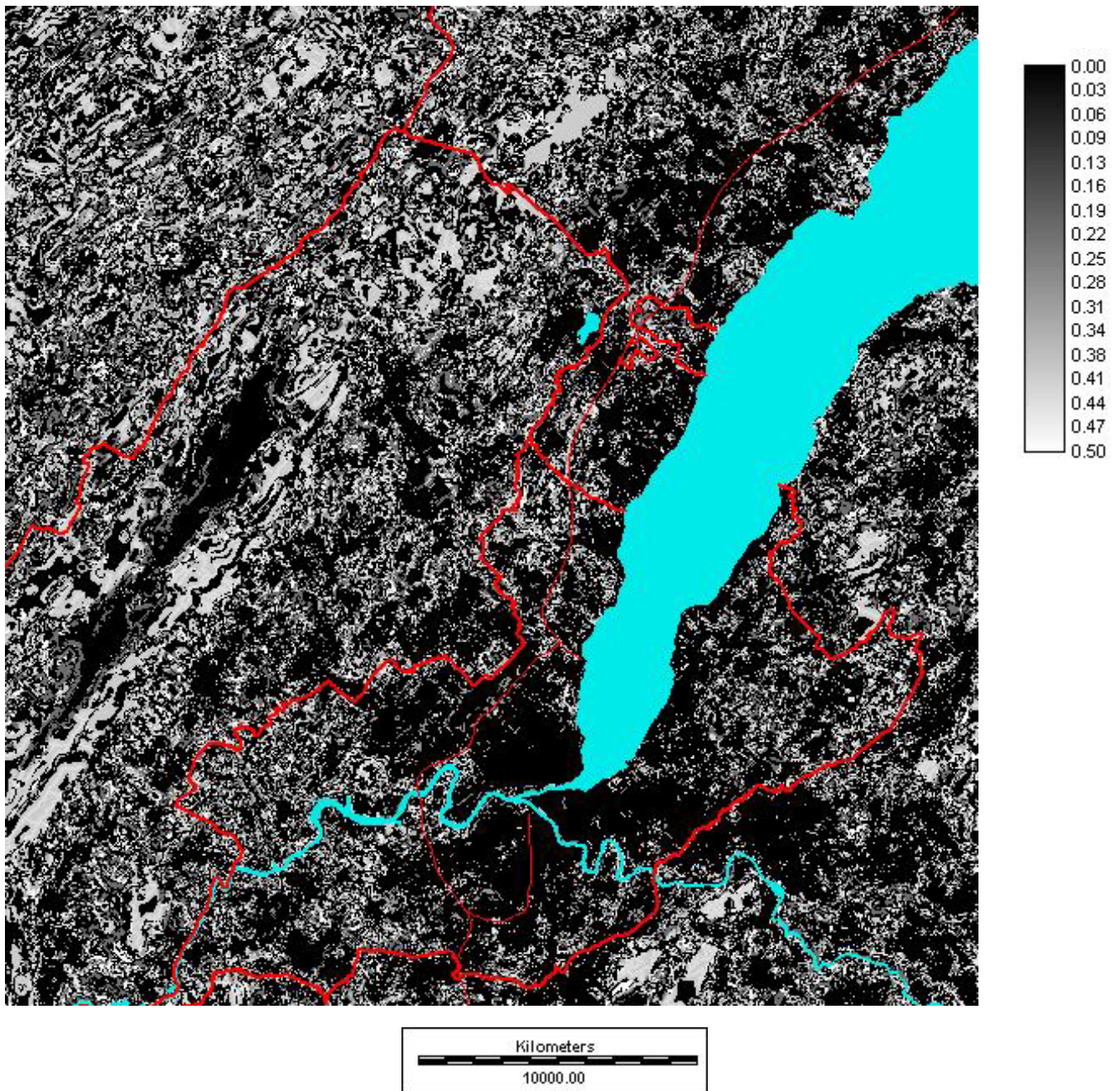
Corridors HS Maps point out not only the linear corridors but also the diffuse areas around these features and interrupted corridors features.

### **5.5.2. *Least-cost distance analyses***

The ENFA do not allow us to use information on highways (score value near zero) as no presence site includes information from the original highway map (Hirzel et al. 2002, Sachot 2002). Therefore we assigned a cost value of 10,000 to highways, preventing the model to find pathway which frequently crossed highways.

We used the Habitat suitability (HS) maps for Geneva Bassin developed in chapter 2 to define 17 suitable habitat patches. Areas with a HS value greater than 0.5 were therefore assessed to be suitable areas and HS values under this cutting value were considered as inadequate areas. The cost distance map indicates that cost distances are lower where corridors are observed (Figure 5-4).

We used the Habitat suitability (HS) maps for Geneva Bassin developed in chapter 2 to define 17 suitable habitat patches. Areas with a HS value greater than 0.5 were therefore assessed to be suitable areas and HS values under this cutting value were considered as inadequate areas. The cost distance map indicates that cost distances are lower where corridors are observed (Figure 5-4).

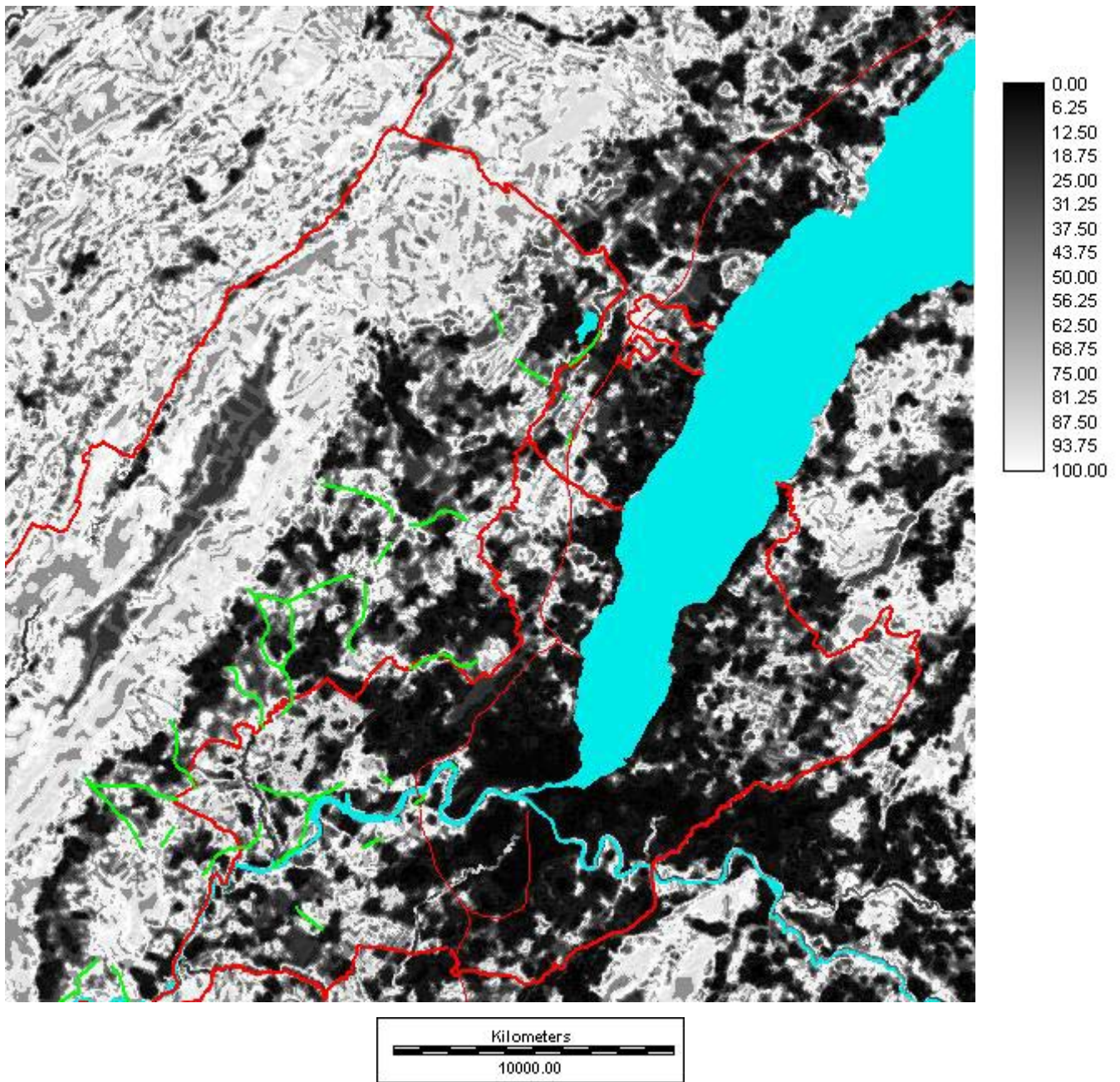


**Figure 5-2:** Uncertainties (from the k-fold cross validation) on red deer corridor suitability values for the Geneva Basin, as computed by ENFA. Department borders (red large lines) and (red fine lines) highways are indicated.



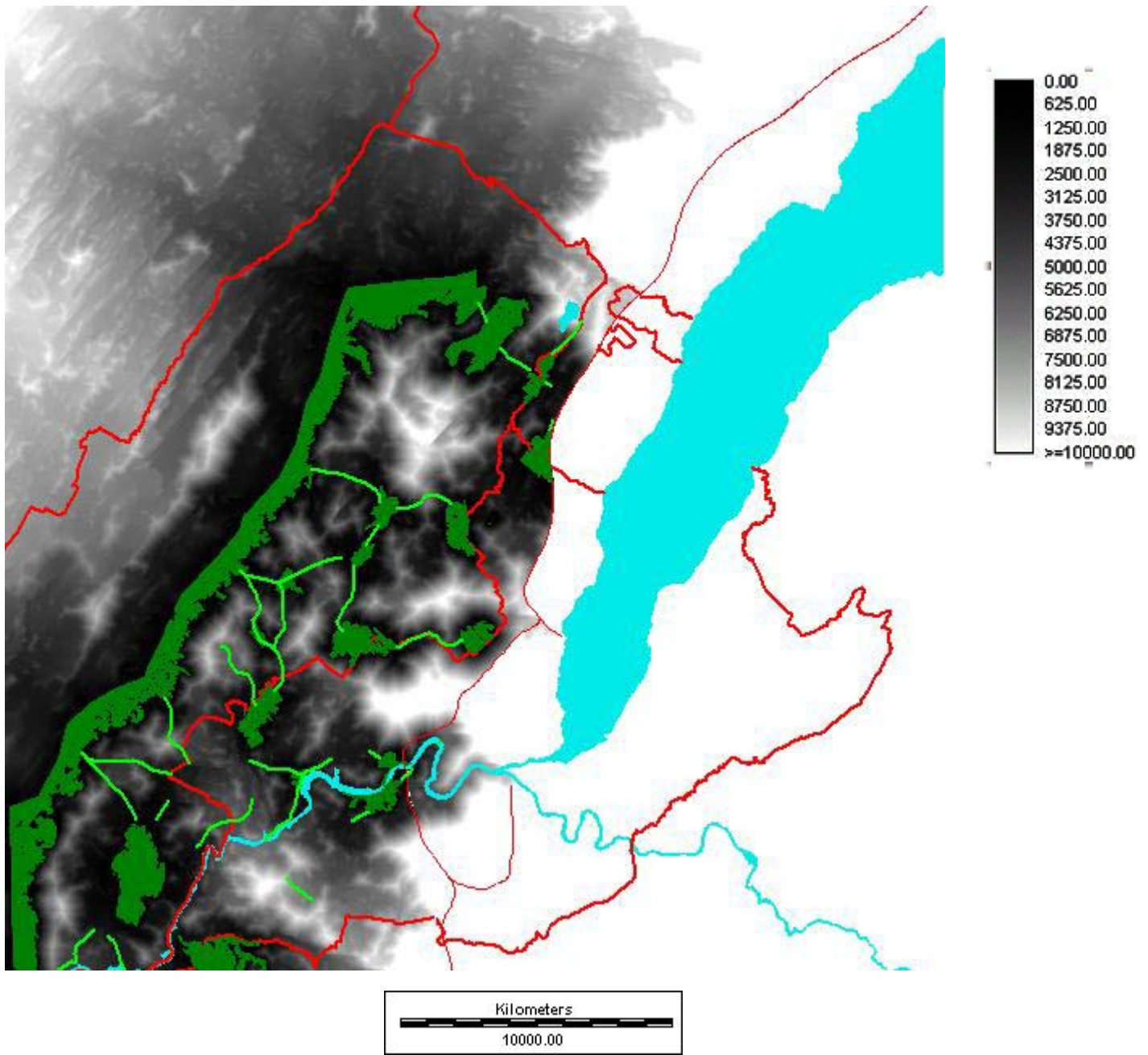
**Table 5-2:** Scores of the variables on the selected factorial axes (out of 49) from the red deer corridors ENFA analyses in the Geneva Bassin (Switzerland). Percentages indicate the amount of variance explained by each factor. M= marginality, S1 to S4= specialization factors. The marginality scores indicate the correlation between each variables and the factor. The greater the absolute value of the coefficient, the higher this variable contributes to the marginality. Positives marginality scores values mean that red deer prefers location with higher values than average location in study area, a negative value means that red deer prefers the low values. The absolute values of specialization scores indicate the correlation of each variable to each specialization factor but here the sign has no meaning. The higher the value, the more restricted is the range of the red deer on the corresponding variable.

	<b>M</b>	<b>S1</b>	<b>S2</b>	<b>S3</b>	<b>S4</b>
	9%	9%	7 %	5 %	4 %
HighWays_FQr10	0.00	0.00	0.00	0.00	0.00
HighWays_FQr100	0.00	0.00	0.01	-0.01	-0.01
HighWays_FQr50	0.00	0.00	0.00	0.00	0.00
Road2_FQr10	-0.01	0.00	0.00	0.00	0.00
Road2_FQr100	-0.03	0.01	-0.01	0.01	0.01
Road2_FQr200	-0.04	0.04	-0.01	-0.01	0.03
Road2_FQr50	-0.02	0.00	-0.01	0.01	0.00
Road3_FQr10	0.00	0.01	0.01	0.00	0.00
Road3_FQr100	0.01	-0.02	0.00	0.00	0.01
Road3_FQr200	0.04	0.00	-0.01	0.01	0.00
Road3_FQr50	0.00	0.00	0.00	0.00	0.01
Road4_FQr10	-0.02	0.00	0.00	0.00	0.00
Road4_FQr100	-0.05	0.01	0.01	0.03	0.01
Road4_FQr200	-0.04	0.04	-0.02	-0.01	-0.01
Road4_FQr50	-0.04	0.01	0.01	-0.02	-0.02
Road5_FQr10	0.00	0.00	0.01	0.00	0.00
Road5_FQr100	0.01	0.01	-0.01	0.00	0.03
Road5_FQr200	0.07	0.02	-0.02	-0.01	0.03
Road5_FQr50	0.00	-0.01	0.01	0.00	0.00
Road6_FQr10	0.07	0.00	0.00	0.00	0.00
Road6_FQr100	0.19	0.02	0.01	0.01	0.00
Road6_FQr200	<b>0.26</b>	0.03	-0.03	-0.02	0.03
Road6_FQr50	0.13	0.01	0.00	-0.01	0.00
RoadAll_FQr100	0.12	0.00	-0.01	0.00	0.01
RoadAll_FQr200	0.12	0.04	-0.03	0.00	0.05
RoadAll_FQr50	0.10	0.00	0.00	0.00	-0.01
Build_FQr100	<b>-0.27</b>	0.04	0.06	-0.15	<b>0.50</b>
Build_FQr200	<b>-0.28</b>	0.00	0.04	0.00	-0.04
Build_FQr50	<b>-0.25</b>	<b>0.21</b>	<b>-0.76</b>	<b>0.28</b>	<b>-0.45</b>
Other_FQr100	0.07	-0.15	0.04	0.04	-0.12
Other_FQr200	0.10	<b>0.39</b>	-0.19	-0.11	<b>0.21</b>
Other_FQr50	0.05	0.03	-0.01	-0.03	0.05
Thicket_FQr100	-0.06	0.01	0.06	-0.08	<b>-0.25</b>
Thicket_FQr200	-0.07	-0.06	0.04	0.05	<b>0.53</b>
TreeAll_FQr100	0.03	0.01	-0.03	0.02	-0.03
TreeAll_FQr200	0.10	0.01	-0.06	0.05	-0.02
TreeAll_FQr50	0.00	0.01	-0.02	0.01	0.02
River_FQr50	<b>0.27</b>	0.00	0.00	0.00	-0.01
Forest_FQr100	<b>0.34</b>	-0.13	0.13	0.07	-0.24
Forest_FQr200	<b>0.33</b>	<b>0.40</b>	<b>-0.35</b>	-0.06	0.17
Forest_FQr50	<b>0.33</b>	0.06	-0.06	-0.02	0.07
Orchard_FQr100	-0.14	0.04	-0.14	<b>-0.73</b>	<b>-0.19</b>
Orchard_FQr200	-0.16	0.02	-0.05	0.00	0.05
Orchard_FQr50	-0.11	<b>0.76</b>	<b>0.45</b>	<b>0.57</b>	0.02
Vine_FQr100	0.12	-0.02	-0.03	0.01	0.00
Vine_FQr200	0.18	-0.01	0.01	0.01	0.00
Vine_FQr50	0.08	0.03	-0.02	0.00	-0.01
Marsh_FQr100	0.14	0.00	0.00	0.00	0.00
Marsh_FQr200	0.16	0.00	-0.01	0.00	-0.01



**Figure 5-3:** Red deer corridor habitat suitability map for the Geneva Basin, as computed by ENFA. The mean corridor suitability values from the Jack-knife cross validation range from 0% (black) to 100% (white). Red deer linear corridors used to construct the map (green lines), department borders (red large lines) and highways (red fine lines) are indicated.





**Figure 5-4:** Cost distance map from 17 forest patches (green polygons) in western Geneva Basin. Cost values were derived from the corridor suitability map computed by ENFA (Figure 5-3). Cost distances ranges from 1 to infinite. Red deer linear corridors (green lines), department borders (red large lines) and highways (red fine lines) are indicated.



## 5.6. Discussion

### 5.6.1. *Model strengths and limits*

The validation process indicates high consistency in model predictions. We believe that the relatively low contrast value does not indicate a poor model, but reveals that a larger number of grid cells than the one observed are adequate for red deer movements. Indeed, visualization of these cells on the suitability corridor map shows that they probably belong to broken or unclear corridors. In some cases, these cells may fit into real corridors that have not been recognized in the field. Moreover, red deer have traditions (Gonzales and Pépin 1996) and therefore may not use potentially valuable corridors, especially with their currently low population.

### 5.6.2. *Corridor features*

Our results are consistent with our predictions as well as findings of a few other studies. Suitable sites for corridors are not compatibles with built-up areas (Alexander and Waters 2000). Instead they are preferentially associated with areas with a high tree density, such as forests or thickets (Alexander and Waters 2000). There is no radius or scale that appears to be more important than another.

In our study area, we did not find an important road effect indicating that spatial arrangements or current size of roads do not affect inter-patch movements. Dyer et al. (2002) have shown that GPS collar fitted caribou cross real roads less frequently than a sample of simulated roads randomly located in their landscape, which suggests that roads have a quantitative effect on caribou behavior. As we do not have quantitative information on road crossing occurrence in our study area, we could not test or model it.

Surprisingly, highways do not seem to play an important role. We have two explanations for this unexpected result. The first is methodological: ENFA needs presence data. In fact, our corridor network does not cross any highway and therefore ENFA does not assess whether highway has an influence on movements. Secondly, red deer density is low and a lot of areas free of red deer exist on the same side of the highway. Perhaps red deer do not normally attempt to cross risky landscape features such as highways but are more when habitat is at its carrying capacity.

Although our model has good performance overall, it may be improved by inclusion of other relevant habitat features such as finer scale variables. Alexander and Waters (2000) used a comparison between habitats where animals crossed a focus highway with habitats where they do not, and showed that flatter areas with greater visibility were selected. Unfortunately, our database (and moreover any actual GIS database) does not provide that kind of information at the grain of our study area extent.

## **5.7. Management implications**

Our model provides a statistical and mathematical relationship between any point of the landscape and its probability to belong to a corridor. However, although our observed correlation between avoidance of human disturbed features and preference for forested areas seems to be obvious, it allows a quantification of this relationship and therefore is no longer an assessment of corridor habitat quality based on a complete expert judgment (as all presence data used for modeling potential species distribution, Guisan and Zimmermann 2000). The relationship may be used by the means of corridors suitability maps to improve actual landscape management by locating the relative permeability (corridor habitat suitability values) of the landscape. The confidence maps also provide model uncertainties, which is an important information for managers. Moreover, the model may help to test the effect of landscape management scenario on corridor distribution.

Corridors have a conservation and management value as long as animals actually use them and accordingly, increase connectivity and viability of populations. Effectiveness of management decisions needs field verification, and if necessary, models must be adapted or reformulated with new data or findings (Zabel et al. 2002, Wilhere 2002).

Managers have to consider the potential corridor disadvantages (Neet 1992). Although corridors may theoretically function as prey-traps (Hobbs 1992), most studies record no evidence of predation (Little et al. 2002 for a review). Corridors may also be boundaries for other species that may facilitate pest species dispersal or epizooties (Puth and Wilson 2001). These effects must be controlled in the field, or when information is available in a GIS, spatial tools may be used, i.e. to overlay the different species maps and thus point out the conservation conflict or favorable sites (Lathrop and Bogner 1998, Sanderson 2002).

Our results do not provide a quantitative measure of connectivity between patch networks. Although the functionality of a between-patch corridor may be lost (i.e. due to the construction of a new road), the remaining corridor matrix may be sufficient to ensure enough inter-patch connectivity for the species. Therefore, in the next chapters, we will apply an individual-based dispersal random based model to the corridor suitability map in order to estimate connectivity between forest habitat patch networks.

## 5.8. Overview

The corridor habitat suitability model we constructed has several new advantages in comparison with previous studies:

- 1) It provides a statistical relationship between landscape and probability of being a corridor.
- 2) It is not limited to linear features and permits visualization of diffuse, continuous or discontinuous corridors.
- 3) It allows testing of management scenarios

Nevertheless, the model should be enhanced by the integration of finer scale parameters, such as slope for example, and be tested in the field.

*A red deer habitat point of view*

## **6. DEERDISPERSER, A SPATIALLY EXPLICIT INDIVIDUAL-BASED MODEL TO MEASURE CONNECTIVITY BETWEEN HABITAT PATCHES**

---

*Habitat sensitive random walk modeling*

### **6.1. Summary**

- 1) We constructed a spatially explicit grid-based random walk model that simulates animal movements between habitat patches.
- 2) The model was developed to estimate connectivity between habitat patches in the sense of transferring rates probabilities. The model was shaped to allow different kind of random behavior and can be parameterized by the user.
- 3) The importance of key parameters may be evaluated by the means of sensitivity analysis. The model can be used to gain insight into the total connectivity network of an area or to locate inaccessible areas where animals have difficulty in dispersing.

## **6.2. Introduction**

Animal populations and habitats are increasingly fragmented as a consequence of human population increases, road network and city size increase (e.g. Bennett 1999). Therefore many species inhabit patchy landscapes surrounded by human-induced landscape. Habitat loss/and or loss of habitat connectivity may have a severe effect on population viability (Hanski 2001). A low level of connectivity reduces the chance for individuals to disperse successfully between habitat patches (Berggren et al. 2002) and therefore increases the extinction probabilities of the populations (e.g. Hanski 2001). This is particularly true for species with highly specialized habitat requirements or limited dispersal ability. High landscape connectivity may be particularly important for species with conservation status (Bennett 1999). Knowledge of how landscape composition affects connectivity and consequently population viability of managed, endangered or alien populations is therefore essential (Roff 1974, Berggren et al. 2001, Reed et al. 2002).

Conservationists, wildlife managers and urban planners have difficulties taking decisions on what to do and where to act to improve habitat connectivity (Bennett 1999). PVA analysis or genetic analysis may allow them to point out which are the isolated, source or sink populations if parameters estimations are reliable (Coulson et al. 2001, Reed et al. 2002). Unfortunately these studies are commonly conducted with pseudo spatially explicit dispersal functions as connectivity or migration is assumed to be only distance-dependent (Table 6-1). Habitat patches may be more or less effectively isolated than simple distance would indicate (Ricketts 2001, Travis and French 2000). The connectivity of a landscape depends not only on the distance between habitat patches but also on the presence of corridors of natural habitat and their specific resistance to movements. Dispersal habitat quality and landscape structure should be integrated into a spatially realistic model (Moilanen and Hanski 2001, Wiens 2001), as it may be one of the key processes for population persistence in a landscape network (Opdam 1988, Wiens 1997). Consequently information on how individuals behave in the landscape becomes crucial.

Recent works on dispersal used spatially explicit models to evaluate connectivity or to measure the effect of management scenarios on connectivity between habitat patches. Two model types are currently used: percolation or diffusion models, and random walk models (Table 6-1). The diffusion models cannot represent the complex behavior of an individual and

are generally parameterized from expert knowledge. Our dispersal understanding is generally very poor, firstly because population models have been developed for much of the last century while the study of spatial processes in spatial ecology is recent (Travis and French 2000) and secondly, studies on dispersal are very time consuming especially with larger species, as a consequence of tracking-costs of individual animals during their dispersal or movement processes.

Therefore, we developed a spatially explicit individual based model (seIBM) of the dispersal process that incorporates several modeling approaches. The approach may be use to

1. Parameterize a specific model in order to estimate connectivity between habitat patches
2. Visualize corridors and barriers to dispersal
3. Quantify the effect of management scenarios on overall connectivity of a habitat patches network.

In this chapter, we describe and comment on the model. In the next chapter, this seIBM will be parameterized for red deer with real data and then applied to a real landscape.

## 6.3. Model description

### 6.3.1. Model overview

We constructed DeerDisperser, a spatially explicit individual-based model that simulates movement occurrence between habitat patch pairs. Movements were simulated over Geographic Information System (GIS) representations of the landscape in the form of digital gridded land cover map (raster maps). The resolution (pixel size and study area extent) of environment is defined by the user and is only limited by the computer performances. Movements across the landscape occurred as a sequence of steps to adjacent cells. Simulated animals move according to input landscape files (Section 6.3.2) and movement rules (chapter 6.3.3). The movement rules defined how animals move and interact with the landscape. DeerDisperser provides several user-friendly outputs (Section 6.3.4) such as between-patch

connectivity estimation, and allows performance of powerful sensitivity analyses (Section 6.3.5).

DeerDisperser model structure is based on the approach of Gustafson and Garner (1996). We implemented other random movement behavior and sensitivity analyses. DeerDisperser is not specific to red deer. The model was written in Delphi (Borland 1998) and used GIS IDRISI32 files (Eastman 2001) as input landscape maps.

### **6.3.2. Model inputs**

Landscape is divided into several functional raster maps as follows (Figure 6-1):

- Patch map.

The patch map contains localizations of habitat patches (i.e. populations).

- Corridor suitability map.

The pixel values of the corridor suitability map are the probability that an animal will enter that grid cell. This map may be derived from a land-use habitat map where each habitat has an associated probability representing the facility or the difficulty for the animal to enter that habitat type.

- Mortality map.

The mortality grid map contains the probability of dying on each pixel. The animal may have a higher probability of dying when it stays in a particular habitat type such as roads.



**Table 6-1:** None exhaustive literature review on dispersal models links or not with population models IBM: individual-based model, MM: metapopulation model, LCP: least-cost path models, RW: random walk models.

Species	Reference	Linked with population Model?	Movement Model					
			Model Type	Landscape	Habitat sensitive with Real data		Sensitivity Analysis	
Marmot	<i>Marmota marmota</i>	Stephens et al. 2002	IBM	Def, Random	Real	Pseudo	-	No
Wildlife		Vuillemier and Prélaz-Droux 2002	No	LCP	Real	Yes	No	No
Lynx	<i>Lynx lynx</i>	Schaadt et al. 2002	No	LCP	Real	Yes	Mixed	No
Butterfly	<i>Prodossiana eunomia</i>	Petit et al. 2001	IBM	RW	Real	No	-	No
Squirrel	<i>Sciurus vulgaris</i>	Lurz et al. 2001	MM	RW	Real	No	-	Yes
Hedgehog	<i>Erinaceus europaeus</i>	Doncaster et al. 2001	No	RW	Real	Yes	Yes	No
Panther	<i>Puma concolor</i>	Cramer et al. 2001	No	RW	Real	Yes	No	Yes
Trout	<i>Oncorhynchus mykiss</i>	Clark et al. 2001	IBM	RW	Real	Yes	No	No
Glider	<i>Petauroides volans</i>	Lindenmayer et al. 2001	MM	RW	Real	No	-	No
Geese	<i>Branta sp.</i>	Pettifor et al. 2000	IBM	RW	-	No	-	Yes
Glider	<i>Petauroides volans</i>	Tyre 1999	No	RW	No, territory	Yes	No	No
Robin	<i>Erithacus rubecula</i>	Reuter and Breckling 1999	IBM	Not dispersal	Real	Yes	-	No
Fairy-wrens	<i>Malurus pulcherrinus</i>	Brooker et al. 1999	No	RW	Real	Yes	Yes	No
Bear	<i>Ursus arctos</i>	Wiegand et al. 1999	IBM	RW	Virtual	Yes	No	No
Orthoptera	<i>Metrioptera bicolor</i>	Kindvall 1999	No	RW	Real	Yes	Yes	?
Badger	<i>Meles meles</i>	Schippers et al. 1996	No	RW	Real	Yes	No	Yes
		Van Apeldoorn et al. 1998	Yes					
Lark	<i>Alaudidae</i>	Fahse et al. 1998	Yes	Not dispersal	Virtual	Yes	No	No
Woodpecker	<i>Picoides borealis</i>	Letcher et al. 1998	IBM	RW	Real, territory	No	-	Yes
Gull	<i>Larus ridibundus</i>	Johst and Brandl 1997	MM	RW	No	No	-	No
Gnatcatcher	<i>Polioptila californica</i>	Akçakaya and Atwood 1997	MM	RW	Real	No	-	Yes
Bear	<i>Ursus arctos</i>	Boone and Hunter 1996	No	RW	Real	Yes	No	Yes
Possum	<i>Gymnobelideus leadbeateri</i>	Lindenmayer and Possingham 1996	MM	Mixed	Real	No	-	Scenario on mixed
Monkey	<i>Cercopithecus mitis</i>	Swart and Lawes 1996	MM	Mixed	??	Pseudo	-	“
Not real		Schumaker 1996	No	RW	Real, territory	No	-	No
Not real		Gustafson and Gardner 1996	No	RW	Virtual	Yes	No	No
Prairie dog	<i>Cynomys ludvicianus</i>	Bowser	No	LCP	Real	Yes	No	No

### **6.3.3. Movements rules**

Each animal begins its dispersal in a patch (from the patch map). Departure location in the patch is random (Figure 6-2). Movements on the landscape occur as a sequence of steps from cell to cell. A cumulative probability distribution of the values of the probabilities  $c$  of the seven remaining contiguous cells is constructed and the probability of moving into cell  $i$  ( $p_i$ ) was a function of the eight adjacent cells ( $c_j$ ) (Figure 6-2 "Look").

$$p_i = \frac{c_i}{\sum_{j=1}^8 c_j}$$

Cell probabilities ( $c_j$ ) depend on the three classes of movement's rules that we have implemented in DeerDisperser, as follows:

- Self-avoiding random walk models (SAW)
- Into SAW models, probabilities  $c_j$  are randomly attributed. Consequently, movements are independent of habitat. Animals were simulated in SAW as walkers were not allowed to go back into previously visited cells until after 2 steps by giving a probability of zero to enter the cell. SAW prevents oscillations between two cells (Gustafson and Gardner 1996).
- Correlated random walk models (CRW)

Animals may choose a direction of movement that depends on their previous direction. This type of movement is named correlated random walk model (CRW) and was observed mainly in insects (McCullogh and Cain 1989, Kereiva and Shigesadan 1993). Turning angles between moves are calculated according to a circular normal function with a mean direction fixed at  $0^\circ$  and a turning angle concentration parameter (K parameter, appendix 13-5). Corresponding probabilities to enter each contiguous pixel  $c_j$  are estimated on the bases of an approximate cumulative circular normal density function as described in Cain (1985) (Appendix 13-5). The first movement direction of a simulated walker is determined randomly.

- Probabilistic random walk model (PRW)

Through the input corridor suitability map, the user assesses the probabilities of moving into each cell. An SAW is superposed to avoid oscillations between cells.

- Combinations of CRW and PRW can be done (CPRW) corresponds to a CRW that is habitat sensitive. In this case, resulting probabilities are the product of PRW pixel probabilities by CRW pixel probabilities.

A uniform random number was then selected to choose the cell into which the walker will move based on one of the selected random walk models (Figure 6-2 "Choose").

When the walker stays on a grid cell it has a probability of dying given by the mortality map (Figure 6-2 "Death").

Each surviving walker continues to move until it reaches a patch that is different from the initial patch, or until it reaches a dispersal length limit (Figure 6-2). The user may choose between a maximum number of pixel movements, a real maximal distance or a maximal cost distance.

#### **6.3.4. Model runs and outputs**

A simulated individual moves according to the model rules. Because of the stochastic character of the model, animals have different walking patterns and may arrive or not in different arrival patches. The connectivity between two patches ( $C_{st}$ ) was estimated by calculating the “probabilities of disperser transfer between patches” (Gustafson and Gardner 1996, Tischendorf and Fahrig 2000), which is the ratio of the number of animals arriving in a target patch ( $N_t$ ) by the number of animals that started from the source patch ( $N_s$ ):

$$C_{st} = \frac{N_t}{N_s}$$

Thus connectivity varies between 0 and 1. This was done for each patch as a source patch. Estimations therefore provide a connectivity matrix, which describe the relationship between all patches based on arrival of walkers. Movement history and dispersal success were registered in order to give the followings results (Gustafson and Gardner 1996, Tischendorf 1997, Tischendorf and Fahrig 2000) (Figure 6-1, Appendix 13-4):

- Emigration and immigration probabilities between patches given the ratio of successful walkers by the total number of walkers (Appendix 13-4 c).
- Mean distances (+/- SE) walked between patches for successful dispersal.
- Dying probabilities between patches given by the number of dead walkers divided by the total number of simulated walkers.
- Visitation frequency maps of accumulated walking patterns represented by the number of dispersers that pass a cell in the grid landscape (Appendix 13-4 d).
- Vectorial pathway maps (Appendix 13-4 d).

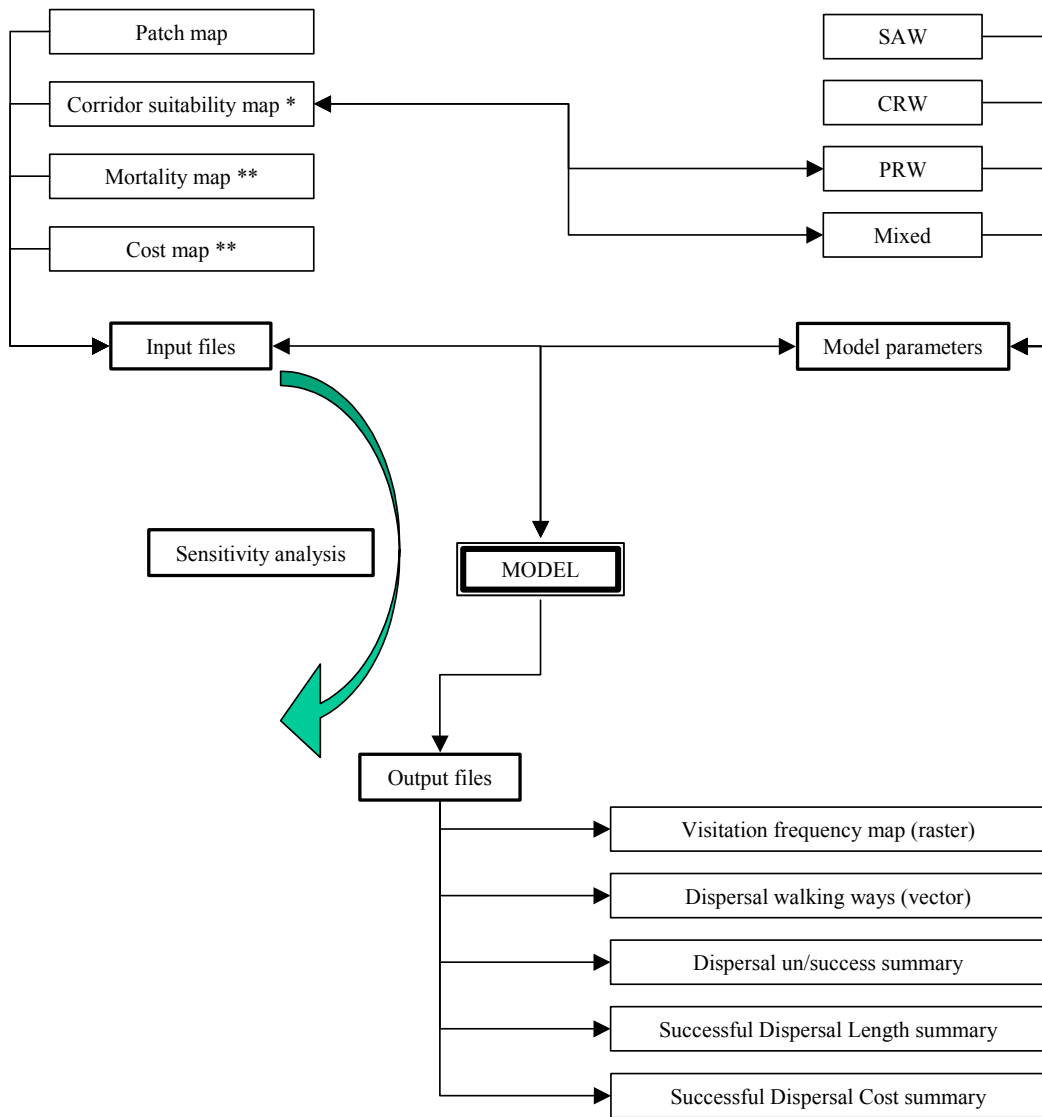
### **6.3.5. Sensitivity analysis**

Model input parameters may be values associated with a standard error or a range of possible values. Therefore sensitivity analyses should be undertaken by changing one parameter or one group of parameters at a time, and consequently, results of the sensitivity analysis are compared with the reference run (Ruckelhaus et al. 1997).

## **6.4. Discussion**

### **6.4.1. Random walk model assumptions**

DeerDisperser offers a range of random walk model complexity, depending on the degree of our biological understanding of the species, as it provides the choice from a spatially random walk model to a habitat sensitive random walk model. The models can be parameterized for a wide range of terrestrial species whose perception scale may be conceived in the form of a gridded landscape. The movement rules are basically simple. If dispersal behavior of a species is well understood, our object-oriented model may be improved in the future by inclusion of more biological and complex behavior. For example, the random movers may consider a larger neighborhood (Fahlse et al. 1998), have a landscape memory, or behavioral variability between individuals (Morales and Ellner 2002). At our current development stage, we prefer to offer a lower range of model complexity instead of more complex models that are difficult to parameterize and may lead to incorrect results (Kareiva et al. 1996).

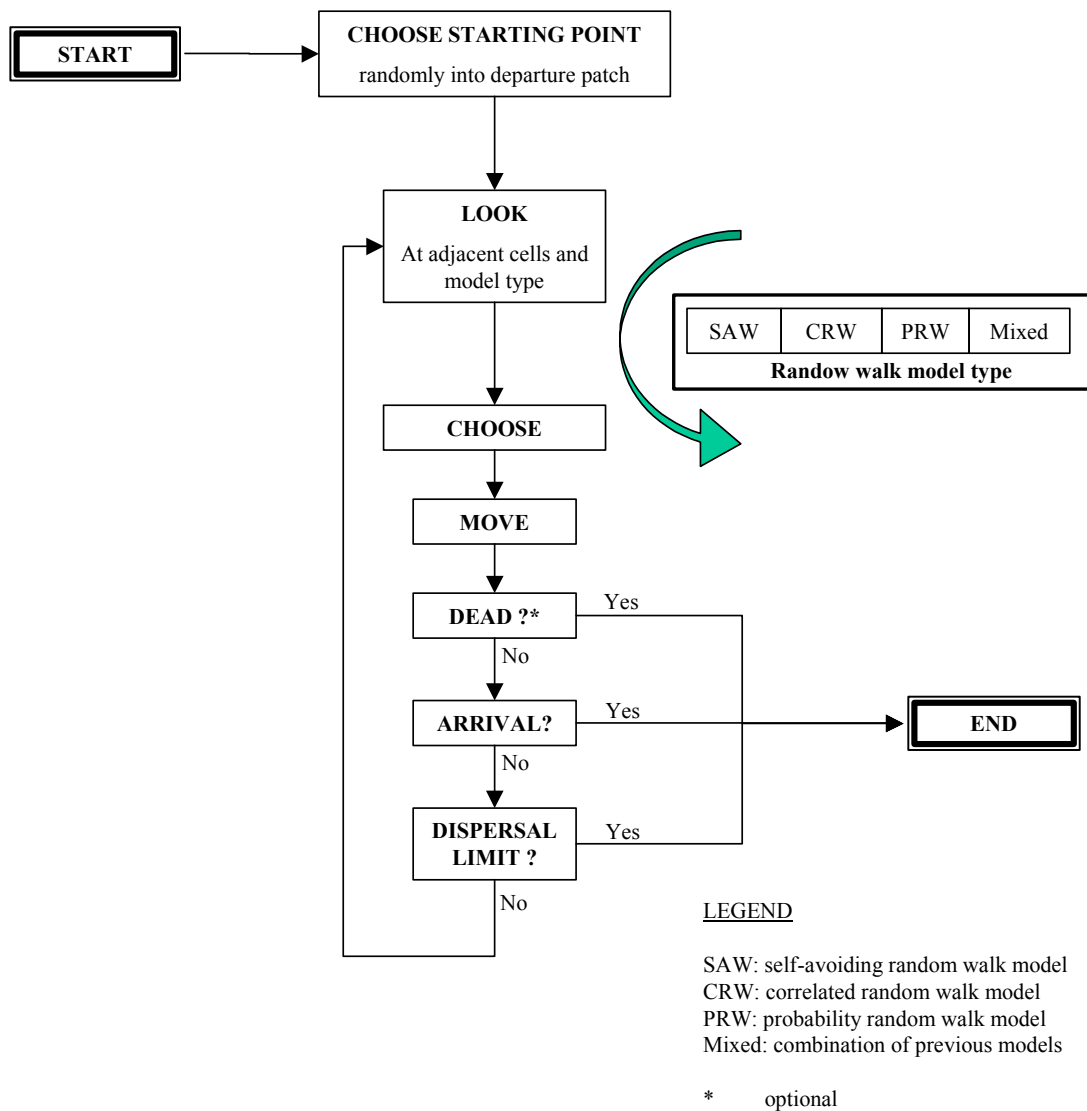


**LEGEND**

SAW: self-avoiding random walk model  
 CRW: correlated random walk model  
 PRW: probability random walk model  
 Mixed: combination of previous models

\* only necessary with PRW  
 \*\* optional

**Figure 6-1:** Diagramm of DeerDisperser model structure. See section 6.3 for explanations and details.



**Figure 6-2:** Flow diagram of DeerDisperser random walk models into DeerDisperser. See sections 6.3.2 and 6.3.3 for explanations.

#### **6.4.2. Random walk model results**

DeerDisperser can be used to gain insight into the total connectivity network of an area through connectivity matrices. The model can also locate inaccessible areas where animals have difficulty in dispersing, by visualization of the random walk movement patterns across the landscape (Gustafson and Gardner 1996, Schippers et al. 1996) (Appendix 13-4 d).

Nevertheless, modeling results need to be combined with sensitivity analysis or to be validated in the field (Ruckelhaus et al. 1997). In fact, models may be especially sensitive to errors in parameters that are difficult to estimate, such as mortality rates. Sensitivity analyses therefore can give quick insight into consequence of assumptions and point out the important features value that need to be precisely measured in the field (Burgman 1993, Reed et al. 1998). On the other hand, field validation of such models is tricky because the necessary dispersal field data are costly and difficult to acquire. Genetic analysis may provide estimates of connectivity that may be compared with those estimates from random walk approaches, and this seems to be a promising combination of tools.

#### **6.4.3. Scenario tests**

The IBM simulation results can be used in a number of ways to assess and compare the dispersal qualities of landscapes (Gustafson and Gardner 1996, Schippers et al. 1996). Wildlife managers and land managers may use such procedures to evaluate the suitability of particular landscapes for a species reintroduction or to evaluate effects of landscape changes on the connectivity network (Van Apeldoorn et al. 1998). Therefore, they can determine the best or the less risky scenario.

#### **6.4.4. Links with population viability analysis**

The connectivity matrix contains the probabilities of disperser transfer between patches and thus may be directly integrated in the dispersal toolbox of metapopulations PVA (Ruckelhaus et al. 1997, Brooker et al. 1999). In the same way, if sensitivity analysis were performed, the connectivity confidence error matrix may also be included in the sensitivity toolbox of metapopulation PVA.

## **6.5. Conclusion**

DeerDisperser estimates between-patch connectivity (probabilities of disperser transfer) according to different kinds of random walk models. It may be used by land managers to improve their connectivity management scenarios, and secondly, may help wildlife managers and conservationists as they may input connectivity estimations into population viability analyses and therefore represent more explicitly spatial dynamics within metapopulation models (Wiegand et al. 1999).



## **7. PREDICTING HABITAT PATCH COLONIZATION PROBABILITIES FOR AN EXPANDING RED DEER SUBURBAN POPULATION**

---

*Between habitat-patches connectivity estimations*

### **7.1. Summary**

- 1) We tested random walk approaches (Gustafson and Gardner 1996) to assess presence or absence of red deer corridors between habitat patches in the suburban area of Geneva. Suitable habitat patches of this highly fragmented landscape had already been located, but in addition prediction potential distribution of red deer is important for wildlife management.
- 2) We used information from one part of our study area, where red deer are present, to parameterize a spatially explicit individual-based model (DeerDisperser). The virtual individuals move stochastically on a corridor suitability map and the model allows estimation of transfer rates between habitat patches. A cut-off value of these transfer rates was found to discriminate between presence and absence of corridors. We next applied the model on the remaining study area to predict whether red deer may reach other suitable habitat patches.
- 3) The results confirm that random walk models are useful tools for estimating connectivity and for corridor identification with spatial data. In our case, correlated random walk models give better results than random walk models.

## **7.2. Introduction**

Habitat destruction and fragmentation are cited as major causes of species loss (e.g. Hanski 2001). Fragmentation generally results in a landscape consisting of remnant areas of isolated habitat patches surrounded by a matrix of non-suitable habitat. The survival probability of a species in isolated populations depends partially on its ability to disperse and the probability of extinction generally increases with the level of fragmentation (Saunders 1990, Hanski et al. 1994, Lindenmayer and Possingham 1996). It is therefore important to understand how landscape characteristics affect connectivity between habitat patches (Bennett 1999).

Until recently, very little information has been published on how animals use the landscape during their dispersal process. This is especially true for large mammals mainly as a consequence of the high cost of obtaining a statistically sufficient sample size of individual animals (Alexander and Waters 2000, Palomares 2001, Zimmermann and Breitenmoser 2002, Dyer et al. 2002 and review by Tischendorf and Fahrig 2000). Population models have nevertheless become increasingly popular in conservation biology (Wiens 1997, Coulson et al. 2001, Reed et al. 2002). Traditional approaches assume a binary landscape of habitat and a uniform matrix of nonhabitat surrounding the habitat patches and this assumption simplifies modeling. Connectivity between habitat patches is generally input simply as a function of the distance between two habitat patches and sometimes combined with size of habitat patches (Dock et al., 1992, Thomas et al. 1992, Johst and Brandl 1997, Akçakaya and Atwood 1997, Lurz et al. 2001, Petit et al. 2001, Stephens et al. 2002), that corresponds to a “pseudospacial” model (Gough and Rushton 2000). However, the surrounding matrix may significantly influence the “effective isolation” of habitat patches (Gustafson and Gardner 1996, Travis and French 2000, Ricketts 2001) resulting in more or less isolated patches than expected according to a distance function. As an example, landscape structures may create barriers to dispersal (Dmoswki and Kozakiewicz 1990, Baur and Baur 1995). Moreover, of the few studies that integrate spatially-explicit dispersal, most 1) are theoretical models that test hypothesis on landscape fragmentation (Gustafson and Gardner 1996, Tyre et al. 1999), 2) are usually parameterized with expert values (Shippers et al. 1996, Cramer and Portier 2001, Vuillemier and Prélaz-droux 2002) or 3) have used empirical information on breeding habitat (Wiegand et al. 1999, Clevenger et al. 2002) assuming that the dispersal habitat use is the same as the annual habitat use, even though it may not be the case (Merriam and Lanone 1990, Kindvall 1999, Palomares 2001).

Here we use the approach developed by Gustafson and Gardner (1996) to parameterize a GIS individual-based dispersal model for the red deer *Cervus elaphus* population in the suburban area of Geneva city (Figure 5-1) which are currently colonizing this highly fragmented area. As a consequence, local managers would like to know whether red deer might reach other suitable habitats within this area.

The GIS dispersal model is used to simulate dispersal-transfer rates between habitat patches, which are matched with field information on the presence-absence of corridors. By comparing these two data sets, we are able to define a cut-off value of simulated transfer rates that discriminates between presence and absence of corridors between two habitat patches. Simulated individuals walk on a corridor suitability map that was developed in a previous chapter (5).

### 7.3. Methods

#### 7.3.1. Model overview

We used the DeerDisperser software (Patthey 2002) that permit the estimation of the landscape connectivity between habitat patches (Chapter 5). This tool simulates individual random moves on a grid cell landscape map containing dispersal probabilities for each cell. Different kinds of random walk models may be applied. Simulated individuals start randomly in a source patch, then move according to the model rules and will therefore arrive or not in other patches. The connectivity between a source patch and a target patch is estimated as the proportion of animals that arrive in the target patch divided by the number of animals starting in the source patch (Gustafson and Gardner 1996, Tischendorf and Fahrig 2000). Each patch of the landscape is considered to be a source while the others are target patches.

#### 7.3.2. Model inputs

A map of *red deer linear corridors* was established for our study area (Chapter 5) and considered as the reference map. This map contains information on usage frequency of deer occurrence (yes, no) but no information on the direction of movements (Figure 7-2).

We used the habitat suitability (HS) map constructed in chapter 2 to create a map of *suitable habitat patches*. Patches were defined as forested areas with a HS value greater than 0.5

(Figure 7-2). The Jura Mountains were divided into 4 small patches of the same size as lowland patches, to limit a size effect (Gustafson and Gardner 1996).

In chapter 5, we built a *corridor suitability map* and its associated confidence error maps. These maps contain probability pixel values to belong to a corridor, from absolute barriers (0) to ideal corridors (1). Pixel size of the map was 10 meters squares.

The patch map and the corridor suitability map were input to the individual based random walk model.

### **7.3.3. Model parameters**

The number of individuals dispersing per habitat patch was fixed to 10,000, because preliminary tests with lower numbers reveal too large irreproducibility in results.

Maximal walking distance was limited to 10,000 pixel steps per individual, which is a distance three times higher than the mean distance between habitat patches, and allowed movers to reach adjacent habitat patches.

### **7.3.4. Calibration/validation process**

Our study area was divided into two parts. The first region is the western Geneva bassin. In this area, we have information on presence/absence of red deer corridors. We limited this region to the west by the highway N1, as we do not have valuable estimation of highway effect on dispersal (see chapter 5). This area was used to calibrate and validate our models. We parameterized a self-avoiding random walk (SAW) model, several correlated random walk (CRW) models with different turning angle concentration parameters (K parameters, Appendix 13-5) and simulated individual dispersals. Simulated transfer rate values were related to presence/absence of a corridor using a confusion matrix and kappa statistics (Cohen 1960, Fielding and Bell 1997) in order to determine a cut-off value of simulated transfer rate that allow discrimination between presence or absence of corridor.

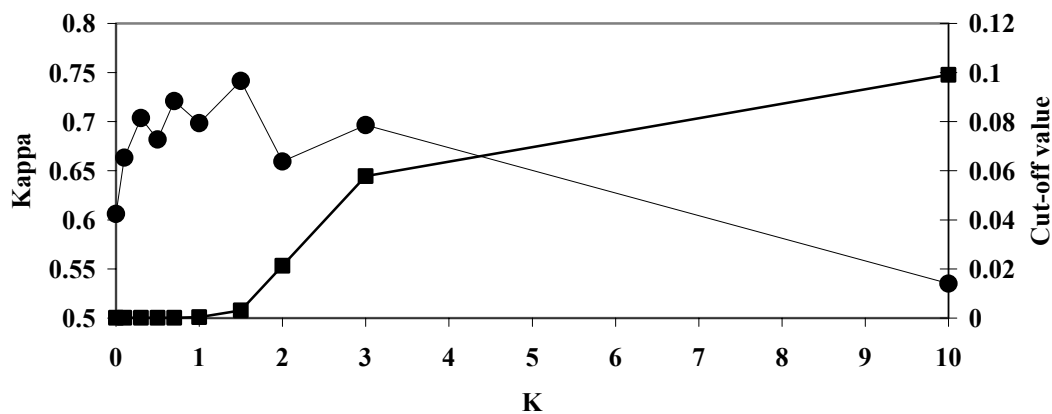
Sensitivity to parameter change was tested in order to evaluate the model. Sensitivity analysis were performed by simulating random walk on the corridor suitability and also on its confidence error maps (See section 1.6.3 for error maps construction). Kappa statistics was calculated with the cut-off value determined from the reference map.

Next our model was applied to the second part of our study area, in which we have only corridor information based on expert knowledge, in order to predict patch colonization.

## 7.4. Results

### 7.4.1. Calibration

The kappa statistic of our different model parameterizations from random ( $k=0$ ) to correlated random walk models revealed that the best model is obtained with a turning angle concentration parameter of 1.5 associated with a kappa value of 0.74 (Figures 7-1 and 7-2).

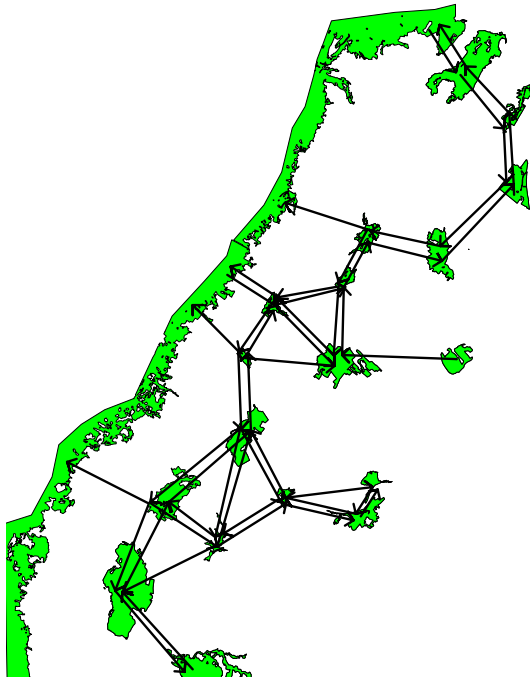


**Figure 7-1:** Kappa statistics (circles, left scale) and transferring cut-off value (squares, right scale) as function of turning angle concentration parameter (K, appendix 13-5). The kappa index is a measure of association ranging from 0.0 (no agreement) to 1.0 (identical).

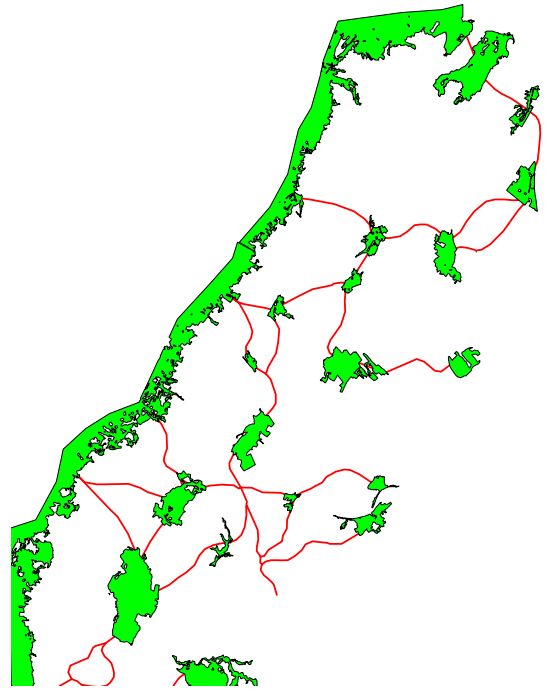
We applied the correlated random walk model with a turning angle concentration parameter of 1.5 on the confidence error corridor suitability maps. The resulting kappa statistics (0.76 and 0.71) are very close to the kappa statistic of the reference map, showing low variability in model predictions.

A red deer habitat point of view

a)

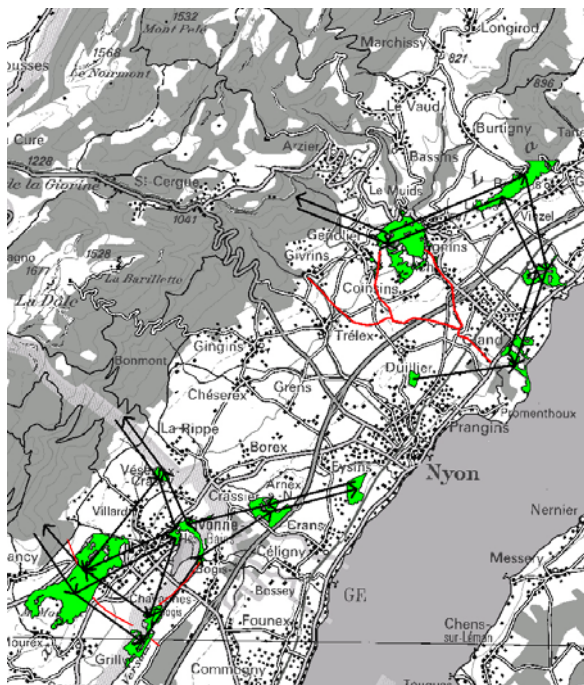


b)

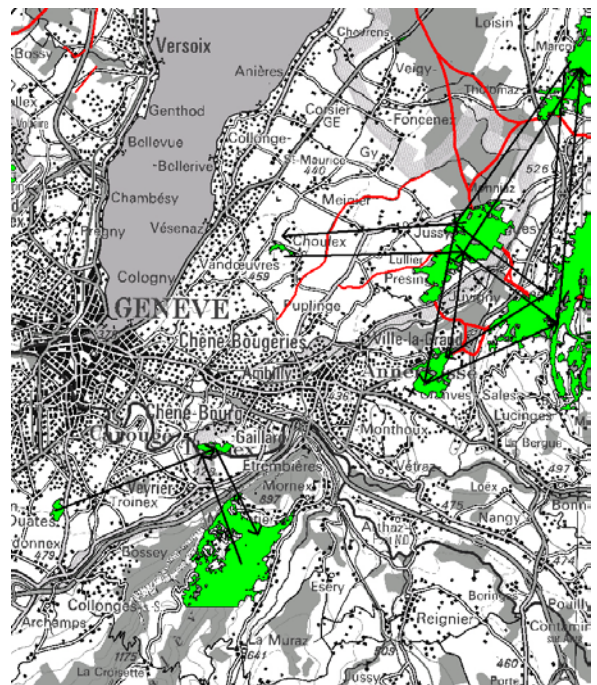


**Figure 7-2:** a) Between red deer habitat patches connectivity estimated with the best correlated random walk model and b) observed red deer corridors used to calibrate this model in the Geneva suburban area.

a)



b)



**Figure 7-3:** Between red deer habitat patches connectivity estimated with the correlated random walk model calibrated in a) south of Vaud state and b) east of Geneva. Habitat patches (green polygons), simulated connection (black lines) and observed wildlife corridors (expert assessment) (red lines) are indicated.

### 7.4.2. Tests on the second part of the study area

Connectivity estimations from application of the best model on other regions that are situated near our calibration area are concordant with observed wildlife corridors (Figures 7-3a and 7-3b).

## 7.5. Discussion

### 7.5.1. Strengths and weaknesses of the model

Overall, our results show that habitat-patch connectivity may be sufficiently estimated by the random walk modeling approach. Firstly, simulations performed with confidence errors corridor maps reveal low differences in connectivity estimations (Wennergren et al. 1995). Secondly, reclassifications of connectivity estimation into presence/absence of corridors between habitat patches are “very good”, based on the Monserud and Leemans (1992) scale of agreement (Figure 7-1). Reclassifications are not true validations. Exact validation has to be performed in an other area than the one used for calibration (Manel et al. 1999). Unfortunately, we could not perform this model validation in such an area, as we lacked information on connectivity for red deer. Nevertheless, our predicted connectivity values are concordant with reference to current wildlife corridors based on expert assessments (Figure 7-3 and 7-4).

Our model is based on grid cell maps that are obtained by “rasterizing” habitat polygons and road lines (Chapter 5). As movement distances between cells are not equal, this may bias behavior. In our case, we assumed that red deer would not be affected by this small resolution bias, considering the low mean distance between habitat patches as compared to its potential daily movement length (Haller and Filli, *unpublished data*).

The DeerDisperser user has the opportunity to input his own corridor suitability map. We incorporated a corridor suitability map that considers different habitat influence radii (Chapter 5). In this way, random walk movements are not strictly limited to pixel-to-pixel actions. Integrating complex spatial information would undoubtedly be an improvement of current individual based movement models (Vuillemier and Prélaz-Droux 2002), which generally use habitat information only at the pixel level.

DeerDisperser random walk structure is currently limited to very simple movement behaviors and consequently does not integrate other potentially important parameters. For instance, animals may; 1) switch between different behaviors during their dispersal process (Moralles and Ellner 2002), 2) learn and register landscapes, 3) perceived suitable habitat at distance and try to reach them directly (Fahse et al. 1998) and/or 4) die during their dispersal process due to environmental factors such as occurrence of roads. DeerDisperser may probably be improved by integrating these behaviors (it is already the case for habitat mortality). However, as we do not currently have the necessary field information on red deer dispersal behavior, integrating these additional parameters would have increased model complexity and made it more difficult to parameterize adequately. Ruckelshaus et al. (1997) suggested that less detailed models should improve the match between model complexity and the quality of the available data.

### **7.5.2. Predicting inter-patch connectivity**

It appears that the best results are obtained with the correlated random walk (CRW) model. Their kappa statistics are slightly better than the SAW, but their transfer rate values are higher, meaning that more individuals achieved dispersal (Figure 7-1). A higher transfer rate cut-off value is therefore less sensitive to stochastic behavior. Moreover, dispersal patterns of CRW have a higher range than those from SAW (Figure 7-1). Although CRW models seem to have several advantages, their main drawback is their higher simulation time, making their calibration (change of the turning angle concentration parameter  $k$ ) time consuming. CRW simulation time is about 10 times higher than the SAW simulation time.

The better result obtained with the correlated than with the random walk model is not surprising. Correlated pathways are more likely to connect to habitat patches (by using short gaps) than random walk models, which may be lost or do not pass through these short-in-length poor-value corridor areas.

Model output also demonstrates that connectivity may be asymmetric (Figure 7-2). This result is in agreement with theoretical findings (Gustafson and Gardner 1996) and probably with real species dispersal behavior. Therefore modeling provides more information than expert-field assessments. Presumably, kappa statistic values would have been higher if we had not considered corridor direction in simulation results (field expert assessment of corridor use do



not allow discrimination of direction). In most cases, an observed presence is predicted as an absence in one direction and as a presence in the other direction (Figure 7-2).

## **7.6. Management implications and future prospects**

Conservation and land-use planning require an understanding of the relationship between landscape patterns and the dynamics of populations, a task that requires understanding of species movements and dispersal (Kareiva and Wennergren 1995, McDonald and Johnson 2001).

The random walk approach seems to be an appropriate tool in the context of corridor management. Firstly our results suggest that random walk models are valuable tools to estimate connectivity between habitat patches given that sufficient information on dispersal habitat use is acquired (King and With 2002). This reinforces the urgent need for information on individual dispersal behavior to improve landscape connectivity management. Secondly, the visitation frequency maps show where the corridors used by dispersal movers are, and therefore provide useful maps for management purposes. They also point out precisely where corridors may be interrupted and where road-conflict areas may be located. Thirdly, connectivity estimation may be implemented in metapopulation models in order to enhance the dispersal toolbox of population dynamics models (McDonald and Johnson 2001). In addition, land-user planners and conservationists may also test landscape effects changes on connectivity networks and on population dynamics, by modifying the landscape in the GIS (Van Apeldoorn et al. 1998, Clark et al. 2001, Sachot 2002).

Since model behavior is sensitive to its own parameters (Ruckelshaus et al. 1997, Clevenger et al. 2002), models should generally be used with caution. Tests for sensitivity to parameters must be performed as they reveal the strength of the model (Reed et al. 1998) or allow to point out the parameter that needs to be examined in priority (Burgman et al. 1993). Models need to be validated before being applied to real landscapes and/or used as conservation tools. We believe that our model may be used at least to test land use management scenarios in our study area and may probably be used for extrapolations to other similar areas, given that a highway does not separate habitat patches.

An alternative method to estimate connectivity would be to analyze genetic differentiation among populations. Population genetic structure is an indirect measure of dispersal between groups of individuals or between parents and offsprings (e.g. Vos et al. 2001). Between-patch connectivity may be then related to habitat between patches in order to find a habitat effect on connectivity (Lee et al. 2001).

## **7.7. Conclusion**

The goal of this chapter was to parameterize a dispersal model as a tool for estimating habitat patch connectivity. Results show that the random walk model can adequately reveal the connectivity network and enables location of dispersal bottlenecks. Moreover, visitation frequency maps indicate where animals disperse and where the key regions are located. Future prospects might be to analyze dispersal behaviors and dispersal habitat use at a finer scale in order to incorporate a better knowledge into our models.

## 8. CONCLUSIONS AND PERSPECTIVES

---

### *Links with management applications*

#### 8.1. Habitat selection and habitat suitability maps

Our results are consistent with previous findings on red deer habitat selection in well-established populations and offer new insights in red deer ecology and its associated management (Table 8.1).

Both in lowland (Geneva Bassin) and Jura Mountains, red deer presence is correlated open forests with low-level human disturbance. Distance to buildings and roads, density of forest and open forest, summer herbaceous plant cover (sedges, *Festuca altissima* and red raspberry) are important habitat predictors that are positively correlated with red deer presence. Moreover, our results emphasize the importance of microhabitat for thermoregulation, especially during winter mornings. Some of these habitat features are derived from GIS and thus allow management scenario testing on red deer habitat suitability maps. As an example, we may simulate the construction of a road or a new village and assess its impact on red deer habitat by comparing the habitat suitability maps before and after the landscape modification (Rushton et al. 2000, Whitfield et al. 2001). Some relevant habitat factors are only measurable in the field (i.e. solar radiation) rendering GIS based management scenarios unreliable. However these habitat factors are related to forest structure on which a management control is possible.

We based our habitat analysis on a hierarchical habitat selection framework as recommended by several authors (e.g. Orians and Witenberger 1991, George and Zack 2001, McLoughin et al. 2002). Our results support the utility of this approach: the same ecological factors may have a different impact on red deer distribution according to the level of selection concerned, as in the case of slope. We have also found that a comparison of habitat outside red deer range with bedding sites habitat (combination of population and home range selection levels) failed to detect important factors for one of the selection level (Dunand 2001). This hierarchical approach also facilitates the definition of management plans. Managers may follow the hierarchical process to propose management options for each selection level. For instance, they should first act on broad scale ecological factors, such as human disturbance to delimit

red deer population ranges (population selection level) and then within defined population ranges, act on finer scale factors (home range selection level) such as canopy cover.

**Table 8-1:** Important habitat factors for red deer distribution according to selection level, scale of observation, seasons, region, and the reference chapter. Management applicability is indicated. J: Jura Mountains, G: Geneva basin, W: winter, S: summer, ○: already mentioned in other *Cervus elaphus* studies, ◐: already mentioned in other *Cervus elaphus* studies but for the home range selection level \*, ◑: hypothesized in other *Cervus elaphus* studies, ●: new important habitat predictor.

Selection level	Region	Scale	Season	Habitat feature	Status	Ref.*	Management applicability	Chapter
<b>Population</b>								
	J, G	Broad	W, S	Low building density, High distance to building	◐	6	-	2, 3, 4
	J, G	Broad	W, S	High distance to roads	◐		Yes	2, 3, 4
	J, G	Broad	W, S	High forest density	●		Yes	3, 4
	J	Broad, Local	S	Higher open forests density	●		Yes	2, 3, 4
	J	Broad	W	High meadow and agriculture density	●		Yes	4
	J	Broad	S	Low roe deer hunting pressure	◐	8,9	Yes	4
	J	Local	W, S	Higher <i>Festuca altissima</i> cover	◐	12	No	3
	J	Local	S	High grass cover	◐		Yes	3, 4
	J	Local	S	Higher elevation	●		No	3, 4
<b>Home range</b>								
	J	Broad	W	High forest density,	●		No	4
	J	Broad	W	High agriculture density	●		No	4
	J	Broad	W, S	Low human disturbance	○	1,3,4,5,6,11	Yes	4
	J	Broad	S	Low agriculture density	●		No	4
	J	Local	S	Open stands with high cover of grass and red raspberry	○	3,6,10,11	Yes	4
	J	Micro	W	High morning solar radiation flux	◐	7	Yes	4
	J	Micro	W, S	High coniferous cover	●,○	2,4	Yes	4

\* Nearly all studies used home range selection level or did not clearly indicate it. We added briefly after the reference, shortly the type of data and extent comparison:

- 1 Rowland et al. 2000; elk locations vs.fenced study area
- 2 Staines 1976; visual observation vs. random plots inside study area
- 3 Edge et al. 1987; elk location vs. random points inside study area
- 4 Millspaugh et al. 1998; elk bed vs. random plots inside home range

- 5 Grover and Thomspson 1986; elk feeding use for random plots inside study area
- 6 Morellet et al 1996; pellets densities in study area
- 7 Cook et al. 1998; elks inside pens
- 8 Millspaugh et al. 2000; elk location vs. hunter locations
- 9 Conner et al. 2001; elk collar fitted movements
- 10 Welch et al. 1990; pellets counts on permanent plots
- 11 Catt and Staines 1987; locations vs. habitat at home range scale

The major limitation of this work concerns a potential difference in habitat selection between sexes that should be taken into account for further research. Stags in well-established populations have shown different pattern of habitat use than females (Conradt et al. 1999). Some authors even proposed to consider male and female red deer as two distinct species (e.g. Staines et al. 1982). Regarding red deer-forestry conflicts, male specific management may be important because males not only strip barks but also fray trees (Gill 1992).

Some of our human disturbance variables are important habitat predictors at both population and home range selection level. We are aware that our disturbance variables need to be improved, especially at the home range selection level. Distance to inhabited areas may well reflect human perturbation at broad scales, but at local scale visual cover (Edge et al. 1987) or forest penetration rate by the public may be the most important key factors. Red deer are known to accommodate to predictable human perturbations (Milspaugh et al. 2000) and may live in an area with high road frequentation without public penetration into forests (Patthey 2003). In this sense, mapping different human disturbances (i.e. hunting, dog recreation areas) may greatly improve red deer habitat suitability models.

Radiotracking may also certainly improve our understanding of red deer habitat selection. This technique allows the analysis of specific behavior such as feeding and differentiating male and female behavior. Nevertheless, the efficiency of this method closely depends on the high number of required radiotracked animals (Mainy 1993, Roloff and Kernohan 1999).

## **8.2. Corridor selection and colonization probabilities**

Management of ecological networks is nowadays an important task for urban and wildlife managers (e.g. Bennett 1999 for IUCN). Our work is the first 1) to provided a spatially explicit corridor suitability map, and 2) to allow the estimation of between-patch colonization probabilities that are both not parameterized with expert values. The combination of these two models applied over all our study area, allowed us to define the potential red deer distribution. Moreover, our tools are applicable to other terrestrial species (after parameterization) and they should allow ecological network management at a large scale through simulation of land-use management scenarios. Connectivity estimation may also be implemented in population

viability analysis (PVA) to improve their dispersal box. Hence, we offer a new methodology for managers to deal with ecological network management of red deer and other species.

According to our dispersal habitat analyzes, high density of habitat containing trees (such as forest and hedges) favor corridor occurrence. In contrast, densities of and distance to buildings decrease the chance of finding a corridor. This result seems *a priori* obvious but the relationship is explained in a statistical way and is no more a expert view of what is a good or a bad corridor. This scientific based relationship may undeniably improve expert-based opinions (Warnken and Buckley 1998).

Although our models reveal robustness and reliability, they need to be improved in the future. Our data set is unable to reveal a potential highway effect on between-forest patch connectivity (Chapter 5). This point needs further investigations, as highways may be important barriers to animal dispersal (Bennett 1999 for a review).

Some studies on movement behavior tracked insects (i.e. butterfly) or small animals (i.e. frogs, small mammals) in nature. They captured, marked, released and followed individuals in a controlled landscape (Cain 1985, Haddad 1999, Kindwall 1999, Wiens 2001), in the landscape from which they came (Sjögren-Gulve 1998, Zimmermann et Breitenmoser 2002, Tigas et al. 2002) or in real but unknown landscape (Charrier et al. 1997, Bright 1998, Brooker et al 1999, Jonsen and Taylor 2000, Doncaster et al. 2002). In this way habitat-based dispersal behavior may be split up and dispersal habitat selection analyzed, thereafter leading to direct applications to management of these species at a broader scale (Beier and Noss 1998). Current radiotracking tools (GPS) permit tracking of animal movements intensively and precisely. Releasing marked red deer in an unknown fragmented landscape is evidently risky with this large and potentially dangerous species. Although this procedure may offer the best results, the radiotracking of young males that are the most inclined to disperse (Hamann and Klein, *unpublished data*) or of resident individuals in a patchy landscape should, even so, provide useful data to improve our understanding of red deer movement behavior.

An alternative to the correlation analyzes between habitat factors and dispersal would be the use of genetics. Genetic analyzes allow estimation of connectivity between populations and also natal dispersal through determination of parental links. Connectivity estimates may then be related to habitat pattern between the two populations (Lee et al. 2001, Fontanillas et al., *in prep*) or to habitat pattern between mother and offspring.

### 8.3. Management applications of modeling results: illusion or reality?

Our modeling approaches have been used to understand habitat relationships of red deer, to evaluate its habitat quality, to develop tools to estimate between-patch connectivity and to deal with management scenarios (Figure 1-7, Table 8.2). However the use of models may be limited because they are simplifications of reality. Model results are dependent on what we give (or are able to give) them and on their own (i.e. mathematical) construction. Thus model quality relies 1) on the *a priori* knowledge of the species pointing at the importance of the field experience for the species concerned, and 2) on our ability to adequately measure the ecological factors and 3) to relate it to the model's objectives in a statistical way. Therefore, model validation is essential to evaluate performance and range of application and consequently to allow managers to point out model limits and strengths.

Modeling procedures may also reveal potentially important ecological factors that can be further investigated, such as human disturbance in the case presented here. Thus, models can be improved by successive parameterization and testing on new data (e.g. Lint et al. 1999 or Zabel et al. 2002 for the well known case of Spotted Owl in USA, Wilhere 2002).

The power of geographic information systems (GIS) has been demonstrated throughout this work. Nevertheless, as GIS models use a lot of data and perform complex calculations, they are reliant on computer performance. Although rapide developments in technology has improved the power of analyses, population-level analysis still have high data storage and processing requirements. Therefore, in some cases, habitat parameters that have been found to be significant at a local scale may not be applied on a broader scale (i.e. a 10m resolution gridded GIS map of Switzerland). Moreover, it is often difficult to collect same data for management purposes due to limited availability over administrative limits or due to high costs.

One important improvement of red deer management initiated by this study is linked to the use of statistical modeling. Such tools allow us to answer complex management questions such as which are the most important factors, where to apply management measures and at what scale? Models allow the ranking of ecological factors or management scenarios. For instance, we used multivariate analyses that weight effects of each ecological factor. Therefore, our results provide the opportunity to wildlife and land managers to propose

objective and scientifically based management measures instead of the expert based decisions (Dee Boersma and DeWeerts 2001).

**Table 8-2:** Modeling tools developed for a spatially-explicit management of red deer.

<b>Modeling tools</b>	<b>Chapter</b>
Habitat suitability model at the population selection level	2, 3, 4
Bedding-site suitability model at the home range selection level	4
Corridor suitability model for a suburban area	5
Between-patch connectivity estimator tool ( <i>DeerDisperser</i> )	6
Parameterization framework to estimate between-patch connectivity	7

#### **8.4. Towards spatial wildlife management modeling of red deer populations**

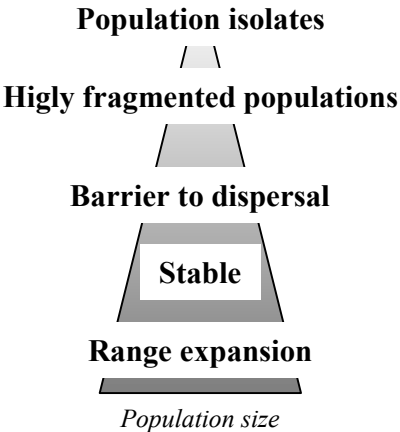
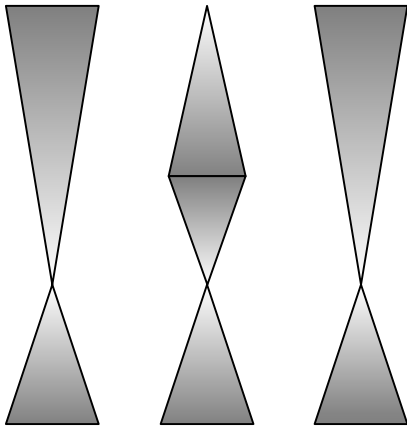
We produced seasonal habitat suitability models and parameterized a tool to estimate when suitable habitats are or not connected. With these tools, we may construct future potential red deer distribution maps. Thus, we have answered our questions, achieved our objectives and offered tools to improve the spatial wildlife management of red deer (Figure 8-1). Nevertheless, red deer potential distribution maps are static in the sense that they are a snapshot of an unknown future time. Temporal information may be important for managers, allowing them to improve planning. Are we able to simulate spatial red deer recolonization? To answer that question, we need to add red deer survival and reproduction to our tools in order to construct a spatially explicit population model that integrates habitat-specific demographic parameters such as growth, reproduction, natal dispersal, death and hunting mortality (for game management).

Our results show that red deer habitat may not be reduced to a simple habitat/non-habitat landscape, but is a continuous landscape with variable habitat quality and with no well-defined suitable habitat boundaries. For instance, a single red deer population is likely to occupy the entire Jura Mountains. In the future, probably only highways will present barrier to dispersal and this may even induce a metapopulation pattern. Consequently, we may not apply a metapopulation model to simulate the recolonization of Swiss Jura Mountains for instance, and wonder whether we should consider instead a cellular automaton or an individual based population model. Red deer habitat selection is different among seasons. The red deer social structure and social behavior are complex; sex segregation is observed (Clutton-brock et al. 1982), and individual reproduction parameters depend on year (Albon et al. 2000), habitat (Birtles et al. 1998, Conradt et al. 1999), climate (Myserud et al. 2000), age,



hierarchical rank (Clutton-brock et al. 1984), genotype (Coulson et al. 1998) and density (Kruuk et al. 1999, Bonenfant et al. 2002). Dispersal is poorly documented but differs between the sexes (Hamann and Klein, *unpublished data*). Although computer performances promise in the near future to create population individual based models (IBMs) for large populations, these IBMs need to be parameterized. Kareiva et al. (1996) proposed to use modeling approaches that take into account the limitations of existing knowledge instead of more complex models, as their output may be especially sensitive to errors in difficult-to-estimate parameters such as dispersal-mortality rates. Thus, cellular automaton seems to be a more appropriate tool because demographic parameters may be summarized and stochasticity may be added (e.g. Hirzel 2002).

This work is also a contribution to a comprehensive development of spatial wildlife management a currently growing field, in addition to classical population management tools (Figure 8-1). In the past, wildlife modeling was mainly used to improve conservation of endangered species or to test fundamental theories in biology. Only recently have models been applied to management of unthreatened or pest species.

POPULATION SPATIAL PATTERN	SPATIALLY-EXPLICIT POPULATION MODELING	POPULATION MANAGEMENT PRIORITIES
 <p>Population isolates</p> <p>Highly fragmented populations</p> <p>Barrier to dispersal</p> <p>Stable</p> <p>Range expansion</p> <p>Population size</p>	<p><i>Habitat modeling</i>    <i>Dispersal modeling</i>    <i>Dynamics Modeling</i></p>  <p>Modeling importance</p>	<p><i>viability</i></p> <p>Habitat restoration</p> <p>Wildlife corridors</p> <p><i>management</i></p> <p>Range control</p>

**Figure 8-1:** Links between animal population spatial pattern, spatially-explicit population modeling and population management priorities (adapted from Neet, *unpublished*)

## **8.5. General conclusion**

One of the difficulties encountered in this applied research was to find a place in the academic scientists, government biologists and implicated landscape users system. This status question that I discussed with several people, followed me during these last four years. The researcher involved in applied research are often considered to be poor scientists by academics, and unaccomplished naturalists by involved landscape users, and as a result, is placed in an uncomfortable place. Moreover, Dee Boersma and DeWeerd (2001) wrote about this complex relationship: “Academics wonder why agencies don’t know more about the biology of the species ... and why they take so long to get anything done, agency scientists grumble that academics are too quick to criticize and often undertake research projects that are difficult to apply to real-world concerns”. The job of the applied researcher is to improve biological understanding of problems, to find the best methods to resolve them according to their potential applications in the “real-world”. This task requires both academic and naturalist’s skills. This multidisciplinary approach is essential to improve our biological knowledge of specie ecology and for development of appropriate management tools.

To conclude, I believe that we have constructed biologically and spatially more realistic habitat and dispersal models than those currently used for red deer. Although they will be improved in the future, our population and home range level predictive models will be critical tools for insuring forestry, recreation and landscape management of red deer in western Switzerland and nearby France.

## 9. BIBLIOGRAPHY

---

- ANDERSON G.S., and DANIELSON B.J. 1997. The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. *Landscape Ecology* 12(5):261-271.
- AKCAKAYA H.R., and ATWOOD J.L. 1997. A habitat based metapopulation model of the California gnatcatcher. *Conservation Biology* 11(2):422-434.
- ALBON S.D., COULSON T.N., BROWN D., GUINNESS F.E., PEMBERTON J.M., and CLUTTON-BROCK T.H. 2000. Temporal changes in key factors and key age groups influencing the population dynamics of female red deer. *Journal of Animal Ecology* 69:1099-1110.
- ALEXANDER S.M., and WATERS N.M. 2000. The effects of highway transportation corridors on wildlife: a case study of Banff National Park. *Transportation research part c* 8:307-320.
- APPS C.D., McLELLAN B.N., KINLEY T.A., and FLAA J.P. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, british Columbia. *J. Wildl. Manage* 65(1):65-77.
- AUSTIN M.P., CUNNINGHAM R.B., and FLEMING P.M. 1984. New approaches to direct gradient analysing using environmental scalars and statistical curve-fitting procedures. *Vegetatio* 55:11-27.
- BAGUETTE M., PETIT S., and QUEVA F. 2000. Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal of Applied Ecology* 37(1):100-108.
- BAUR B., and BAUR A. 1995. Habitat-Related Dispersal in the Rock-Dwelling Land Snail *Chondrina-Clienta*. *Ecography* 18(2):123-130.
- BEIER P., and NOSS R.F. 1998. Do habitat corridors provide connectivity ? *Conservation Biology* 12(2):1241-1252.
- BENNETT A.F. 1999. Linkages in the landscape: the role of corridors and connectivity in wildlife conservation. Gland, Switzerland and Cambridge, UK: IUCN. x+254 p.
- BERGGREN A., CARLSON A., and KINDVALL O. 2001. The effect of landscape composition on colonization success, growth rate and dispersal in introduced bush-crochets *Metrioptera roeseli*. *Journal of Animal Ecology* 70:663-670.
- BIRTLES T., GOLDSPIK C.R., GIBSON S., and HOLLAND R.K. 1998. Calf site selection by red deer (*Cervus elaphus*) from three contrasting habitats in northwest England: Implications for welfare and management. *Animal Welfare* 7(4):427-443.
- BISSONETTE J.A. 1997. *Wildlife and landscape ecology*. Bissonnette JA, editor. New-York: Springer-Verlag. 410 p.
- BLANKENHORN H.J., BUCHLI C., and VOSER P. 1978. Migration and Seasonal Distribution of Red Deer (*Cervus elaphus* L) in Swiss National Parc and Its Surroundings. *Revue Suisse De Zoologie* 85(4):779-789.
- BRIGHT P.W. 1998. Behaviour of specialist species in habitat corridors: arboreal dormice avoid corridor gaps. *Animal Behaviour* 56:1485-1490.
- BROOKER L., BROOKER M., and CALE P. 1999. Animal dispersal in fragmented habitat: measuring habitat connectivity, corridor use, and dispersal mortality. *Conservation Ecology* 3(1).
- BONENFANT C., GAILLARD J.M., KLEIN F., and LOISON A. 2002. Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. *Ecography* 25(4):446-458.
- BOONE R.B., and HUNTER M.L. 1996. Using diffusion models to simulate the effects of land use on grizzly bear dispersal in the Rocky Mountains. *Landscape Ecology* 11(1):51-64.
- \_\_\_\_\_, and KROHN W.B. 2000. Predicting broad-scale occurrences of vertebrates in patchy landscapes. *Landscape Ecology* 15(1):63-74.
- BORLAND. 1998. Borland Delphi Professional, Inprise corporation. Url: <http://www.inprise.com/delphi/>

- BOYCE, M.S., VERNIER, P.R., NIELSEN, S.E., and F.K.A. SCHMIEGLOW. 2002. Evaluating resource selections functions. *Ecological Modelling* 157: 281-300.
- BRAUN-BLANQUET J. 1964. *Pflanzensoziologie*. Springer-Verlag, editor. New-York.
- BURGMAN M.A., FERSON S., and AKÇAKAYA H.R. 1993. Risk assessment in conservation biology. Hall C, editor. London.
- CAIN M.L. 1985. Random Search by Herbivorous Insects - a Simulation-Model. *Ecology* 66(3):876-888.
- CARGNELUTTI B., REBY D., DESNEUX L., ANGIBAULT J.M., JOACHIM J., and HEWISON A.J.M. 2002. Space use by roe deer in a fragmented landscape some preliminary results. *Revue D Ecologie-La Terre Et La Vie* 57(1):29-37.
- CATT D.C., and STAINES B.W. 1987. Home Range Use and Habitat Selection by Red Deer (*Cervus elaphus*) in a Sitka Spruce Plantation as Determined by Radio- Tracking. *Journal of Zoology* 211:681-693.
- CHEN H.P., LI F., LUO L.Y., WANG H., and MA J.Z. 1999. Winter bed-site selection by red deer *Cervus elaphus xanthopygus* and roe deer *Capreolus capreolus bedfordi* in forests of northeastern China. *Acta Theriologica* 44(2):195-206.
- CHARRIER S., PETIT S., and BUREL F. 1997. Movements of *Abax parallelepipedus* (Coleoptera, Carabidae) in woody habitats of a hedgerow network landscape: a radio-tracing study. *Agriculture Ecosystems & Environment* 61:133-144.
- CHEN H.P., LI F., LUO L.Y., WANG H., and MA J.Z. 1999. Winter bed-site selection by red deer *Cervus elaphus xanthopygus* and roe deer *Capreolus capreolus bedfordi* in forests of northeastern China. *Acta Theriologica* 44(2):195-206.
- CLARK M.E., ROSE K.A., LEVINE D.A., and HARGROVE W.W. 2001. Predicting climate change effects on Appalachian trout: combining GIS and individual-based modeling. *Ecological Applications* 11(1):161-178.
- CLEVENGER A.P., and WALTHO N. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. *Conservation Biology* 14(1):47-56.
- \_\_\_\_\_, WIERZCHOWSKI J., CHRUSZCZ B., and GUNSON K. 2002. GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. *Conservation Biology* 16(2):503-514.
- CLUTTON-BROCK T.H., GUINNESS F.E., and ALBON S.D. 1982. The structure of social groups in hinds and stags. Red deer: behavior and ecology of two sexes. Chicago: The University of Chicago Press. p 201-218.
- \_\_\_\_\_, ALBON S.D., and GUINNESS F.E. 1984. Maternal Dominance, Breeding Success and Birth Sex-Ratios in Red Deer. *Nature* 308(5957):358-360.
- \_\_\_\_\_, IASON G.R., and GUINNESS F.E. 1987. Sexual Segregation and Density-Related Changes in Habitat Use in Male and Female Red Deer (*Cervus elaphus*). *Journal of Zoology* 211:275-289.
- COHEN, J. 1960. A coefficient of agreement for nominal scales. *Educational Psychology*. 41: 687-690.
- COLE E.K., POPE M.D., and ANTHONY R.G. 1997. Effects of road management on movement and survival of roosevelt elk. *Journal of Wildlife Management* 61(4):1115-1126.
- CONNER M.M., WHITE G.C., and FREDDY D.J. 2001. Elk movement in response to early-season hunting in Northwest Colorado. *Journal of Wildlife Management* 65(4):926-940.
- CONRADT L., CLUTTON-BROCK T.H., and GUINNESS F.E. 1999. The relationship between habitat choice and lifetime reproductive success in female red deer. *Oecologia* 120(2):218-224.
- \_\_\_\_\_, \_\_\_\_\_, \_\_\_\_\_. 2000. Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. *Animal Behaviour* 59:1049-1060.
- COOK J.G., IRWIN L.L., BRYANT L.D., RIGGS R.A., and THOMAS J.W. 1998. Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. *Wildlife Monographs* 141(1-61).
- COULSON T., MACE G.M., HUDSON E., and POSSINGHAM H. 2001. The use and abuse of population viability analysis. *Trends in Ecology & Evolution* 16(5):219-221.

- COULSON T.N., ALBON S.D., PEMBERTON J.M., SLATE J., GUINNESS F.E., and CLUTTON-BROCK T.H. 1998. Genotype by environment interactions in winter survival in red deer. *Journal of Animal Ecology* 67(3):434-445.
- \_\_\_\_\_, ALBON S., PILKINGTON J., and CLUTTON-BROCK T. 1999. Small-scale spatial dynamics in a fluctuating ungulate population. *Journal of Animal Ecology* 68(4):658-671.
- CRAMER P.C., and PORTIER K.M. 2001. Modeling Florida panther movements in response to human attributes of the landscape and ecological settings. *Ecological Modelling* 140:51-80.
- DEBELJAK M., DZEROSKI S., JERINA K., KOBLER A., and ADAMIC M. 2001. Habitat suitability modelling for red deer (*Cervus elaphus* L.) in South-central Slovenia with classification trees. *Ecological Modelling* 138(1-3):321-330.
- DECALESTA D.S., and STOUT S.L. 2000. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. *Wildlife Society Bulletin* 25(2):252-258.
- DEE BOERSMA P., and DEWEERDT S. 2001. Tapping the Ivory tower. *Conservation Biology In Practice* 2(3):30-34.
- DELARZE R., GONSETH Y., and GALLAND P. 1998. Guide des milieux naturels de Suisse: écologie, menaces, espèces caractéristiques. Office fédéral de l'environnement dfedp, editor. Lausanne, Switzerland: Delachaux et Niestle. 415 p.
- DIDIER K.A., and PORTER F.P. 1999. Large-scale assessment of potential habitat to restore elk to New York State. *Wildlife Society Bulletin* 27(2):409-418.
- DONCASTER C.P., RONDININI C., and JOHNSON P.C.D. 2001. Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. *Journal of Animal Ecology* 70(1):33-46.
- DUNAND I. 2001. Le cerf, un amoureux des petites fleurs ? sélection de l'habitat chez le cerf (*Cervus elaphus*) au sein d'une population en voie d'expansion dans le massif jurassien [Master's thesis]. Lausanne: University of Lausanne, Ecology Institute. 41 p.
- DUNNING J.B., STEWART D.J., DANIELSON B.J., NOON B.R., ROOT T.L., LAMBERSON R.H., and STEVENS E.E. 1995. Spatially Explicit Population-Models - Current Forms and Future Uses. *Ecological Applications* 5(1):3-11.
- DYER S.J., O'NEILL J.P., WASEL S.M., and BOUTIN S. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 80(5):839-845.
- EASTMAN, J. R. 2001. IDRISI32 2.0. Clark labs, Workester.
- EDGE W.D., MARCUM C.L., and OLSONEDGE S.L. 1987. Summer Habitat Selection by Elk in Western Montana - a Multivariate Approach. *Journal of Wildlife Management* 51(4):844-851.
- FAHRIG L., and MERRIAM G. 1985. Habitat Patch Connectivity and Population Survival. *Ecology* 66(6):1762-1768.
- FAHSE L., WISSEL C., and GRIMM V. 1998. Reconciling Classical and Individual-Based Approaches in Theoretical Population Ecology - a Protocol For Extracting Population Parameters From Individual-Based Models. *American Naturalist* 152(6):838-852.
- FIELDING A.H., and BELL J.F. 1997. A review of methods for the assesments of prediction errors in conservation presence/absence models. *Environmental Conservation* 24(1).
- FOURNIER C. 1997. Bilan actuel et les perspectives d'évolution de diverses espèces animales dans le PNR du Haut-Jura.: ONFS.
- FRANKLIN S.E., STENHOUSE G.B., HANSEN M.J., POPPLEWELL C.C., DECHKA J.A., and PEDDLE D.R. 2001. An Integrated Decision Tree Approach (IDTA) to mapping landcover using satellite remote sensing in support of grizzly bear habitat analysis in the Alberta yellowhead ecosystem. *Canadian Journal of Remote Sensing* 27(6):579-592.
- FRID A., and DILL L. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6(1):art. n0-11.
- GAWRONSKI E. 2002. La sélection hivernale et estivale de l'habitat par le cerf (*Cervus elaphus*) dans le Jura [Master's thesis]. Genève: University of Geneva, Science Faculty. 57 p.

- GEBERT C., and VERHEYDEN-TIXIER H. 2001. Variations of diet composition of Red Deer (*Cervus elaphus* L.) in Europe. *Mammal Review* 31(3):189-201.
- GEORGE T.L., and ZACK S. 2001. Spatial and temporal considerations in restoring habitat for wildlife. *Restoration Ecology* 9(3):272-279.
- GEORGII B., and SCHRODER W. 1983. Home Range and Activity Patterns of Male Red Deer (*Cervus elaphus* L) in the Alps. *Oecologia* 58(2):238-248.
- GIBEAU M.L., CLEVINGER A.P., HERRERO S., and WIERZCHOWSKI J. 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biological Conservation* 103(2):227-236.
- GILL R.M.A. 1992. A Review of Damage by Mammals in North Temperate Forests .1. Deer. *Forestry* 65(2):145-169.
- GONZALES G., and PÉPIN D. 1996. Le cerf (*Cervus elaphus*) en milieu montagnard et nordique. I. Paléontologie, occupation de l'espace, utilisation du temps et des ressources, revue bibliographique. *Gibier Faune Sauvage* 13:27-52.
- GONG P., SHENG Y., and BIGING G.S. 2002. 3D model-based tree measurement from high-resolution aerial imagery. *Photogrammetric Engineering and Remote Sensing* 68(11):1203-1212.
- GOUGH M.C., and RUSHTON S.P. 2000. The application of GIS-modelling to mustelid landscape ecology. *Mammal Review* 30:197-216.
- GROVER K.E., and THOMPSON M.J. 1986. Factors influencing spring feeding site selection by elk in the Elkhorn mountains, Montana. *Journal of Wildlife Management*. 50(3):466-470.
- GROOT BRUINDERINK G.W.T.A. and E. HAZEBROEK. 1996. Ungulate traffic collisions in Europe. *Conservation Biology* 10: 1059-1067.
- GUISAN A., and ZIMMERMANN N.E. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135(2-3):147-186.
- \_\_\_\_\_, Edwards, T.C., and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling* 157: 89-100.
- GUSTAFSON E.J., and GARDNER R.H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77(1):94-107.
- HADDAD N.M. 1999. Corridor use predicted from behaviors at habitat boundaries. *American Naturalist* 153(2):215-227.
- HAIG S.M., MEHLMAN D.W., and ORING L.W. 1998. Avian movements and wetland connectivity in landscape conservation. *Conservation Biology* 12(4):749-758.
- HAIGHT R.G., CYPHER B., KELLY P.A., PHILLIPS S., POSSINGHAM H.P., RALLS K., STARFIELD A.M., WHITE P.J., and WILLIAMS D. 2002. Optimizing habitat protection using demographic models of population viability. *Conservation Biology* 16(5):1386-1397.
- HALLER, H. 2002. Der Rothirsh im Schweizerischen Nationalpark und dessen Umbegebung. Eine alpine Population von *Cervus elaphus* zeitlich und räumlich documentiert. *Nat. park-Forsch. Schweiz* 91.
- HANSKI I. 1994. A Practical Model of Metapopulation Dynamics. *Journal of Animal Ecology* 63(1):151-162.
- \_\_\_\_\_. 2001. Population dynamics consequences of dispersal in local populations and in metapopulations. In: Colbert J, Danchin E, Dhondt A.A, Nichols J, editors. *Dispersal*: Oxford university press. p 283-298.
- HAMANN J.L., KLEIN F., and SAINT-ANDRIEUX C. 1997. Domaine vital diurne et déplacements de biches (*Cervus elaphus*) sur le secteur de la petite pierre (Bas-Rhin). *Gibier Faune Sauvage* 14:1-17.
- HAUSSER, J. 1995. *Mammifères de Suisse*. Birkhäuser. Bâles, p.
- HIGGINS K.F., OLDEMEYER J.L., JENKINS K.J., CLAMBEY G.K., and HARLOW T.F. 1996. Vegetation sampling and measurement. *Research and management techniques for wildlife and habitat*. Bethesda, Md: The Wildlife society. p 740.
- HIRZEL A.H. 2001. When GIS come to life: linking landscape- and population ecology for large population management modelling: the case of Ibex (*Capra ibex*) in Switzerland [Ph-D Thesis]. Lausanne: University of Lausanne. 106 p.

- HIRZEL A.H., and GUIBAN A. 2002. Which is the optimal sampling strategy for habitat suitability modelling. *Ecological Modelling* 157(2-3):331-341.
- \_\_\_\_\_, HAUSSER J., CHESSEL D., and PERRIN N. 2002. Ecological-niche factor analysis: How to compute habitat- suitability maps without absence data? *Ecology* 83(7):2027-2036.
- \_\_\_\_\_, HAUSSER J., and PERRIN N. 2002. Biomapper 2.0. Version 2.0. Lausanne: Laboratory for Conservation Biology, University of Lausanne. url: <http://www.unil.ch/biomapper>.
- \_\_\_\_\_, HELFER V., and METRAL F. 2001. Assessing habitat-suitability models with a virtual species. *Ecological Modelling* 145(2-3):111-121.
- HEGG, O., BEGUIN, C. and H., ZOLLER. 1993. Atlas de la végétation à protéger en Suisse. Ed. OFEFP, Berne, 160pp.
- HESS G.R., and FISCHER R.A. 2001. Communicating clearly about conservation corridors. *Landscape and Urban Planning* 55(3):195-208.
- HOBBS R.J. 1992. The role of corridors in conservation: solution or bandwagon? *Tree* 7(11).
- HOBBS N.T. 1996. Modification of ecosystems by ungulates. *Journal of wildlife ecology* 60(4):695-713.
- HODGETTS B.V., WASS J.R., and MATTHEWS L.R. 1998. The effects of visual and auditory disturbance on the behaviour of red deer (*Cervus elaphus*) at pasture with and without shelter. *Applied Animal Behaviour Science* 55:337-351.
- HOFMANN R.R. 1985. Digestive physiology of the Deer - their morphophysiological specialisation and adaptation. *The Royal Society of new Zealand Bulletin* 22:393-407.
- HOLZANG O., PFISTER H.P., HEYNEN D., BLANT M., RIGHETTI A., BERTHOUD G., MARCHESI P., MADDALENA T., MÜRRI H., WENDELSPIESS M. and others. 2001. Les corridors faunistiques en Suisse. Sempach, Bern: Office fédéral de l'environnement, des forêts et du paysage, Société suisse de biologie de la Faune, Station ornithologique suisse. Report nr 326. 120 p.
- HUBERTY, C.J. 1994. Applied discriminant analysis. Wiley Interscience. New-York.
- HUTCHINSON, G.E. 1957. Concluding remarks. Cold Spring Harbour symposium on quantitative biology.
- JABERG C., and GUIBAN A. 2001. Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. *Journal of Applied Ecology* 38:1169-1181.
- JAQUIERY, J and BRANDLI, L. 2003. Dispersion, structure d'habitat et génétique des populations chez *Crocidura russula*. Travail de Certificat, Université de Lausanne, 26pp.
- JOBIN A., MOLINARI P., and BREITENMOSER U. 2000. Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. *Acta Theriologica* 45(2):243-252.
- JOHST K., and BRANDL R. 1997. The effect of dispersal on local population dynamics. *Ecological Modelling* 104(1):87-101.
- JOHNSON D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61(1):65-71.
- \_\_\_\_\_, JOHNSON L.B., RICHARDS C., and BEASLEY V. 2002. Predicting the occurrence of Amphibians: an assessment of multiple-scale models. *Predicting species occurrences: issues of accuracy and scaled*. Washington, Covelo, London: Island Press. p 157-170.
- JOHNSON C.M., and KROHN W.B. 2002. Dynamic patterns of association between environmental factors and island use by breeding seabirds. *Predicting species occurrences: issues of accuracy and scale*. Washington, Covelo, London: Island Press. p 171-182.
- JONSEN I., and TAYLOR P.D. 2000. *Calopteryx* damselfly dispersions arising from multiscale responses to landscape structure. *Conservation Ecology* 4(2):art. no.-4.
- KARL, J.W., HEGLUND, P.J., GARTON, E.O., SCOTT, J.M., WRIGHTt, N.M., and R.L., HUTTO. 2000. Sensivity of species habitat-relationship model performance to factors of scale. *Ecological applications* 10: 1690-1705.
- KING A.W., and WITH K.A. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecological Modelling* 147(1):23-39.

- KINDVALL O. 1999. Dispersal in metapopulation of the bush cricket, *Metrioptera bicolor* (Orthoptera: Tetigoniidae). *Journal of Animal Ecology* 68:172-185.
- KLEIN F., and HAMANN J.-L. 1999. Domaines vitaux diurnes et déplacements de cerfs mâles (*Cervus elaphus*) sur le secteur de la Petite Pierre (Bas-Rhin). *Gibier faune Sauvage* 13(3):251-271.
- KOUBEK P., and HRABE V. 1996. Home range dynamics in the red deer (*Cervus elaphus*) in a mountain forest in central Europe. *Folia Zoologica* 45(3):219-222.
- KRUUK L.E.B., CLUTTON-BROCK T.H., ALBON S.D., PEMBERTON J.M., and GUINNESS F.E. 1999. Population density affects sex ratio variation in red deer. *Nature* 399(6735):459-461.
- LATHROP R.G., and BOGNAR J.A. 1998. Applying GIS and landscape ecological principles to evaluate land conservation alternatives. *Landscape and Urban Planning* 41:27-41.
- LIMA S.L., and ZOLLNER P.A. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution* 11(3):131-135.
- LINT J., NOON B., ANTHONY R., FORSMAN E., RAPHAEL M., COLLOPY M., and STARKEY E. 1999. Northern spotted owl: effectiveness monitoring plan for the Northwest forest plan. Portland: U.S. Department of agriculture, Forest Service, Pacific Northwest research station. 43 p.
- LETCHER B.H., PRIDDY J.A., WALTERS J.R., and CROWDER L.B. 1998. An Individual-Based, Spatially-Explicit Simulation Model of the Population Dynamics of the Endangered Red-Cockaded Woodpecker, *Picoides borealis*. *Biological Conservation* 86(1):1-14.
- LIMA S.L., and DILL L.M. 1990. Behavioral Decisions Made under the Risk of Predation - a Review and Prospectus. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 68(4):619-640.
- LINDENMAYER D.B., and POSSINGHAM H.P. 1996. Modelling the inter-relationships between habitat patchiness, dispersal capability and metapopulation persistence of the endangered species, Leadbeater's possum, in south-eastern Australia. *Landscape Ecology* 11(2):79-105.
- LITTLE S.J., HARCOURT R.G., and CLEVENGER A.P. 2002. Do wildlife passages act as prey-traps? *Biological Conservation* 107:135-145.
- LURZ P.W.W., RUSHTON S.P., WAUTERS L.A., BERTOLINO S., CURRADO I., MAZZOGLIO P., and SHIRLEY M.D.F. 2001. Predicting gray squirrel expansion in North Italy: a spatially explicit modelling approach. *Landscape Ecology* 16(5):407-420.
- MCDONALD D.W., and JOHNSON D.D.P. 2001. Dispersal in theory and practice: consequences for conservation biology. In: Colbert J, Danchin E, Dhondt AA, Nichols J, editors. *Dispersal*: Oxford university press. p 283-298.
- MCLOUGHLIN P.D., CASE R.L., GAU R.J., CLUFF H.D., MULDER R., and MESSIER F. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia* 132(1):102-108.
- MACE R.D., and WALLER J.S. 1996. Grizzly Bear Distribution and Human Conflicts In Jewel Basin Hiking Area, Swan Mountains, Montana. *Wildlife Society Bulletin* 24(3):461-467.
- MANLY B., MCDONALD L., and THOMAS D. 1993. Resource selection by animals: statistical design and analysis for field studies. London: Chapman & Hall. 175 p.
- MANEL S., DIAS J.M., BUCKTON S.T., and ORMEROD S.J. 1999. Alternative methods for predicting species distribution: an illustration with Himalayan river birds. *Journal of Applied Ecology* 36(5):734-747.
- MATTIELLO S., BERGAMI G., REDAELLI W., VERGA M., and CRIMELLA M.C. 1997. Ecology and Behaviour Of Red Deer (*Cervus elaphus*) In an Alpine Valley. *Zeitschrift fur Saugetierkunde-International Journal of Mammalian Biology* 62(Suppl 2):129-133.
- MEIER S. 2000. Phyto-Vaud database. Lausanne: Service Forêts-Faune-Nature. 200 p.
- MERRILL E.H. 1991. Thermal Constraints on Use of Cover Types and Activity Time of Elk. *Applied Animal Behaviour Science* 29(1-4):251-267.
- MILLSPAUGH J.J., RAEDEKE K.J., BRUNDIGE G.C., and WILLMOTT C.C. 1998. Summer bed sites of elk (*Cervus elaphus*) in the Black Hills, South Dakota: Considerations for thermal cover management. *American Midland Naturalist* 139(1):133-140.



- MILLSPAUGH J.J., BRUNDIGE G.C., GITZEN R.A., and RAEDEKE K.J. 2000. Elk and hunter space-use sharing in South Dakota. *Journal of Wildlife Management* 64(4):994-1003.
- MLADENOFF D.J., SICKLEY T.A., HAIGHT R.G., and WYDEVEN A.P. 1995. A Regional Landscape Analysis and Prediction Of Favorable Gray Wolf Habitat In the Northern Great Lakes Region. *Conservation Biology* 9(2):279-294.
- MOILANEN A., and HANSKI I. 1998. Metapopulation dynamics: Effects of habitat quality and landscape structure. *Ecology* 79(7):2503-2515.
- MONSERUD R.A., and LEEMANS R. 1992. Comparing global vegetation maps with the kappa statistics. *Ecol. Modelling* 62:275-293.
- MOOTY J.J., KARNS P.D., and FULLER T.D. 1987. Habitat use and seasonal range size of white-tailed deer in northcentral Minnesota. *J. Wildl. Manage.* 51(3):644-648.
- MORARD, E. 2003. Les sites de reproduction d'amphibiens de la plaine de l'Orbe: analyse des relations au paysage et modélisation de dispersion. Travail de diplôme, Université de Lausanne. 50p.
- MORALES J.M., and ELLNER S.P. 2002. Scaling up animal movements in heterogeneous landscapes: The importance of behavior. *Ecology* 83(8):2240-2247.
- MORELLET N., and GUIBERT B. 1999. Spatial heterogeneity of winter forest resources used by deer. *Forest Ecology and Management* 123:11-20.
- \_\_\_\_\_, \_\_\_\_\_, KLEIN F., and DEMOLIS C. 1996. Utilisation de l'habitat forestier par le cerf (*Cervus elaphus*) dans le massif d'Is-sur-Tille (Côte-d'or). *Gibier Faune sauvage* 13:1477-1493.
- MORRISON M.L., and HALL. 2002. Role of temporal and spatial scale. In: Scott JM, Heglund PJ, Morrison ML, Haufler JB, Wall WA, Samson FB, editors. *Predicting species occurrences: issues of accuracy and scaled*. Washington, Covelo, London: Island Press. p 123-124.
- MYSTERUD A., and OSTBYE E. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildlife Society Bulletin* 27(2):385-394.
- \_\_\_\_\_, LANGVATN R., YOCCOZ N.G., and STENSETH N.C. 2002. Large-scale habitat variability, delayed density effects and red deer populations in Norway. *Journal of Animal Ecology* 71(4):569-580.
- NEET, C.R. 1995. Field studies on the population and community consequences of habitat fragmentation. In Bellan, D., Bonin, G., Emig, C, editors *Functioning and dynamics of natural and perturbed ecosystems*: 17-34.
- OFS. 2000. GEOSTAT-Statistique de la superficie 1992/1997. Swiss Federal Statistical Office.
- OFT. 2000. VECTOR 25-Road Network. Federal Office of Topography.
- OKARMA H., JEDRZEJEWSKI W., SCHMIDT K., KOWALCZYK R., and JEDRZEJEWSKA B. 1997. Predation Of Eurasian Lynx On Roe Deer and Red Deer In Bialowieza Primeval Forest, Poland. *Acta Theriologica* 42(2):203-224.
- OPDAM P., FOPPEN R., and VOS C.C. 2002. Bridging the gap between ecology and spatial planning in landscape ecology. *Landscape Ecology* 16:767-779.
- ORIAN G.H., and WITTENBERGER J.F. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137, supp:29-49.
- OSBORNE P.E., and SUAREZ-SEOANE S. 2002. Should data be partitioned spatially before building large-scale distribution models? *Ecological Modelling* 157(2-3):249-259.
- PALOMARES F. 2001. Vegetation structure and prey abundance requirements of the Iberian lynx: implications for the design of reserves and corridors. *Journal of Applied ecology* 38:9-18.
- PATTHEY P. 2002. DeerDisperser. Version 1.0. Lausanne: Laboratory for Conservation Biology, University of Lausanne. <http://www.unil.ch/izea/research.html#softs>.
- \_\_\_\_\_. 2002. IdrisiPlus. Version 1.0. Lausanne: Laboratory for Conservation Biology, University of Lausanne.
- \_\_\_\_\_. 2002. StratSampler. Version 1.0. Lausanne: Laboratory for Conservation Biology, University of Lausanne.

- PATTHEY. 2002. ValueExtractor. Version 1.0. Lausanne: Laboratory for Conservation Biology, University of Lausanne.
- \_\_\_\_\_. 2003. Projet Cerf, recolonisation du bassin genevois et des forêts jurassiennes par le cerf élaphe , rapport final. Lausanne, Switzerland: Office fédéral de l'environnement, des forêts et du paysage, Office national de la chasse et de la faune sauvage, Service des forêts, de la protection du paysage et de la nature (Genève), Centre de conservation de la faune et de la nature (Vaud).
- PELLET, J. HOHEN, S., and PERRIN, N. Multiscale determinants of tree frog (*Hyla arborea* L.) calling ponds in western Switzerland. *Submitted*.
- PETTIFOR R.A., CALDOW R.W.G., ROWCLIFFE J.M., GOSS-CUSTARD J.D., BLACK J.M., HODDER K.H., HOUSTON A.I., LANG A., and WEBB J. 2000. Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. *Journal of Applied Ecology* 37:103-135.
- PETIT S., MOILANEN A., HANSKI I., and BAGUETTE M. 2001. Metapopulation dynamics of the bog fritillary butterfly: movements between habitat patches. *Oikos* 92(3):491-500.
- PETRAK M. 1996. Man as a disturbing factor in the environment of the red deer (*Cervus elaphus* L 1758). *Zeitschrift für Jagdwissenschaft* 42(3):180-194.
- PHILLIPS G.E., and ALLDREDGE A.W. 2000. Reproductive success of elk following disturbance by humans during calving season. *Journal of Wildlife Management* 64(2):521-530.
- PICARD J.F., OLEFFE P., and BOISAUBERT B. 1991. Influence of Oak Mast on Feeding-Behavior of Red Deer (*Cervus elaphus*). *Annales Des Sciences Forestieres* 48(5):547-559.
- POLLARD J.C., and LITTLEJOHN R.P. 1995. Consistency in Avoidance of Humans by Individual Red Deer. *Applied Animal Behaviour Science* 45(3-4):301-308.
- POLZIEHN R.O., and STROBECK C. 2002. A phylogenetic comparison of red deer and wapiti using mitochondrial DNA. *Molecular Phylogenetics and Evolution* 22(3):342-356.
- PORTER W.F., and CHURCH K.E. 1987. Effects of environmental pattern on habitat preference analysis. *J. Wildl. Manage.* 51(3):681-685.
- PUTH L.M., and WILSON K.A. 2001. Boundaries and corridors as a continuum of ecological flow control: lessons from rivers and streams. *Conservation Biology* 15(1):21-30.
- PUTMAN R.J., and MOORE N.P. 1998. Impact of deer in lowland Britain on agriculture, forestry and conservation habitats. *Mammal Rev.* 28(4):141-164.
- RANDIN C, and RICKEBUSH S. 2001. Modélisation de l'habitat potentiel de *Narcissus radiiflorus* (Amaryllaceae) sur la commune de Montreux (VD). Travail de certificat. Lausanne university, Lausanne. 18p.
- REED J.M., MILLS L.S., DUNNING J.B., MENGES E.S., MCKELVEY K.S., FRYE R., BEISSINGER S.R., ANSTETT M.C., and MILLER P. 2002. Emerging issues in population viability analysis. *Conservation Biology* 16(1):7-19.
- REIMOSER F., and GOSSOW H. 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. *Forest Ecology and Management* 88:107-119.
- RETTIE W.J., and MESSIER F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23(4):466-478.
- REUTER H., and BRECKLING B. 1999. Emerging properties on the individual level: modelling the reproduction phase of the European robin *Erithacus rubecula*. *Ecological Modelling* 121:199-219.
- RIBBEN, E. 1957. La forêt et l'économie pastorale dans le Jura. Ph-D thesis, Ecole polytechnique fédérale, Zurich, 250 p.
- RICKETTS T.H. 2001. The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist* 158(1):87-99.
- RIGHETTI A. 1995. *Cervus elaphus* L., 1758. In: Hausser J, editor. Atlas des mammifères de la Suisse. Basel, Boston, Berlin: Birkhäuser Verlag. p 433-439.
- ROFF D.A. 1974. The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. *Oecologia* 15:259-274.

- ROLOFF G.J., and KERNOHAN B.J. 1999. Evaluating reliability of habitat suitability index models. *Wildlife Society Bulletin* 27(4):973-985.
- \_\_\_\_\_, and HAUFLER J.B. 1997. Establishing population viability planning objectives based on habitat potentials. *Wildlife Society Bulletin* 25(4):895-904.
- \_\_\_\_\_, MILLSPAUGH J.J., GITZEN R.A., and BRUNDIGE G.C. 2001. Validation tests of a spatially explicit habitat effectiveness model for Rocky Mountain elk. *Journal of Wildlife Management* 65(4):899-914.
- ROSENBERG D.K., NOON B.R., and MESLOW E.C. 1997. Biological corridors: Form, function, and efficacy. *Bioscience* 47(10):677-687.
- ROWLAND M.M., WISDOM M.J., JOHNSON B.K., and KIE J.G. 2000. Elk distribution and modelling in relation to roads. *Journal of Wildlife Management*. 64(3):672-684.
- RUCKELSHAUS M., HARTWAY C., and KAREIVA P. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology* 11(6):1298-1306.
- RUSHTON S.P., LURZ P.W.W., FULLER R., and GARSON P.J. 1997. Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. *Journal of Applied Ecology* 34(5):1137-1154.
- SACHOT S. 2002. Viability and management of an endangered capercaillie (*Tetrao urogallus*) metapopulation [Ph-D Thesis]. Lausanne: University of Lausanne. 117 p.
- \_\_\_\_\_, PERRIN, N., and NEET, C. 2003. Winter habitat selection by two sympatric forest grouse in western Switzerland: implications for conservation. *Biological conservation*, in press.
- SANDERSON E.W., REDFORD K.H., CHETKIEWICZ C.L.B., MEDELLIN R.A., RABINOWITZ A.R., ROBINSON J.G., and TABER A.B. 2002. Planning to save a species: the jaguar as a model. *Conservation Biology* 16(1):58-72.
- SCARTH P., PHINN S.R., and MCALPINE C. 2001. Integrating high and moderate spatial resolution image data to estimate forest age structure. *Canadian Journal of Remote Sensing* 27(2):129-142.
- SCHADT S., KNAUER F., KACZENSKY P., REVILLA E., WIEGAND T., and TREPL L. 2002. Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. *Ecological Applications* 12(5):1469-1483.
- SCHIPPERS P., VERBOOM J., KNAAPEN J.P., and VAN APELDOORN R.C. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: An analysis with a GIS-based random walk model. *Ecography* 19(2):97-106.
- SCHUMAKER N.H. 1996. Using Landscape Indices to Predict Habitat Connectivity. *Ecology* 77(4):1210-1225.
- SENFTE R.L., COUGHENOUR M.B., BAILEY D.W., RITTENHOUSE L.R., SALA O.E., and SWIFT D.M. 1987. Large Herbivore Foraging and Ecological Hierarchies. *Bioscience* 37(11):789-and.
- SIBBALD A.M., HOOPER R.J., GORDON I.J., and CUMMING S. Using GPS to study the effect of human disturbance on the behaviour of red deer stags on a highland estate in Scotland. In: LOTTEK T, VECTRONIC, editor; 2001 12-13 march 2001; Aberdeen, UK. p 39-43.
- SIEVING K.E., WILLSON M.F., and DE SANTO T.L. 2000. Defining corridor functions for endemic birds in fragmented south-temperate rainforest. *Conservation Biology* 14(4):1120-1132.
- SIMBERLOFF D., FARR J.A., COX J., and MEHLMAN D.W. 1992. Movement Corridors - Conservation Bargains or Poor Investments. *Conservation Biology* 6(4):493-504.
- SINGER F.J., and DOHERTY J.L. 1985. Managing Mountain Goats at a Highway Crossing. *Wildlife Society Bulletin* 13(4):469-477.
- SJÖRGEN-GULVE P. 1998. Spatial movement patterns in frogs: differences between three *Rana* species. *Ecoscience* 5(2):148-155.
- SOKAL R.R., and RHOLF J. 1995. *Biometry: the principles and practice of statistics in biological research*. New-York: W.H. Freeman and Company. 850 p.
- STAINES B.W. 1976. Use of Natural Shelter by Red Deer (*Cervus elaphus*) in Relation to Weather in Northeast Scotland. *Journal of Zoology* 180(SEP):1-8.

- \_\_\_\_\_, CRISP J.M., and PARISH T. 1982. Differences in the Quality of Food Eaten by Red Deer (*Cervus elaphus*) Stags and Hinds in Winter. *Journal of Applied Ecology* 19(1):65-77.
- STAPP P., and VANHORNE B. 1997. Response of Deer mice (*Peromyscus maniculatus*) to shrubs in shortgrass prairie: linking small-scale movements and the spatial distribution of individuals. *Functional Ecology* 11(5):644-651.
- STEPHENS P.A., FREY-ROOS F., ARNOLD W., and SUTHERLAND W.J. 2002. Model complexity and population predictions. The alpine marmot as a case study. *Journal of Animal Ecology* 71:343-361.
- STORCH I. 2002. On spatial resolution in habitat models: Can small-scale forest structure explain capercaillie numbers? *Conservation Ecology* 6(1):6.[online]url : <http://www.consecol.org/vol6/iss1/art6>.
- SFPNP. 2000. Dérangements et dégâts causés par les chiens.: Service des forêts, de la protection de la nature et du paysage. 30 p.
- SWART J., and LAWES M.J. 1996. The effect of habitat patch connectivity on samango monkey (*Cercopithecus mitis*) metapopulation persistence. *Ecological Modelling* 93(1-3):57-74.
- TIGAS L.A., VAN VUREN D.H., and SAUVAJOT R.M. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in a urban environment. *Biological Conservation* 108:299-306.
- TISCHENDORF L. 1997. Modelling Individual Movements In Heterogeneous Landscapes - Potentials Of a New Approach. *Ecological Modelling* 103(1):33-42.
- \_\_\_\_\_, and FAHRIG L. 2000. How should we measure landscape connectivity? *Landscape Ecology* 15(7):633-641.
- TRAVIS J.M.J., and FRENCH D.R. 2000. Dispersal functions and spatial models: expanding our dispersal toolbox. *Ecology letters* 3:163-165.
- TURNER M.G., PEARSON S.M., ROMME W.H., and WALLACE L.L. 1997. Landscape heterogeneity and ungulate dynamics: what spatial scales are important. In: Bissonnette JA, editor. *Wildlife and landscape ecology*. New York: Springer-Verlag. p 331-348.
- TYRE A., POSSINGHAM H.P., and LINDENMAYER D.B. 1999. Modelling dispersal behavior on a fractal landscape. *Environmental modelling and software* 14:103-113.
- UNDERHILL J.E., and ANGOLD P.G. 2000. Effects of roads on wildlife in an intensively modified landscape. *Environmental Review* 8:21-39.
- VAN APELDOORN R.C., KNAAPEN J.P., SCHIPPERS P., VERBOOM J., H. V.E., and H. M. 1998. Applying ecological knowledge in landscape planning: a simulation model as a tool to evaluate scenarios for the badger in the Netherlands. *Landscape and Urban Planning* 41:57-69.
- VITTOZ P. 1998. Flore et végétation du Parc jurassien vaudois: typologie, écologie et dynamique des milieux. PhD thesis, Lausanne: University of Lausanne. 300 p.
- VUILLEUMIER S., and PRELAZ-DROUX R. 2002. Map of ecological networks for landscape planning. *Landscape and Urban Planning* 58(2-4):157-170.
- VOLK F.H. 1999. Bark peeling frequency in the alpine provinces of Austria: the importance of forest structure and red deer management. *Zeitschrift Fur Jagdwissenschaft* 45(1):1-16.
- VOS C.C., ANTONISSE-DE JONG A.G., GOEDHART P.W., and SMULDERS M.J.M. 2001. Genetic similarity as a measure for connectivity between fragmented populations of the moor frog (*Rana arvalis*). *Heredity* 86:598-608.
- WANG B., and MANNING R.E. 1999. Computer simulation modeling for recreation management: A study on carriage road use in Acadia National Park, Maine, USA. *Environmental Management* 23(2):193-203.
- WARNKEN J., and BUCKLEY R. 1998. Scientific quality of tourism environmental impact assessment. *Journal of Applied ecology* 35:1-8.
- WECKERLY F.W., RICCA M.A., and MEYER K.P. 2001. Sexual segregation in Roosevelt elk: cropping rates and aggression in mixed-sex groups. *Journal of Mammalogy* 82(3):825-835.
- WENNERGREN U., RUCKELSHAUS M., and KAREIVA P. 1995. The promise and limitations of spatial models in conservation. *Oikos* 74:349-356.

- WIEGAND T., MOLONEY K.A., NAVES J., and KNAUER F. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *the American Naturalist* 154(6):605-627.
- WIENS J.A. 1997. The emerging role of patchiness in conservation biology. In: Pickett STA, Ostfeld RS, Shachak M, Likens GE, editors. *The ecological basis of conservation. Heterogeneity, ecosystems and biodiversity*. New York: Chapman & Hall. p 446.
- \_\_\_\_\_. 1989. Spatial Scaling in Ecology. *Functional Ecology* 3(4):385-397.
- \_\_\_\_\_. 2001. The landscape context of dispersal. In: Colbert J, Danchin E, Dhondt AA, Nichols J, editors. *Dispersal*: Oxford university press. p 96-109.
- WILHERE G.F. 2002. Adaptive management in habitat conservation plans. *Conservation Biology* 16(1):20-29.
- WHITTINGTON C.J., and CHAMOVE A.S. 1995. Effects of Visual Cover on Farmed Red Deer Behavior. *Applied Animal Behaviour Science* 45(3-4):309-314.
- YOCCOZ N.G., MYSTERUD A., LANGVATN R., and STENSETH N.C. 2002. Age- and density-dependent reproductive effort in male red deer. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269(1500):1523-1528.
- ZABEL C.J., ROBERTS L.M., MULDER B.S., STAUFFER H.B., DUNK J.R., WOLCOTT K., SOLIS D., GERTSCH M., WOODBRIDGE B., WRIGHT A. and others. 2002. A collaborative approach in adaptative management at a large-landscape scale. *Predicting species occurrences: issues of accuracy and scale*. Washington, Covelo, London: Island Press. p 241-254.
- ZANIEWSKI A.E., LEHMANN A., and OVERTON J.M.C. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modeling* 157(2-3):261-280.

## 10. ACKNOWLEDGMENTS

---

This work has benefited from the help of several peoples who contributed at different degree to its conclusion. I would like to thank all of these people and particularly:

This research would have never begun and be concluded without the constant help of Cornelis Neet, who as Ph-D supervisor and wildlife manager offered me the opportunity to work in a comfortable office and always care to counterbalance scientific and applied comments. His global vision significantly improved this work.

I'm also greatly grateful to the team of supervisors and financers; B. Boisaubert, H.-J. Blankenhorn, G. Dändliker, A.-C. Déprez, P. Durand, F. Klein, C. Neet, G. Mulhauser, and S. Sachot who initiated and/or followed this work. All their comments were greatly appreciated.

I thank the Ecology Institute of the Lausanne University for its logistical support and especially N. Perrin to provide me a working place inside his team and to A. Guisan for his GIS support.

I address all my gratitude to all the wildlife rangers associated to this work, especially, Patrick Deleury and Jean-Pierre Perruchoud for their huge and successful commitment in red deer captures, Pascal Mathieu, Eric Monteloy, Patrick Deleury and Jean-Pierre Perruchoud for their radiotracking help and with all of them associated with Bernard Reymond, Jean-Maurice Pesenti, Michel Conti, Francois Corcelle and Alain Rauss for their help during red deer captures and for discussions about red deer distribution, ecology and management. Jean Fournier, Daniel Gétaz, Georges Gremion, Jean-Louis Henriod, William Isoz, Peter Nussbaum and André Vietti as wildlife ranger auxiliaries gave me some welcome field help.

My masters students Isabelle Dunand and Ewa Gawronski for their help with the collection of field data and data preparation that greatly contributed to chapter 4, to Joachim Vos and David Badstuber for their help during fieldwork, to Nicolas Perrin for its statistical support.

I also thanks my offices fellows with whom I shared a lot of funny moments, professional ideas and collaborative works, Brigitte Reutter, John Aeschmann, Alexandre Hirzel, Jérôme Pellet, Véronique Helfer and in particular Sébastien Sachot for its support from field work, GIS data preparation, programming to discussion about red deer habitat use.

I'm very grateful to Alexandre Hirzel, who allowed me to use its IDRISI-DELPHI interface. I thanks Alexandre Hirzel, Vincent Reviol and Sébastien Sachot who assisted me to kill some serious bugs and helped me to prevent creating some others.

I thank Lori Handley for the English revision of the manuscript.

I also benefit of suggestions from informal SPACE group (UNIL-EPFL) members.

François Klein, Jean-Luc Hamann and Jean-Marc Angibault for their precious technical advice concerning capture methods. Dr P. Boujon and the KORA team for their technical assistance in red deer captures.

All of the rutting counters, who I hope, will apologize me for not citing all their names.

GERNAJURA and in particular Gilles Mallejac for its radiotracking contribution.

The Swiss army at Bière and MM P.-A. Monthoux who kindly authorize us to install a big capture fence on their field.

The TIG team (from may 2000) who constructed the corral capture fence at Bière.

M. J. Kilchherr who provide us freely apples kilograms.

The Bière army team and in particular, Col. Glauser, Adj. Bertholet and M. Hediger for their always precious support and interest to our work.

Ms and M Curlier for their information that allowed capturing the red deer named “TANKY”.

Johny Bruny, Vincent Chabloz, Philippe Christe, François Corcelle, Daniel Gétaz, Georges Gremion, Eric Montoloy, Julien Perrot, Sébastien Sachot, Pierre Wegmüller and Laurent Willeneger, who kindly transmitted me their red deer observations and all the observers I met on the field.

Danièle Kattanage, Michel Schuepbach, Blaise Pavillard and Françoise Pham, who always contentedly answered to my “little” administrative or technical requests.

I am also grateful to Jean-Michel Gaillard, Antoine Guisan and François Klein who accepted to expertise this work.

The Conseil du Léman and the Service des forêts, de la faune et de la nature (Canton de Vaud) to provide us freely their GIS data.

This work would never been possible without the financial support of the Swiss Agency for the Environment, Forest and Landscape (ProjektNummer 310.98.M002WILDMAN), the Centre de Conservation de la Faune et de la Nature, Vaud State, Switzerland, the Service des Forêts, de la Protection du Paysage et de la Nature, Geneva state, Switzerland and the Office National de la Chasse et de la Faune Sauvage, France. I also thank the deanship of the University of Lausanne for their financial help that allowed me to go to 5<sup>th</sup> international congress on deer biology (Canada).

Finally, I want to thank Alexandra, whose patience and comprehension are my best support and safeguard during this last four years.

## 11. GLOSSARY

---

- Accuracy* The nearness of a measurement to the actual value of the variable being measured < not synonymous with Precision.
- (Landscape) Connectivity* The fraction of individuals that successfully locate and occupy new habitat
- Corridor*<sup>1</sup> A structure that canalizes and directs the flows of organisms, materials, or energy between patches.
- Breeding Dispersal*<sup>2</sup> The movement between two successive breeding areas or social groups.
- Natal Dispersal*<sup>2</sup> The movement between the natal area or social group and the area or social group where breeding first takes place.
- Dispersal*<sup>3</sup> Movement from one location and the consequences of arriving at the other location
- Distribution* The spread or scatter of an entity within its range.
- Extent* The area over which observations are made and the duration of those observations.
- Grain* The spatial and temporal resolution of observations the smallest resolvable unit of study.
- Habitat selection* A hierarchical process involving a series of innate and learned behavioral decisions made by animal about what habitat it would use at different scales of the environment.
- Habitat use* The way an animal uses or consumes, in a generic sense a collection of physical and biological entities in a habitat
- Home range* The area traversed by an animal during its activities during a specified period of time
- Level* The level of organization revealed by observation at the scale under study
- Model* Any formal representation of the real world. A model may be conceptual, diagrammatic, mathematical, or computational
- Model calibration* The estimation of model parameters from data
- Model parameterization* The process of specifying a model structure
- Model validation* Comparison of a model's predictions to some use-chosen standard to assess if the model is suitable for its intended purpose
- Model verification* The demonstration that a model is formally correct
- Population viability analysis*<sup>4</sup> A modeling tool that estimates the future size and risk of extinction for population of organisms.
- Precision* The closeness to each other of repeated measurements of the same quantity; not synonymous with accuracy
- Range* The limits within each an entity operates or can be found



*Resolution* The smallest spatial scale at which we portray discontinuities in biotic and abiotic factors in map form

*Resource* Any biotic or abiotic factor directly used by an organism

*Scale* The resolution at which patterns are measured, perceived, or represented. Scale can be broken into several components, including grain and extent

*Scale of observation* The spatial and temporal scales at which observations are made. Scale of observation has two parts: extent and grain

*Sensitivity analysis* A process in which model parameters or other factors are varied in a controlled fashion

*Site* An area of uniform physical and biological properties and management status

*Study area* An arbitrary spatial extent chosen by the investigator within which to conduct a study (Contrast with Site and Scale)

*Territory* The spatial area defended (actively or passively) by an animal or group of animals

*Viability* Strictly, the ability to live or grow. In conservation biology, the probability of survival of a population for an extended period of time

**Sources:**

If not specified Morrisson et Hall 2002

1 Puth and Wilson 2001

2 Clobert et al. 2001

3 Wiens 2001

4 Coulson et al. 2001

## **12. ABBREVIATIONS**

---

<i>CRW</i>	Correlated random walk model
<i>CPRW</i>	Correlated probabilities random walk model
<i>CS maps</i>	Corridor suitability maps
<i>IBM</i>	Individual-based models
HS maps	Habitat suitability maps
<i>GIS</i>	Geographic information system
<i>GPS</i>	Global positioning system
<i>MM</i>	Metapopulation model
<i>PRW</i>	Probabilities random walk model
<i>PVA</i>	Population viability analysis
<i>SAW</i>	Self-avoiding random walk model

## **13. APPENDICES**

---

### 13.1. Appendix 1, solar compass

The solar compass used to estimate potential solar flux on red deer bedding site



### 13.2. Appendix 2, bed site selection with ENFA

A) Scores of the variables on the first five selected factorial axes (out of 40) from the winter ENFA (absence/presence range) for red deer in the Jura Mountains. Explained information 65%.

Marginality	M	S1	S2	S3	S4
Tolerance	7%	7%	6%	5%	4%
<b>Local scale variables (in 10m radius circle)</b>					
BeeBush	-0.16	0.04	-0.04	0.11	-0.16
Canopy	0.11	0.07	0.07	-0.06	-0.16
ConBush	-0.08	0.08	-0.18	-0.11	0.00
DecCan	0.06	0.06	-0.09	0.05	0.04
DecSCan	0.04	0.10	0.00	0.04	-0.07
FirBush	0.05	-0.03	0.08	0.08	-0.03
FirCan	-0.02	-0.05	-0.06	0.01	-0.15
FirSCan	0.00	-0.01	-0.11	-0.03	-0.04
MappBush	-0.17	-0.03	0.15	0.11	<b>0.25</b>
SpruBush	-0.12	0.07	<b>0.22</b>	-0.12	-0.12
SpruCan	-0.20	-0.13	0.09	-0.01	0.08
SpruSCan	0.06	0.14	0.06	-0.05	0.04
SubCanopy	-0.05	-0.01	0.03	-0.02	-0.08
UnStory1	-0.05	-0.15	-0.11	-0.01	-0.03
UnStory2	0.02	-0.04	-0.09	-0.10	-0.05
VisMean	0.06	-0.08	-0.08	<b>-0.30</b>	0.07
VisSdev	0.06	0.01	0.17	0.18	<b>-0.22</b>
<b>Topographical variables</b>					
Elev	0.01	0.10	0.04	-0.03	0.02
Asp_E	-0.11	-0.10	-0.05	0.03	0.03
Asp_N	0.00	-0.04	-0.14	-0.13	0.10
Slope	0.14	0.10	0.13	-0.08	0.11
<b>Disturbance variables</b>					
Road1	0.15	0.09	<b>-0.22</b>	-0.14	-0.06
Road2	<b>0.25</b>	0.19	0.12	-0.12	0.10
Road3	-0.09	-0.19	-0.06	0.16	-0.01
Road4	0.05	-0.09	0.11	0.11	-0.06
Road5	0.09	-0.03	0.00	0.00	0.10
Road6	-0.11	-0.04	-0.08	-0.07	-0.06
RoadAll	-0.02	0.17	-0.17	-0.14	0.04
RoadFree	0.10	-0.05	0.10	-0.07	-0.08
Built10	<b>-0.21</b>	<b>-0.26</b>	-0.07	<b>-0.27</b>	-0.11
Built50	<b>-0.22</b>	<b>-0.25</b>	0.09	-0.19	0.16
BuiltDist	0.06	<b>-0.37</b>	<b>-0.55</b>	<b>-0.31</b>	<b>0.40</b>
<b>Broad scale variables</b>					
For10	0.13	<b>-0.23</b>	-0.05	-0.05	<b>-0.57</b>
For50	<b>-0.29</b>	<b>0.53</b>	<b>0.24</b>	<b>0.38</b>	-0.11
Mead10	0.19	0.14	-0.14	-0.13	-0.15
Mead50	<b>0.53</b>	-0.10	<b>0.26</b>	<b>0.35</b>	0.03
OpFor10	-0.06	-0.03	<b>0.33</b>	<b>0.26</b>	-0.04
OpFor50	0.06	<b>0.31</b>	-0.01	-0.02	0.06
Past10	<b>-0.31</b>	0.12	-0.16	<b>-0.20</b>	<b>-0.31</b>
Past50	<b>-0.27</b>	-0.02	0.16	<b>0.27</b>	<b>0.21</b>

B) Scores of the variables on the first four selected factorial axes (out of 51) from the summer ENFA for red deer in the Jura Mountains. Explained information 71%.

Marginality	M	S1	S2	S3
Tolerance	<b>21%</b>	9%	7%	5%
<b>Local scale variables (in 10m radius circle)</b>				
VisMean	0.02	0.03	-0.02	0.03
VisSdev	-0.01	-0.05	0.17	-0.11
BBerGrass	0.04	0.00	0.04	-0.01
BeeBush	0.12	-0.05	0.02	-0.07
BeeGrass	0.02	-0.02	-0.08	0.08
BilGrass	-0.17	0.06	-0.16	0.13
Canopy	0.09	0.08	-0.04	-0.14
ConBush	-0.12	0.03	-0.18	<b>-0.28</b>
DecCan	0.16	-0.02	-0.06	0.14
DecSCan	0.10	-0.05	0.09	0.08
FirBush	0.04	-0.03	0.14	0.15
FirCan	0.05	-0.02	0.03	-0.02
FirGrass	-0.03	-0.01	0.04	-0.02
FirSCan	0.04	0.03	0.06	0.05
GrassGrass	0.00	0.03	0.04	-0.08
HeigGrass	0.08	-0.02	-0.02	0.11
MappBush	-0.03	-0.02	-0.01	-0.07
MappGrass	-0.01	0.00	0.02	-0.05
RRasGrass	0.00	-0.02	-0.08	-0.08
SpruBush	-0.19	-0.08	<b>0.34</b>	0.18
SpruCan	<b>-0.22</b>	-0.04	0.02	-0.08
SpruGrass	-0.08	0.02	-0.01	0.03
SpruSCan	-0.17	0.05	-0.09	-0.01
SubCanopy	0.03	0.02	-0.01	-0.10
UnStory1	-0.07	0.05	0.03	0.09
UnStory2	0.03	0.07	-0.03	0.08
<b>Topographical variables</b>				
Elev	-0.19	-0.07	-0.15	<b>0.37</b>
Asp_E	0.00	-0.01	0.04	0.00
Asp_N	0.12	-0.01	-0.12	0.07
Slope	0.11	-0.01	0.08	-0.02
<b>Disturbance variables</b>				
Road1	-0.01	0.07	-0.14	0.01
Road2	-0.02	0.05	-0.06	0.09
Road3	-0.04	0.00	-0.12	-0.03
Road4	-0.08	-0.04	0.06	-0.01
Road5	0.17	-0.03	0.03	0.02
Road6	<b>-0.28</b>	0.03	-0.07	0.04
RoadAll	-0.10	0.05	-0.02	-0.02
RoadFree	-0.18	-0.06	0.03	-0.06
BuiltDist	0.07	-0.06	<b>0.51</b>	-0.04
Built10	0.01	0.03	0.17	-0.01
Built50	-0.04	0.14	0.17	<b>0.41</b>
<b>Broad scale variables</b>				
For10	<b>0.21</b>	0.00	<b>-0.27</b>	<b>-0.25</b>
For50	0.04	<b>0.66</b>	0.07	0.15
Mead10	0.07	0.02	-0.15	0.09
Mead50	<b>0.41</b>	<b>0.46</b>	0.18	<b>0.40</b>
OpFor10	-0.18	-0.01	<b>-0.27</b>	-0.18
OpFor50	-0.17	<b>0.44</b>	<b>0.28</b>	0.20
Past10	<b>-0.30</b>	0.18	0.19	-0.09
Past50	<b>-0.39</b>	<b>0.20</b>	0.06	<b>0.22</b>

C) Scores of the variables on the first five selected factorial axes (out of 43) from the winter 1999 ENFA (bed site/presence range) for red deer in the Jura Mountains. Explained information 92%.

<i>Marginality=1.16</i>	<b>M</b>	<b>S1</b>	<b>S2</b>	<b>S3</b>
<i>Tolerance=0.21</i>	47%	20%	13%	9%
<b>Local scale variables (in 10m radius circle)</b>				
BeeBush	0.06	0.01	0.20	0.05
Canopy	-0.10	0.06	-0.10	<b>0.31</b>
ConBush	<b>0.29</b>	<b>0.28</b>	0.19	<b>0.40</b>
DecCan	-0.12	0.00	0.02	-0.16
DecSCan	-0.13	-0.02	0.05	-0.01
FirBush	<b>0.24</b>	<b>-0.25</b>	-0.04	<b>-0.33</b>
FirCan	0.20	-0.06	0.02	-0.10
FirSCan	0.18	-0.04	-0.05	0.01
MappBush	0.12	-0.07	-0.07	-0.11
SpruBush	0.13	-0.12	-0.05	-0.19
SpruCan	-0.11	0.04	-0.06	0.13
SpruSCan	<b>-0.22</b>	-0.04	-0.12	-0.03
SubCanopy	<b>0.23</b>	0.00	-0.10	0.07
UnStory1	0.12	-0.05	-0.04	-0.06
UnStory2	0.09	0.05	-0.05	0.04
VisMean	-0.02	0.01	-0.19	0.04
VisSdev	-0.10	-0.02	0.07	-0.08
<b>Microscales variables (in 1m radius circle)</b>				
BushO	<b>0.43</b>	0.08	-0.10	0.07
ConO	0.03	-0.04	0.05	-0.06
DecO	<b>-0.49</b>	-0.14	0.02	0.00
Homo	0.04	-0.01	0.09	0.07
Pene	-0.19	0.08	0.04	-0.03
<b>Topographical variables</b>				
Asp_E	-0.03	-0.16	-0.04	-0.05
Asp_N	0.12	0.02	-0.04	-0.01
<b>Disturbance variables</b>				
Road1	0.08	-0.06	<b>0.21</b>	0.02
Road2	0.06	-0.09	<b>0.26</b>	-0.09
Road3	0.12	-0.09	0.13	-0.07
Road4	0.08	0.01	0.19	0.04
Road5	0.07	-0.10	-0.03	-0.14
Road6	0.03	0.05	-0.01	0.16
RoadAll	0.14	-0.11	0.12	-0.11
RoadFree	0.12	0.06	-0.07	0.20
BuiltDist	0.05	-0.14	<b>-0.28</b>	<b>-0.22</b>
Built10	-0.05	-0.04	0.04	-0.04
Built50	0.01	0.13	<b>0.43</b>	<b>0.28</b>
<b>Broad scale variables</b>				
For10	0.07	0.02	-0.18	<b>0.35</b>
For50	0.02	<b>-0.34</b>	-0.01	0.04
Mead10	-0.04	-0.04	-0.10	<b>0.23</b>
Mead50	0.05	<b>-0.54</b>	-0.03	-0.04
OpFor10	0.04	-0.07	-0.20	-0.09
OpFor50	0.00	-0.07	<b>0.36</b>	-0.02
Past10	-0.09	0.10	0.13	<b>0.26</b>
Past50	-0.01	<b>-0.50</b>	<b>0.35</b>	0.02

D) Scores of the variables on the first five selected factorial axes (out of 44) from the winter 2000 ENFA (bed site/presence range) for red deer in the Jura Mountains. Explained information 86%.

<i>Marginality=0.52</i>	<b>M</b>	<b>S1</b>	<b>S2</b>	<b>S3</b>	<b>S4</b>
<i>Tolerance=0.38</i>	32%	17%	12%	7%	4%
<b>Local scale variables (in 10m radius circle)</b>					
BeeBush	0.04	-0.06	-0.11	-0.06	-0.09
Canopy	0.08	-0.04	-0.06	-0.03	-0.08
ConBush	0.09	-0.11	-0.16	<b>-0.22</b>	-0.11
DecCan	0.18	0.02	0.05	0.01	-0.01
DecSCan	0.00	0.01	0.09	-0.05	0.04
FirBush	-0.06	0.03	-0.11	0.11	0.11
FirCan	0.15	0.11	0.10	-0.04	0.07
FirSCan	0.00	0.03	<b>0.24</b>	0.06	0.10
MappBush	-0.09	0.07	-0.02	-0.02	0.02
SpruBush	0.06	0.06	0.07	<b>0.27</b>	<b>0.23</b>
SpruCan	-0.03	-0.05	0.01	-0.06	-0.04
SpruSCan	-0.08	0.00	0.19	0.05	-0.06
SubCanopy	0.09	0.00	-0.15	-0.15	-0.11
UnStory1	0.17	-0.01	0.02	0.00	-0.10
UnStory2	-0.12	0.01	0.02	-0.08	0.09
VisMean	-0.13	-0.03	0.02	0.06	-0.15
VisSdev	-0.12	0.03	0.00	-0.16	-0.03
<b>Microscales variables (in 1m radius circle)</b>					
BushO	0.06	0.01	0.14	0.06	0.03
ConO	<b>0.30</b>	-0.02	0.05	0.10	-0.04
DecO	-0.16	-0.02	0.04	0.03	-0.05
Homo	<b>0.30</b>	0.02	0.05	-0.11	-0.03
Pene	-0.15	0.12	-0.01	0.08	0.01
<b>Topographical variables</b>					
Elev	-0.04	0.00	0.14	0.07	0.05
Asp_E	-0.04	-0.08	-0.04	-0.02	-0.05
Asp_N	0.17	-0.05	0.11	-0.09	0.09
Slope	<b>-0.31</b>	0.08	0.09	0.01	-0.01
<b>Disturbance variables</b>					
Road1	0.10	-0.11	<b>0.21</b>	-0.06	0.04
Road2	0.10	-0.10	<b>0.28</b>	-0.01	-0.01
Road3	-0.02	-0.01	-0.01	0.08	0.00
Road4	-0.04	0.01	0.01	-0.14	0.09
Road5	0.10	0.09	0.08	0.00	-0.12
Road6	0.06	0.01	0.16	-0.07	-0.16
RoadAll	0.16	-0.07	-0.06	0.13	0.00
RoadFree	0.06	0.05	0.01	-0.01	0.05
BuiltDist	-0.06	<b>0.29</b>	<b>-0.61</b>	-0.11	-0.13
Built10	-0.11	0.17	0.17	-0.14	0.10
Built50	0.18	-0.02	-0.04	0.06	-0.12
<b>Broad scale variables</b>					
For10	<b>0.30</b>	0.16	-0.04	-0.16	0.03
For50	-0.06	<b>0.51</b>	0.00	<b>0.53</b>	<b>-0.61</b>
Mead10	-0.12	-0.06	-0.09	-0.10	-0.17
Mead50	<b>0.28</b>	<b>0.62</b>	-0.09	<b>0.41</b>	<b>-0.33</b>
OpFor10	-0.18	0.02	-0.14	0.14	-0.04
OpFor50	-0.07	<b>0.21</b>	<b>-0.26</b>	<b>0.31</b>	<b>-0.26</b>
Past10	<b>-0.29</b>	0.07	0.09	-0.15	0.09

E) Scores of the variables on the first five selected factorial axes (out of 51) from the summer 2000 ENFA (bed site/presence range) for red deer in the Jura Mountains. Explained information 93%.

<i>Marginality=0.</i>	<b>M</b>	<b>S1</b>	<b>S2</b>	<b>S3</b>	<b>S4</b>	<b>S5</b>
<i>Tolerance=0.32</i>	44%	16%	10%	7%	4%	3%
<b>Local scale variables (in 10m radius circle)</b>						
BBerGrass						
BeeBush	0.08	0.03	0.00	-0.06	-0.01	-0.08
BeeGrass	0.04	0.01	-0.04	0.00	0.05	0.05
BilGrass	0.04	-0.05	0.02	0.02	-0.01	0.02
Canopy	0.00	0.04	0.00	0.04	0.01	-0.05
ConBush	0.05	-0.01	0.00	<b>-0.22</b>	-0.03	0.11
DecCan	0.02	-0.08	-0.06	-0.06	-0.05	-0.07
DecScan	-0.03	0.06	-0.03	-0.04	0.05	-0.23
FirBush	0.07	-0.13	-0.01	0.08	0.08	-0.15
FirCan	-0.01	0.06	-0.11	-0.06	-0.06	0.01
FirGrass	0.10	-0.01	0.06	0.03	-0.02	-0.04
FirScan	-0.03	0.10	-0.01	0.02	0.01	0.00
HeigGrass	<b>0.30</b>	-0.04	-0.10	0.00	-0.08	0.04
MappBush	0.09	0.01	-0.08	-0.01	0.04	0.01
MappGrass	0.00	0.01	0.03	0.04	0.05	-0.02
RRasGrass	0.19	-0.08	0.00	-0.05	-0.01	0.01
SpruBush	-0.01	0.14	0.06	0.05	0.01	-0.14
SpruCan	0.05	-0.07	-0.04	-0.12	-0.02	0.03
SpruGrass	0.05	-0.11	0.00	0.07	0.06	-0.12
SpruScan	0.01	0.04	-0.08	0.03	0.00	-0.08
SubCanopy	-0.13	-0.18	0.02	-0.02	-0.04	0.36
UnStory1	0.11	0.04	0.08	0.17	-0.09	0.11
UnStory2	0.10	0.01	0.10	-0.03	-0.01	-0.13
VisMean	-0.18	-0.08	-0.13	-0.01	0.09	-0.31
VisSdev	-0.18	0.05	0.19	0.03	-0.01	0.32
<b>Microscale variables</b>						
BushO	0.05	0.00	0.05	0.07	0.02	-0.06
DecO	0.19	0.03	0.00	0.05	0.01	0.08
Homo	-0.03	-0.11	-0.01	0.02	0.02	-0.04
Pene	-0.17	0.05	0.04	0.00	-0.02	0.08
<b>Topographical variables</b>						
Elev	<b>0.28</b>	-0.08	-0.07	-0.09	0.11	-0.09
Asp_E	0.10	-0.07	0.02	0.03	0.01	0.04
Asp_N	0.11	0.04	-0.03	0.04	-0.06	-0.12
Slope	-0.11	0.00	-0.01	0.04	0.00	0.20
<b>Disturbance variables</b>						
Road1	<b>0.20</b>	0.05	0.00	-0.13	-0.04	-0.09
Road2	0.07	0.04	-0.02	-0.01	0.05	0.00
Road3	0.17	0.07	-0.06	-0.10	-0.01	0.00
Road4	0.10	0.05	0.03	0.00	-0.05	-0.01
Road5	0.14	0.05	-0.04	-0.04	0.01	0.03
Road6	0.10	0.00	-0.02	-0.04	-0.06	-0.09
RoadAll	<b>0.24</b>	0.01	0.00	0.00	0.01	-0.02
RoadFree	<b>0.21</b>	0.01	0.03	0.00	-0.03	0.18
BuiltDist	<b>0.26</b>	-0.05	0.06	0.09	-0.08	0.16
Built10	<b>-0.28</b>	0.03	-0.03	0.16	-0.10	0.02
Built50	-0.08	-0.05	-0.04	-0.09	0.08	-0.03
<b>Broad scale variables</b>						
For10	0.13	0.19	0.06	0.18	-0.05	0.00
For50	0.08	<b>-0.57</b>	<b>-0.64</b>	<b>0.28</b>	0.66	0.24
Mead10	<b>-0.24</b>	0.04	-0.17	-0.10	-0.03	-0.18
Mead50	-0.18	<b>-0.57</b>	<b>-0.34</b>	<b>0.47</b>	0.53	0.31
OpFor10	0.20	-0.18	0.15	<b>0.46</b>	0.11	-0.02
OpFor50	0.08	<b>-0.22</b>	<b>-0.51</b>	<b>-0.24</b>	0.36	0.25
Past10	0.10	0.14	0.02	-0.10	0.02	0.02
Past50	0.09	-0.19	-0.12	<b>0.39</b>	0.22	0.29

**F)** Scores of the variables on the first five selected factorial axes (out of 52) from the summer 2001 ENFA (bed site/presence range) for red deer in the Jura Mountains. Explained information 88%.

<i>Marginality=0.8;</i>	<b>M</b>	<b>S1</b>	<b>S2</b>	<b>S3</b>	<b>S4</b>	<b>S5</b>
<i>Tolerance=0.34</i>	16%	24%	17%	9%	7%	4%
<b>Local scale variables (in 10m radius circle)</b>						
BeeBush	0.11	-0.05	-0.06	<b>-0.29</b>	-0.04	-0.02
BeeGrass	-0.06	0.10	-0.01	0.00	0.01	0.15
BilGrass	0.15	-0.05	0.05	-0.05	0.05	0.03
Canopy	-0.14	0.12	<b>-0.63</b>	-0.04	0.33	0.10
ConBush	0.11	<b>-0.24</b>	-0.01	<b>-0.30</b>	0.05	-0.46
DecCan	-0.10	-0.02	<b>0.40</b>	0.13	-0.32	-0.07
DecSCan	-0.05	0.07	-0.14	0.06	-0.08	0.00
FirBush	0.04	0.05	-0.01	0.12	-0.03	-0.04
FirCan	-0.06	-0.08	0.19	0.05	0.02	0.01
FirGrass	0.07	0.09	0.02	0.12	-0.02	0.14
FirSCan	0.07	-0.04	-0.02	0.03	-0.14	-0.06
GrassGrass	<b>0.28</b>	0.00	-0.01	-0.02	0.14	-0.06
HeigGrass	<b>0.21</b>	-0.04	-0.08	-0.14	0.01	0.09
MappBush	<b>0.21</b>	-0.03	-0.01	-0.20	-0.09	-0.12
MappGrass	0.07	0.03	-0.06	-0.02	0.00	0.02
RRasGrass	<b>0.21</b>	-0.03	0.09	0.08	-0.05	0.04
SpruBush	0.16	0.18	0.08	<b>0.25</b>	-0.15	0.37
SpruCan	0.16	0.11	0.14	0.01	-0.24	-0.04
SpruGrass	-0.06	0.04	-0.11	0.05	-0.03	-0.05
SpruSCan	0.04	-0.12	-0.05	-0.02	-0.06	0.09
SubCanopy	-0.04	0.07	0.16	-0.07	-0.04	-0.07
UnStory1	0.18	0.09	-0.01	<b>0.25</b>	-0.09	0.13
UnStory2	0.18	-0.08	0.17	0.02	-0.01	0.00
VisMean	<b>-0.22</b>	-0.10	0.14	-0.02	0.22	-0.29
VisSdev	-0.05	0.06	-0.06	-0.13	-0.06	0.07
<b>Microscale variables</b>						
BushO	0.05	-0.05	-0.01	-0.12	0.08	0.07
ConO	0.18	0.05	-0.14	0.04	0.04	0.03
DecO	-0.14	0.02	-0.11	0.08	0.05	0.03
Homo	0.19	-0.03	0.02	-0.08	0.10	0.09
Pene	0.18	<b>0.20</b>	-0.12	0.09	0.21	-0.18
<b>Topographical variables</b>						
Elev	<b>0.24</b>	0.04	-0.01	-0.16	0.22	-0.01
Asp_E	-0.01	-0.06	-0.05	-0.02	-0.20	-0.06
Asp_N	-0.01	0.09	-0.14	-0.10	-0.16	-0.02
Slope	-0.16	-0.08	0.08	-0.06	0.01	0.26
<b>Disturbance variables</b>						
Road1	-0.01	-0.06	0.06	<b>-0.28</b>	-0.26	-0.10
Road2	0.16	-0.07	-0.02	0.00	-0.15	0.00
Road3	0.04	0.14	-0.14	-0.09	-0.08	-0.16
Road4	<b>0.23</b>	-0.01	-0.09	<b>-0.21</b>	-0.02	0.00
Road5	-0.02	0.00	-0.07	0.07	-0.03	-0.20
Road6	0.01	0.07	-0.01	0.05	-0.02	-0.08
RoadAll	0.18	0.06	0.08	0.00	0.08	-0.01
RoadFree	0.14	-0.06	-0.07	0.18	-0.10	-0.09
BuiltDist	0.19	0.09	0.10	0.18	0.44	0.06
Built10	-0.13	<b>0.22</b>	0.17	0.08	0.19	0.05
Built50	-0.12	-0.11	0.01	-0.01	-0.03	0.15
<b>Broad scale variables</b>						
For10	0.06	-0.12	<b>-0.22</b>	-0.14	-0.05	-0.23
For50	0.09	<b>0.54</b>	-0.05	-0.18	-0.14	0.09
Mead10	-0.18	-0.03	-0.11	<b>-0.27</b>	-0.11	-0.24
Mead50	<b>-0.22</b>	<b>0.44</b>	-0.08	<b>-0.29</b>	0.08	0.20
OpFor10	0.11	-0.02	-0.04	0.00	-0.04	0.17
OpFor50	0.03	<b>0.33</b>	0.03	<b>-0.24</b>	0.00	0.10
Past10	0.09	0.02	-0.12	-0.09	0.10	-0.05



### 13.3. Appendix 3, bed site selection with univariate tests

A) Environmental variables (untransformed) recorded at random points inside red deer absence range and at random points inside red deer presence range during winter in the Jura Mountains (1999-2000).

Variables	T-test		Absence range		Presence range	
	t	P	Mean	SD	Mean	SD
<i>Local scale variables</i>						
Canopy	-1.06	0.28939	16.42	18.54	18.84	18.56
SubCanopy	0.36	0.72147	7.40	13.69	6.91	13.35
UnStory1	0.72	0.47085	9.36	15.80	8.15	13.02
UnStory2	-0.88	0.37793	3.59	6.54	4.29	7.53
FirCan	-0.41	0.67879	1.87	4.62	2.14	5.97
SpruCan	-0.47	0.63634	3.42	7.36	2.27	6.50
DecCan	1.43	0.15313	7.78	15.51	8.88	16.23
FirSCan	-0.59	0.55503	2.18	10.86	1.87	9.48
SpruSCan	0.26	0.79517	2.24	5.88	2.92	7.22
DecSCan	-0.93	0.35145	5.70	14.37	5.40	12.86
ConBush	0.28	0.77939	1.50	3.13	1.46	3.81
FirBush	-1.29	0.19765	0.67	1.75	1.07	3.64
SpruBush	2.00	0.04653	0.84	2.63	0.40	0.97
BeeBush	0.89	0.37653	4.89	12.61	3.44	11.14
MappBush	2.54	0.01206	0.38	1.29	0.11	0.39
<i>Topographical variables</i>						
Elev	0.88	0.38164	1086.69	234.84	1044.42	209.10
Asp.N	-0.39	0.69570	0.60	0.29	0.61	0.26
Asp.E	1.69	0.09159	0.45	0.27	0.40	0.26
Slope	-2.04	0.04231	14.99	11.96	17.65	11.62
<i>Disturbance variables</i>						
Road1	-1.96	0.05077	1472.82	1024.62	1780.67	1292.05
Road2	-3.88	0.00013	1470.70	1143.98	1945.09	1211.82
Road3	1.52	0.12943	309.58	246.81	263.21	224.73
Road4	-0.44	0.65721	227.24	241.66	254.33	314.62
Road5	-2.01	0.04552	147.40	107.13	179.78	137.59
Road6	1.65	0.10033	310.35	292.26	267.86	253.34
RoadAll	0.20	0.83971	58.21	50.26	54.58	42.56
RoadFree	-1.32	0.18714	8466.48	15260.47	10976.50	18481.27
BuiltDist	-0.76	0.44979	1320.55	893.89	1323.10	714.86
Built10	4.61	0.00001	3.56	6.48	1.02	2.53
Built50	5.62	0.00000	4.67	2.83	3.28	1.36
<i>Broad scale variables</i>						
Mead10	-2.62	0.00912	7.66	12.84	11.74	15.01
For10	-2.21	0.02784	74.72	21.06	79.42	18.87
OpFor10	1.25	0.21121	2.74	9.05	1.74	4.95
Past10	4.42	0.00001	11.23	13.46	5.40	9.36
Mead50	-8.73	0.00000	20.35	8.68	28.03	7.04
For50	5.46	0.00000	56.08	7.09	50.95	9.44
OpFor50	-2.48	0.01359	3.61	4.45	4.99	5.55
Past50	4.68	0.00000	14.52	5.95	11.59	5.37

**B)** Environmental variables (untransformed) recorded at random points inside red deer absence range and at random points inside red deer presence range during summer in the Jura Mountains (2000-2001).

Variables	T-test		Absence range		Presence range	
	t	P	Mean	SD	Mean	SD
<b>Local scale variables</b>						
Canopy	1.76	0.07915	35.38	22.93	30.51	21.84
SubCanopy	0.42	0.67613	13.85	16.08	12.83	16.75
UnStory1	0.73	0.46340	9.30	14.08	8.23	11.49
UnStory2	0.57	0.56724	7.46	9.68	6.48	10.65
Grass	-3.31	0.00107	36.96	34.91	51.18	37.74
FirCan	-0.94	0.34591	5.15	9.74	6.37	11.84
SpruCan	0.33	0.74010	11.13	13.08	10.62	11.19
DecCan	2.19	0.02959	16.83	21.12	11.94	16.18
FirSCan	0.80	0.42735	2.30	8.40	1.57	6.27
SpruSCan	0.83	0.40705	4.90	10.67	3.87	8.71
DecSCan	0.60	0.55098	6.05	11.21	5.25	10.17
ConBush	0.08	0.93674	5.37	7.58	5.20	9.37
FirBush	-0.19	0.85237	1.57	3.90	1.66	4.16
SpruBush	0.16	0.87000	3.80	7.08	3.55	8.93
BeeBush	1.73	0.08438	7.71	14.02	5.19	9.22
MappBush	-0.91	0.36380	0.76	1.94	0.99	2.29
FirGrass	0.34	0.73554	0.15	0.38	0.13	0.58
SpruGrass	0.81	0.41721	0.32	0.63	0.25	0.63
BeeGrass	1.47	0.14292	3.30	11.62	1.63	6.22
MappGrass	0.80	0.42538	0.32	0.97	0.25	0.58
GrassGrass	-0.66	0.50757	18.89	30.95	21.06	33.46
BilGrass	1.71	0.08828	5.51	13.31	3.07	9.47
BBerGrass	-0.70	0.48562	0.32	1.51	0.58	4.09
HeigGrass	-0.83	0.41010	0.79	1.11	1.26	1.97
RRasGrass	1.31	0.19236	1.12	4.11	0.62	1.72
<b>Topographical variables</b>						
Elev	-1.46	0.14440	1171.79	205.83	1206.85	192.13
Asp.N	-0.59	0.55582	0.52	0.33	0.55	0.30
Asp.E	1.04	0.29728	0.42	0.26	0.39	0.25
Slope	-1.64	0.10	20.38	12.26	22.66	10.50
<b>Disturbance variables</b>						
Road1	1.19	0.23527	1943.46	1195.36	1764.99	1120.78
Road2	-2.29	0.02256	1808.71	1125.47	2132.04	1182.11
Road3	0.46	0.64627	348.42	297.75	342.67	321.14
Road4	-1.86	0.06407	263.39	293.01	316.37	316.87
Road5	1.18	0.24012	175.49	152.87	150.46	129.64
Road6	-0.97	0.33445	353.66	316.29	396.01	351.45
RoadAll	-1.23	0.21968	58.52	57.02	67.07	66.46
RoadFree	0.59	0.55248	31041.76	60246.15	25484.69	50872.56
BuiltDist	-1.20	0.23105	1449.62	828.98	1574.74	885.53
Built10	-0.34	0.73317	0.77	2.37	0.87	2.49
Built50	1.29	0.19932	3.45	2.05	3.13	1.96
<b>Broad scale variables</b>						
Mead10	0.95	0.34214	7.27	13.92	5.88	11.07
For10	2.17	0.03093	74.01	23.16	65.97	27.84
OpFor10	-2.26	0.02444	5.05	10.39	8.43	13.88
Past10	-3.11	0.00209	12.57	14.39	18.75	18.30
Mead50	2.92	0.00376	19.01	11.26	15.16	10.32
For50	-0.10	0.91802	53.33	10.61	53.46	10.83
OpFor50	-1.53	0.12710	5.64	5.87	6.78	6.40
Past50	-2.74	0.00651	17.02	7.78	19.80	8.88

C) Environmental variables (untransformed) recorded at red deer bed sites and at random points inside red deer range during summer 2000 and 2001 in the Jura Mountains with means independently significant. Differences were examined with t-tests.

Variables	SUMMER 2000				SUMMER 2001							
	T-test t	P	Bed site Mean	SD	Presence range Mean SD		T-test t	P	Bed site Mean	SD	Presence range Mean SD	
<b>Local scale variables</b>												
Canopy	-0.15	0.87971	36.83	24.40	37.61	25.45	-3.02	0.00297	26.49	19.31	37.61	26.40
SubCanopy	-1.48	0.14292	10.65	13.07	15.22	19.91	-1.73	0.08528	11.05	11.26	15.32	19.09
UnStory1	0.66	0.50912	15.18	17.05	13.02	16.58	1.00	0.31683	8.79	9.48	6.37	12.39
UnStory2	0.58	0.56425	10.20	15.26	7.94	15.50	1.89	0.06122	12.79	12.81	8.77	11.26
FirCan	-0.85	0.39618	6.75	11.88	8.91	15.60	-1.99	0.04868	3.19	6.03	6.18	11.62
SpruCan	0.76	0.44977	12.62	17.64	10.28	15.06	1.51	0.13441	8.48	8.46	6.05	9.98
DecCan	0.06	0.94969	15.23	19.29	15.15	18.48	-2.27	0.02449	14.95	15.96	22.39	23.18
FirSCan	-0.92	0.19375	1.20	2.86	2.37	9.10	-1.07	0.28783	1.65	3.05	2.95	10.64
SpruSCan	0.36	0.71811	3.10	6.92	2.67	6.00	-0.65	0.51409	2.87	5.94	3.73	11.10
DecSCan	0.05	0.95734	6.33	13.85	6.19	12.46	-1.86	0.06541	4.73	7.18	8.06	13.61
ConBush	-0.04	0.97013	8.05	9.41	7.91	14.03	-0.16	0.87231	3.54	3.68	3.66	7.28
FirBush	1.31	0.19375	4.57	7.74	2.87	6.00	0.05	0.95771	1.05	2.13	1.03	2.59
SpruBush	-0.80	0.42458	3.48	7.46	5.06	13.72	-0.17	0.86146	2.51	3.28	2.63	7.05
BeeBush	1.75	0.08357	13.32	19.98	7.85	12.66	0.54	0.59291	9.43	10.27	8.05	13.51
MappBush	-0.12	0.90783	0.93	2.19	0.98	2.19	3.15	0.00234	2.94	5.23	0.73	2.09
FirGrass	1.08	0.28482	0.53	1.43	0.30	0.88	1.07	0.28764	0.06	0.25	0.03	0.16
SpruGrass	0.85	0.39647	0.65	1.42	0.46	0.88	-1.18	0.23877	0.03	0.18	0.08	0.27
BeeGrass	0.39	0.69913	4.30	7.76	3.59	9.48	-0.66	0.50955	0.65	2.19	1.04	4.67
MappGrass	0.50	0.62038	0.57	1.03	0.48	0.79	1.16	0.24895	0.17	0.42	0.10	0.30
GrassGrass	0.52	0.60497					3.65	0.00045	3.32	4.21	1.22	1.96
BilGrass	0.14	0.88768	3.55	13.50	3.43	10.73	-0.07	0.94469	1.16	3.05	1.14	7.87
BBerGrass	-1.42	0.16276	0.00	0.00	1.24	6.41	-0.35	0.72677	0.32	0.91	0.39	1.61
RRasGrass	2.09	0.04072	3.48	8.84	0.98	2.53	2.43	0.01788	4.60	11.78	0.82	3.08
HeigGrass	3.29	0.00133	0.44	0.25	0.29	0.22	3.35	0.00108	0.52	0.50	0.24	0.43
BushO	1.24	0.21805	9.73	24.74	4.48	16.14	1.67	0.09815	14.68	29.17	7.46	18.07
ConO	3.28	0.00153	24.25	39.84	5.46	18.69	2.52	0.01360	10.86	16.66	4.94	9.22
DecO	1.66	0.09897	16.32	32.23	6.85	23.07	-3.44	0.00080	3.27	4.97	7.95	10.74
VisMean	-2.09	0.03916	17.45	12.78	28.85	26.01	-4.56	0.00001	13.84	7.21	22.41	12.63
VisSdev	-2.85	0.00584	7.82	8.05	17.04	22.51	-1.52	0.13201	8.21	5.56	10.14	7.47
<b>Topographical variables</b>												
Elev	3.22	0.00176	1262.50	157.69	1139.39	237.47	4.94	0.00000	1264.35	136.83	1118.38	220.76
Asp.N	1.11	0.26885	0.60	0.32	0.53	0.32	-0.09	0.92652	0.64	0.24	0.64	0.25
Asp.E	1.06	0.29202	0.40	0.24	0.35	0.22	0.04	0.96597	0.44	0.31	0.44	0.29
Slope	-1.07	0.28625	16.17	12.78	18.72	12.65	-2.81	0.00577	23.02	7.91	26.84	8.25
<b>Disturbance variables</b>												
Road1	2.41	0.01773	2262.93	1346.80	1673.59	1130.69	0.19	0.84962	2072.57	1397.77	1995.59	1323.65
Road2	0.78	0.43776	2411.33	1136.92	2266.00	1300.52	2.68	0.00824	2244.38	1113.87	1733.11	1176.54
Road3	1.66	0.09904	384.47	299.94	312.17	289.76	0.46	0.64674	324.89	245.01	329.08	288.22
Road4	0.83	0.40936	401.87	366.96	368.94	410.59	3.71	0.00030	411.97	408.06	228.66	298.11
Road5	1.80	0.07489	240.83	181.61	185.26	144.51	-0.17	0.86723	219.08	177.28	218.23	166.68
Road6	1.06	0.28981	280.90	229.18	244.59	247.39	0.37	0.71369	247.65	236.21	232.41	207.03
RoadAll	2.73	0.00747	88.67	58.88	62.33	74.01	3.07	0.00258	69.48	42.07	50.32	54.55
RoadFree	-3.37	0.00130	20874.67	25230.12	13440.81	24248.72	2.25	0.02599	22938.65	27460.00	15278.18	22775.39
BuiltDist	3.00	0.00353	2029.55	619.07	1662.61	872.76	3.55	0.00052	1967.75	666.33	1549.59	762.01
Built10	-2.32	0.02397	0.03	0.26	0.48	1.40	-2.46	0.01586	0.10	0.35	0.58	1.71
Built50	-1.14	0.25761	2.62	1.30	2.96	1.86	-2.41	0.01736	2.60	1.36	3.24	1.79
<b>Broad scale variables</b>												
Mead10	-3.64	0.00059	1.40	2.60	8.83	14.65	-5.09	0.00000	1.25	1.91	8.43	12.27
For10	1.37	0.17420	83.48	18.26	76.44	26.20	1.01	0.31341	82.76	17.74	80.27	15.94
OpFor10	0.38	0.70565	7.40	12.81	6.31	14.78	1.88	0.06233	7.14	13.00	3.56	8.47
Past10	-0.04	0.96734	7.75	8.97	7.78	11.72	1.01	0.31518	8.76	9.24	7.14	9.57
Mead50	-2.14	0.03448	20.25	7.15	23.57	9.32	-3.99	0.00010	19.71	6.75	24.95	9.01
For50	0.79	0.42997	56.78	11.94	55.09	11.16	1.51	0.13496	56.13	12.80	53.27	10.62
OpFor50	0.81	0.41923	5.78	6.56	4.80	6.40	1.20	0.23192	6.30	6.75	5.03	5.69
Past50	1.05	0.29805	14.17	5.92	12.91	6.74	2.09	0.03806	14.97	5.25	13.09	5.40

**D)** Environmental variables (untransformed) recorded at red deer bed sites and at random points inside red deer range during winter 1999 and 2000 in the Jura Mountains with means independently significant. Differences were examined with t-tests

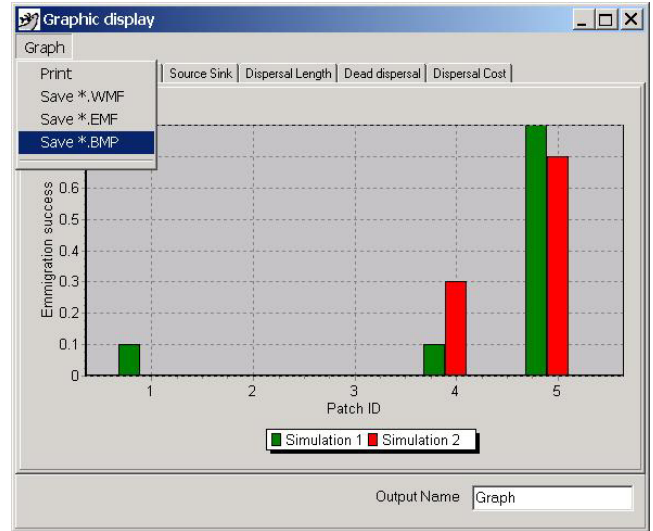
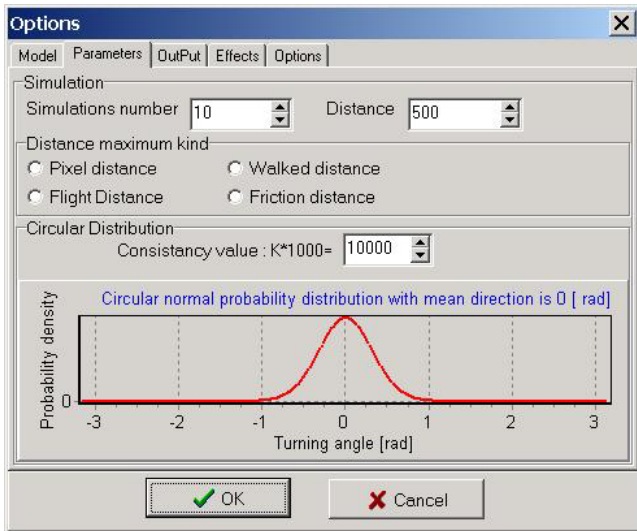
Variables	WINTER 1999						WINTER 2000					
	T-test t	P	Bed site Mean	SD	Presence range Mean	SD	T-test t	P	Bed site Mean	SD	Presence range Mean	SD
<b>Local scale variables</b>												
Canopy	-1.31	0.19139	20.67	20.99	25.42	20.71	0.61	0.54385	12.03	10.05	10.73	11.35
SubCanopy	3.47	0.00091	24.59	28.78	8.30	16.59	0.93	0.35141	6.38	7.27	5.16	7.55
UnStory1	1.77	0.08136	18.16	21.63	11.47	15.62	0.10	0.91856	4.26	5.20	4.08	7.16
UnStory2	0.54	0.59202	4.92	6.12	4.25	7.87	-1.65	0.10073	2.78	3.91	4.29	7.13
FirCan	3.47	0.00109	11.67	21.35	0.36	1.18	1.90	0.05959	8.00	14.22	4.23	8.28
SpruCan	0.13	0.89927	1.47	6.58	1.37	3.63	-1.15	0.25076	2.09	4.12	3.31	8.66
DecCan	-2.23	0.02738	6.86	16.62	14.71	20.11	1.37	0.17388	2.26	2.11	1.79	1.91
FirSCan	2.60	0.01216	9.04	23.48	0.15	0.68	1.31	0.19228	7.79	22.49	3.90	13.76
SpruSCan	0.37	0.71619	4.29	16.93	3.97	5.90	1.19	0.23826	4.06	16.75	1.62	8.37
DecSCan	-2.44	0.01612	3.57	10.41	9.36	16.26	-1.32	0.19038	0.25	0.80	0.61	2.31
ConBush	3.24	0.00215	14.53	28.76	0.41	1.32	0.53	0.59531	3.19	5.17	2.70	5.19
FirBush	2.62	0.01175	10.27	25.06	0.30	1.11	-1.41	0.16170	1.13	1.54	1.97	5.11
SpruBush	1.68	0.09896	4.25	16.78	0.11	0.58	2.16	0.03336	2.08	5.24	0.74	1.20
BeeBush	-1.38	0.17010	2.35	3.33	4.48	14.69	0.02	0.98362	2.19	3.51	2.16	3.44
MappBush	2.04	0.04626	0.27	0.92	0.01	0.10	-1.06	0.29292	0.16	0.40	0.23	0.54
BushO							2.47	0.01549	9.64	21.57	3.26	7.50
ConO	5.51	0.00000	50.49	47.26	16.51	15.81	1.29	0.20033	10.99	20.73	6.43	18.42
DecO	-9.40	0.00000	0.18	0.79	19.55	25.11	-1.93	0.05596	0.56	0.99	0.90	1.23
VisMean	-0.39	0.69386	32.16	21.30	32.96	20.03	-1.88	0.06262	37.24	14.68	57.03	89.11
VisSdev	-0.93	0.35296	17.02	19.95	18.05	16.30	-1.91	0.05945	16.81	12.42	48.50	153.45
<b>Topographical variables</b>												
Elev							0.11	0.91253	1043.05	158.02	1030.86	239.41
Asp.N	2.66	0.00895	0.70	0.22	0.58	0.29	0.56	0.57802	0.66	0.23	0.63	0.25
Asp.E	-1.28	0.20428	0.33	0.20	0.37	0.24	-0.20	0.83816	0.42	0.27	0.42	0.29
Slope							-4.13	0.00006	13.19	7.03	18.87	10.52
<b>Disturbance variables</b>												
Road1	1.64	0.10470	2073.57	1337.95	1700.25	1356.31	1.53	0.12853	2182.42	1234.84	1853.62	1222.34
Road2	1.06	0.29318	1888.27	1238.98	1673.58	1142.25	1.05	0.29498	2559.44	1446.30	2244.23	1238.75
Road3	2.19	0.03072	287.14	196.96	230.91	213.78	-0.29	0.77288	287.77	229.29	298.39	233.77
Road4	1.12	0.26548	236.78	250.26	218.80	317.98	-0.16	0.87256	300.92	349.76	293.47	306.94
Road5	1.63	0.10678	210.73	180.75	159.59	128.89	0.85	0.39629	226.60	164.28	201.57	145.46
Road6	0.42	0.67651	289.61	242.10	282.42	250.51	0.58	0.56157	254.27	227.29	246.97	257.17
RoadAll	4.21	0.00005	76.80	45.27	48.34	40.34	1.77	0.07920	70.64	39.88	61.32	44.46
RoadFree	2.29	0.02435	22516.61	31275.95	11894.85	20411.76	0.84	0.40123	12270.09	19878.25	9736.70	15832.34
BuiltDist	0.98	0.32829	1275.90	505.60	1199.71	551.47	0.21	0.83715	1401.03	524.29	1453.34	863.81
Built10	-0.51	0.60816	0.80	1.80	0.97	1.85	-2.30	0.02399	0.23	0.69	1.08	3.16
Built50	0.65	0.51871	3.51	1.99	3.30	1.45	1.89	0.06135	3.61	1.10	3.21	1.30
<b>Broad scale variables</b>												
Mead10	0.00	0.99824	11.71	20.25	12.68	14.56	-1.74	0.08349	6.75	11.49	10.45	15.50
For10	1.05	0.29702	80.71	21.99	77.47	20.43	3.72	0.00028	90.27	12.55	80.71	18.96
OpFor10	0.33	0.74247	1.98	4.46	1.68	5.64	-1.25	0.21407	1.05	3.55	1.79	3.97
Past10	-0.82	0.41575	4.61	9.66	6.03	11.01	-3.55	0.00060	1.61	2.82	4.57	6.81
Mead50	0.56	0.57928	30.00	8.05	29.33	6.23	2.74	0.00691	29.40	5.09	26.12	8.20
For50	-0.16	0.87007	48.39	8.60	48.63	9.02	-0.53	0.59618	53.03	8.74	53.05	11.03
OpFor50	0.29	0.77568	5.98	5.98	5.68	5.83	-0.03	0.97304	4.12	5.21	4.14	5.11
Past50	-0.33	0.74410	11.22	5.95	11.54	5.01	-2.55	0.01166	9.34	5.38	11.64	5.80

### 13.4. Appendix 4, Snapshots of *DeerDisperser* software

See section 6-3 for further explanations

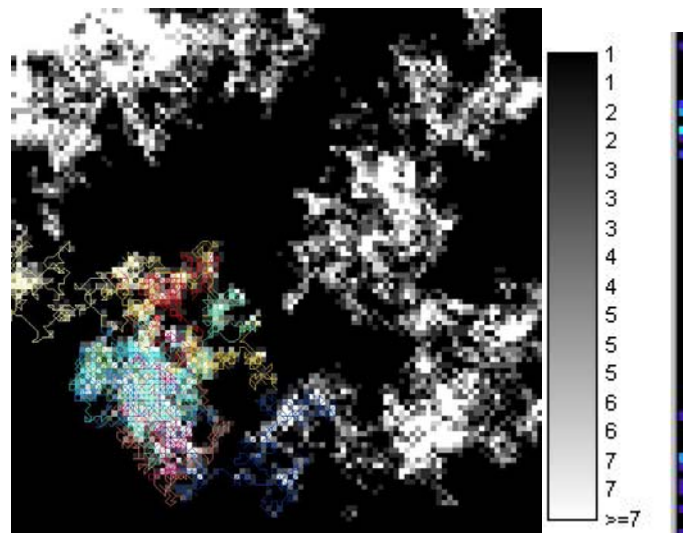
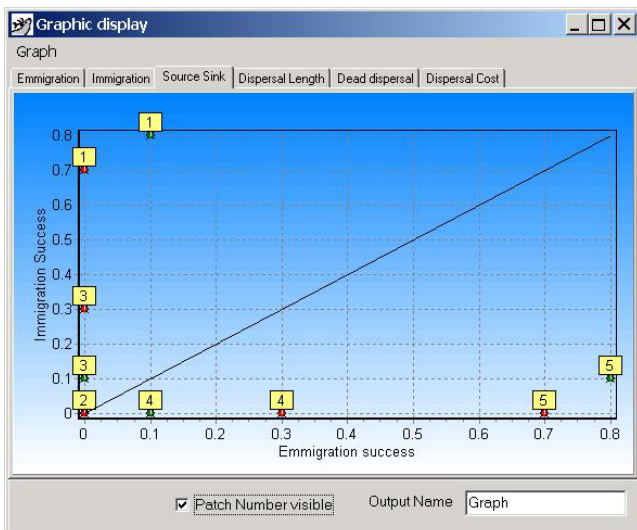
A) Random walk parameters.

B) Plot of tranfert rate probabilities for each habitat patch and for two different simulations.



C) Plot of Immigration success vs emmigration success for each habitat patch and for two simulations.

D) Visitation frequency raster map (white to black) and simulating pathways (color lines) of movers (one color per individual mover) from one patch.



### 13.5. Description of circular random walk function

From CAIN M.L. 1985. Random Search by Herbivorous Insects - a Simulation-Model. Ecology 66(3):876-888:

Here I describe a simple Monte Carlo technique for generating random numbers with a circular normal probability distribution. The technique may be applied to any probability distribution that possesses a density function (see Butler 1970 for a different approximation method, and Freiberger and Grenander 1971 for a mathematical discussion of random number generation).

The circular normal distribution has the density function:

$$f(x) = \frac{1}{2\pi I_0(K)} e^{K \cos(x-m)}, \quad (A.1)$$

where  $K$  and  $m$  are parameters describing turning angle concentration and mean direction of motion, respectively, and  $I_0(K)$  is the Bessel function of purely imaginary argument of order zero.

To generate circular normal random numbers, first divide the unit circle into  $N$  sections so that each section has an arc length of  $2\pi/N$ . I will refer to the  $N$  intervals so created as  $I_j$ , where  $I_j = \left[ \frac{2\pi}{N}(j-1), \frac{2\pi}{N}j \right]$ , for  $j = 1, 2, \dots, N$ . For large  $N$ , a reasonable approximation to the probability  $p_j$  that a circular normal random variable  $X$  takes on a value  $x \in I_j$  is:

$$p_j \propto \frac{2\pi}{N} \frac{1}{2\pi I_0(K)} e^{K \cos(x_j - m)}, \quad (A.2)$$

where  $x_j = \frac{2\pi}{N} \left( j - \frac{1}{2} \right)$  is the midpoint of the  $j^{\text{th}}$  interval ( $I_j$ ).

Thus,  $p_j$  is proportional to the length of the interval  $I_j \left( \frac{2\pi}{N} \right)$  multiplied by the circular normal density function evaluated at the midpoint of  $I_j$ :  $\frac{1}{2\pi I_0(K)} e^{K \cos(x_j - m)}$ .

For convenience I will call the right-hand side of Eq. 2  $Pr_j$ . A constant of proportionality ( $1/\sum_j Pr_j$ ) is necessary to make

the sum of the approximate probability masses  $p_j$  equal to one. Thus, to find the probability that an angle is in  $I_j$ , first compute  $Pr_j$  for  $j = 1, 2, \dots, N$ , and then normalize to obtain:

$$p_j = Pr_j / \sum_{j=1}^N Pr_j \quad (A.3)$$

An approximate cumulative distribution function may now be formed:

$$F_i = \sum_{j=1}^i p_j \quad (A.4)$$

where  $i = 1, 2, \dots, N$ . As suggested by Fig. A1, a random number  $x$  chosen between zero and one will fall between  $F_{j-1}$  and  $F_j$  with the same probability ( $p_j$ ) that a circular normal angle will lie in the interval  $I_j$ . Thus, if random numbers  $x$  and  $y$  are selected between zero and one and it is found that

$F_{j-1} \leq x < F_j$ , the angle should be set equal to  $\frac{2\pi}{N}(j-1+y)$ .

Angles so chosen will be circular normal with parameters  $m$  and  $K$ .

This method was tested by generating 800 observations and comparing them to the circular normal distribution using the chi-squared goodness-of-fit test (40 degrees of freedom). In generating test data the unit circle was divided into 100, 200, or 400 sections. A close fit was obtained in each simulation; in none did the observed distribution significantly differ from a circular normal distribution ( $N = 100$ :  $\chi^2 = 34.0$ ,  $P = .74$ ;  $N = 200$ :  $\chi^2 = 46.4$ ,  $P = .22$ ;  $N = 400$ ,  $\chi^2 = 21.7$ ,  $P = .99$ ).

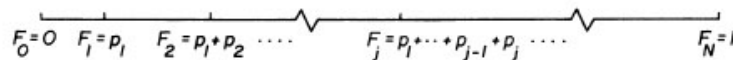


FIG. A1. A graphic representation of the approximate cumulative distribution function.  $F_0 = 0$  by definition;  $F_N = 1$  by substitution.