



UNIVERSITÉ CLAUDE BERNARD - LYON 1,
UNIVERSITÉ DE LYON UMR CNRS 5558,
LABORATOIRE DE BIOMÉTRIE ET BIOLOGIE ÉVOLUTIVE
43, BOULEVARD DU 11 NOVEMBRE 1918,
F-69622 VILLEURBANNE, FRANCE
[HTTP://LBBE.UNIV-LYON1.FR/?LANG=EN](http://lbbe.univ-lyon1.fr/?lang=en)

HABITAT SELECTION AND MOVEMENT BY BROWN BEARS IN MULTIPLE-USE LANDSCAPES

JODIE MARTIN

NORWEGIAN UNIVERSITY OF LIFE SCIENCES • UNIVERSITETET FOR MILJØ- OG BIOVITENSKAP
DEPARTMENT OF ECOLOGY AND NATURAL RESOURCE MANAGEMENT
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Jodie Martin

PhD thesis

Laboratoire de Biométrie et Biologie Evolutive
Université Claude Bernard Lyon 1

&

Dept. of Ecology and Natural Resource Management
Norwegian University of Life Sciences

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- **PhD Supervisors**

Pr. Dominique Allainé

Université Claude Bernard Lyon 1
UMR CNRS 5558 – Laboratoire de Biométrie et Biologie Évolutive
43, boulevard du 11 novembre 1918
F-69622 Villeurbanne, France

Pr. Jon E. Swenson

Norwegian University of Life Sciences
Department of Ecology and Natural Resource Management
Post Box 5003, N-1432 Ås, Norway

- **Adjudication Committee**

Dr. Eloy Revilla

Estación Biológica de Doñana CSIC
Department of Conservation Biology
Avenida de Maria Luisa s/n, Pabellón del Perú
E-41013 Sevilla, Spain

Dr. Stephanie Kramer-Schadt

Universitetet i Bergen
Institutt for biologi
Postboks 7800,
5020 Bergen, Norway

Dr. Olav Hjeljord

Norwegian University of Life Sciences
Department of Ecology and Natural Resource Management
Post Box 5003, N-1432 Ås, Norway

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ABSTRACT

Habitat selection is a preponderant field of evolutionary biology, ecology and conservation biology, as it is one of the driving forces influencing wildlife distribution in the landscape. In essence, it is a hierarchical process, occurring at different spatial and temporal scales. In this thesis, I studied habitat selection at different spatial scales in three European populations of brown bears (*Ursus arctos*) distributed in contrasting landscapes, differentially impacted by anthropogenic pressure.

The results showed that habitat selection within the Scandinavian population was not congruent across spatial scales. However, human infrastructures influence brown bear space occupancy both at large scale (population establishment) and at finer scale (individual selection of habitats within their home range). I also documented a temporal avoidance of anthropogenic structures and a functional response of females to these disturbances. At intermediate scale, no common pattern of habitat selection was identified, probably because of the social structure of females (philopatry), which might supplant choice of habitats.

At the landscape scale, habitat selection of the Cantabrian Mountains and Pyrenean populations was very similar; bears selected forest connectivity at large scale (15 km), forested areas that produce hard mast, and areas with low human impact. The predictive model allowed to identify the quantity and connectivity of suitable habitats within each population, thus providing a valuable tool for conservation planning.

Movement is the mechanism by which individuals can choose among available habitats. I analyzed movements of Scandinavian brown bears, which revealed the joint influence of internal and external factors on movements and its variability according to biological requirements. I also discuss the need for linking habitat selection and movement ecology to obtain insights into behavioral processes involved in habitat selection.

RÉSUMÉ

La sélection de l'habitat est un domaine prépondérant en biologie évolutive, en écologie et en biologie de la conservation car c'est un des processus majeurs influençant la distribution de la faune sauvage dans le paysage. Il s'agit d'un processus hiérarchique intervenant à différentes échelles spatiales et temporelles. Dans cette thèse, je me suis intéressée à la sélection de l'habitat à différentes échelles spatio-temporelles de trois populations européennes d'ours brun (*Ursus arctos*) qui évoluent dans des habitats contrastés et affectés différemment par les pressions anthropiques.

Nos résultats ont montré que la sélection de l'habitat par la population Scandinave diffère en fonction des échelles spatiales et temporelles considérées. En revanche, l'activité humaine influence les ours à la fois à l'échelle du paysage (établissement de la population) et à fine échelle (sélection des habitats par les individus à l'intérieur des domaines vitaux). Nous avons également mis en évidence un évitement temporel des structures anthropiques et une réponse fonctionnelle des femelles en réponse à ces perturbations. A une échelle spatiale intermédiaire, aucun patron commun de sélection n'a cependant été identifié, probablement du à la structure sociale des femelles (philopatrie) qui pourrait supplanter le choix des habitats.

Grâce à un modèle quantitatif de sélection de l'habitat, nous avons également pu démontrer qu'à large échelle, les populations des monts Cantabriques et des Pyrénées sélectionnaient les mêmes caractéristiques d'habitat : une importante connectivité des forêts à large échelle (15 km), des zones de forte production de fruits forestiers et des zones de faible influence humaine. Notre modèle prédictif nous a donc permis de quantifier les habitats de bonne qualité pour ces deux populations et les connections potentielles entre les noyaux d'individus au sein de chacune des populations, et constitue donc un important outil de conservation.

Le mouvement étant le mécanisme permettant aux individus d'effectuer des choix parmi les habitats disponibles, nous avons également conduit une analyse des règles de mouvement des ours scandinaves qui a révélé une influence conjointe des facteurs internes et externes sur les déplacements et une optimisation des mouvements selon leurs exigences biologiques. Je discute également du lien entre l'écologie du mouvement et la sélection de l'habitat, et du potentiel d'une intégration de ces deux processus dans la compréhension des mécanismes comportementaux impliqués dans la sélection des habitats par les animaux.

SAMMENDRAG

Habitatseleksjon er en av de viktigste faktorene som former fordeling av dyr i landskapet og er et viktig felt innenfor evolusjonsbiologi, økologi og forvaltningsbiologi. Habitatseleksjon er en hierarkisk prosess som opptrer på ulike romlige og temporære skala. I denne avhandlingen har jeg studert habitatseleksjon på ulike romlige skala i tre europeiske bjørnepopulasjoner (*Ursus arctos*), fordelt i ulike landskap og med forskjellig grad av menneskelig påvirkning.

Jeg fant at habitatseleksjon i den skandinaviske populasjonen varierte mellom romlige skala. Menneskeskapt infrastruktur påvirket områdebruken til brunbjørn både på stor skala (etablering av populasjon) og på en finere skala (individuell habitatseleksjon innenfor leveområder). Jeg fant også en temporær unngåelse av menneskeskapte strukturer og en funksjonell respons i habitatseleksjonen for disse forstyrrelsene hos hunner. Ingen felles mønster av habitatseleksjon ble identifisert på den intermediære skala, sannsynligvis på grunn av at sosial strukturering hos hunner (philopatry) kan redusere mulighetene for habitatvalg.

Populasjonene i de cantabriske fjell og i Pyreneene hadde lik habitatseleksjon på landskapsnivå; bjørn selekterte storskala sammenhengende skog (15 km), skogsområder med god tilgjengelighet på nøtter og områder med lav menneskelig påvirkning. En prediktiv modell identifiserte hvor mye store og sammenhengende egnede områder som var tilgjengelig for de ulike populasjonene. Dette er et verdifullt verktøy for bevaringstiltak.

Mekanismen som gjør individer i stand til å velge mellom tilgjengelige habitat er bevegelse. Jeg analyserte brunbjørns bevegelse i Skandinavia og fant en felles innflytelse av interne og eksterne faktorer som påvirker bevegelse og variasjon i bevegelse gjennom biologiske behov. Jeg diskuterer også behovet for å koble økologiske problemstillinger relatert til habitatseleksjon og bevegelse for å oppnå innsikt i adferdsprosesser som påvirker habitatseleksjon.

LIST OF PAPERS

PAPER I

MARTIN J., CALENGE C., QUENETTE P.-Y. & ALLAINÉ D. (2008) Importance of movement constraints in habitat selection studies. *Ecological Modelling*, 213 :257-262.

PAPER II

MARTIN J., TOLON V., VAN MOORTER B., BASILLE M. & CALENGE C. (2009) On the use of telemetry in habitat selection studies. In *“Telemetry: Research, Technologies and Applications*.

PAPER III

MARTIN J., BASILLE M., KINDBERG J., VAN MOORTER B., ALLAINÉ D., & SWENSON J.E. Scale-dependent effects of human disturbance on large mammals: brown bears in Scandinavia. *Submitted*

PAPER IV

MARTIN J., VAN MOORTER B., BLANCHARD P., ALLAINÉ D., QUENETTE P.-Y. & SWENSON J.E. Moving along seasons: changing environment and requirements affect brown bear movement patterns? *Manuscript*

PAPER V

MARTIN J., QUENETTE P.-Y., ALLAINÉ D., & SWENSON J.E. Understanding and predicting habitat selection patterns of brown bears at global and local scales. *Manuscript*

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SYNOPSIS

INTRODUCTION

CONTEXT OF THE THESIS

Though we live in a geological time with the highest species richness and diversity, we are at the beginning of a major mass extinction (Primack, 2006). This current biodiversity crisis is mainly caused by growing human alteration of the Earth (Vitousek et al., 1997; Primack, 2006; Sinclair, Fryxell & Caughley, 2006). Indeed, the increasing world human population and human activities have entailed rapid and massive changes to landscapes (transformation of one-third to one-half of the land surface, Vitousek et al., 1997; Hoekstra et al., 2005). For example, overconsumption of resources and expansion of anthropogenic areas have led to direct destruction and fragmentation of habitats (e.g. due to road networks, expanding agricultural areas, and development of cities). Indirectly, human-induced processes also cause degradation of numerous species' habitats through pollution (pesticides, herbicides, industrial chemical emissions from factories and cars which lead to anomalous global climate change, Houghton et al., 2001) and introduction of invasive species (Primack, 2006). Due to these drastic changes of ecosystems, numerous native species have become extinct or are currently endangered due to the negative impact of habitat reduction and degradation (Tilman et al., 1994; Brooks et al., 2002; Primack, 2006). Land transformation is the driving force in the threat to biodiversity worldwide (Vitousek et al., 1997), and this process is operating so fast that most species do not have time to adapt to these modifications and nor can evolutionary compensate them (Teyssèdre, 2005).

In modifying the former habitats of numerous species, humans have become an integral part of their environment. This influence has an effect at different spatial scales and on different biological levels, such as the geographical range of species distribution, spatial organisation of populations, and individual behavior at fine scale. For example, habitat fragmentation¹ may entail division of existing widespread populations into subpopulations or metapopulations², influencing their dynamics (e.g. Banks et al., 2005); human activity may modify daily activity rhythms of individuals (e.g. Olson, Squibb & Gilbert, 1998).

¹ There is a wide diversity of definition for "Habitat fragmentation". I will define it here as the process during which large habitat is transformed into small patches of habitats (see the review by Fahrig 2003).

² I will use the definition of Moilanen et al. (1998): "a metapopulation is an assemblage of local populations inhabiting spatially distinct habitat patches"

Within this context, understanding the relationship between organisms and their environment and particularly how and they distribute themselves in human-modified environments has fundamental implications in several scientific disciplines such as *Ecology* (e.g. how do environmental changes affect individuals or population dynamics?), *Evolution* (e.g. how do these changes affect individual fitness¹, how do species adapt to these changes, what are the best adapted phenotypes to these changes?) and *Conservation Biology* (e.g. what are the “best” habitats that should be prioritized for species conservation?).

Species’ distribution in environments (also valuable for populations and individuals, but for reading convenience I use the term species in this section) emerge from interactions between deterministic and stochastic events (see Corsi, de Leeuw & Skidmore, 2000). Indeed, it is the result of interacting biological events (e.g. foraging, natal or breeding dispersal; determinist) and unpredictable events (e.g. fires, storms; stochastic). During these biological events, animals can choose the best place to meet their ecological requirements (e.g. a place with food when the animal is starving), i.e. they can select their habitat through movements. In an ecological context, species’ requirements therefore are identified in the framework of **habitat selection**, a concept I further develop in the following section. Habitat selection is a central concept in ecology, as it has a strong influence on population dynamics and persistence, species interactions, and ecological communities (Morris, 2003). In the context of conservation biology, the study of habitat selection and the way it is influenced by human-caused alteration of habitats therefore has important implications. In addition, predictive habitat models are reliable tools for the conservation and management of threatened species and they allow the identification of relative¹ suitable habitats that can be then protected or managed properly to mitigate the effects of habitat alterations.

The objective of this thesis is to understand ecological requirements of wildlife at different biological levels (species, population, individuals) through the study of habitat selection of a large carnivore living in different multiple-use landscapes: the brown bear (*Ursus arctos*).

¹ I used the term “relative” to stress that nowadays, due to human alteration of landscape, the word suitable should be interpreted with caution. In my opinion, this is more “the best of the bad job” than purely good habitat quality. For convenience, I will use “habitat suitability” in this sense.

Large carnivores are generally sensitive to human disturbance. Humans have been and still are their main cause of mortality (see Box 1, Woodroffe & Ginsberg, 1998), particularly for populations living in small areas surrounded by high human density and infrastructures. As mortality is often a critical population parameter for those species with low reproductive rates, they might be strongly affected by human presence.

Box 1. Humans and large carnivores

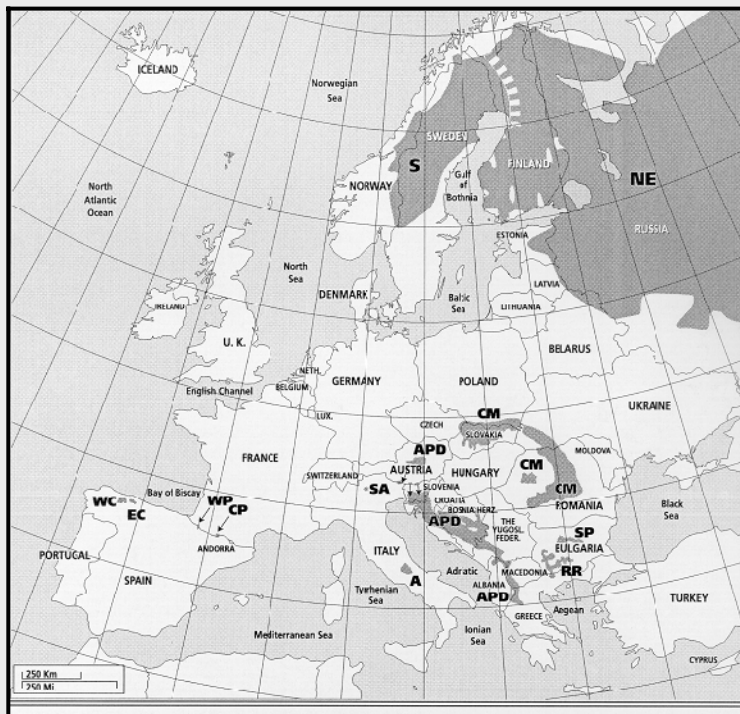
During past centuries, large carnivores have been persecuted by humans and their populations have suffered dramatic reductions worldwide (Linnell, Swenson & Andersen, 2001). They were exterminated in most of the western countries of Europe in the 18th and 19th centuries (Enserink & Vogel, 2006). At the same time, the human-induced reduction of their habitat quickened their decline (Breitenmoser, 1998; Linnell et al., 2001). Recently however, “carnivores have been making a come back” (Enserink & Vogel, 2006), particularly in several European countries. Indeed, in the 1970s strong policies for conservation of biodiversity restricted hunting and removed bounties for killing carnivores, which helped the natural recovery of carnivore populations in Europe (Breitenmoser, 1998). However, their conservation in human-used landscapes remains challenging for two reasons. First, people’s attitude towards carnivores is not always positive, because of their potential depredation on livestock, the competition for resources (e.g. game species), and/or the ancestral fear they have (Breitenmoser, 1998). Therefore, their conservation not only relies on scientific aspects but also on politics and public relations (Linnell et al., 2001). Second, they require considerable spatial areas, as one single home range may encompass extensive expanses of landscape (Noss et al., 1996; Schadt et al., 2002). The preservation of their habitat is therefore challenging in the actual context of human-caused habitat reduction and fragmentation, because of the increasing proximity between carnivores and humans (Treves & Karanth, 2003). Maintaining sufficient protected landscapes therefore requires knowledge about the relationships between these species and their environments and the evaluation of human influence on their distribution and movements.

After avoiding extinction in some countries of Europe (see Box 2), the brown bear is now recovering in some parts of its former range. Interestingly, these populations occur in areas with different environmental characteristics and differentially affected by human land transformations. The Scandinavian population is no longer threatened with extinction (around 2900 individuals) and is expanding mainly in forested areas heavily managed by forestry (which creates open lands) and with relatively low human densities. At the opposite extreme, the Pyrenean population is endangered (around 20 individuals left) and occurs in areas of higher elevation, with little forestry but surrounded with areas with high human densities. About in between, the Cantabrian Mountains population lives in similar habitats as the Pyrenean brown bear, but is slowly recovering from the brink of extinction, although it is still considered to be endangered (110 – 150 individuals).

Box 2. The “fall and rise” of the brown bear

Even if the brown bear (*Ursus arctos*) is currently not threatened with extinction, its distribution and numbers decreased considerably during the 19th century, particularly in North America and Europe. About 50% of brown bear populations have declined since 1800 due to humans (overhunting and habitat loss), resulting in small and isolated populations (Servheen, 1990; Breitenmoser, 1998). In 1970, the species became protected at the international level by the Washington convention and was classified as an “endangered species” in 1976 by the International Union for Conservation of Nature (IUCN). Nowadays, the species is not threatened with extinction, because some of the remaining populations are expanding (e.g. Canada, Russia, Alaska, northern and eastern Europe). It therefore has been classified in IUCN’s “Least concern” category.

Although the brown bear formerly occurred throughout all Europe, it has disappeared progressively from most areas due to human growth and activities (Breitenmoser, 1998; Zedrosser et al., 2001, Figure 2). After its protection by the Bern Convention in 1984, several countries launched restoration programs for the brown bear with the financial assistance of the European Union (Austria, France, Spain, Italy, Greece). Some of the European populations are now expanding (e.g. Scandinavia), but bears still face the human threats, both direct (e.g. poaching) and indirect (e.g. habitat degradation and reduction, increase human access to their habitats, isolation of habitats and therefore populations). Brown bear conservation therefore relies on their integration into human land use (Noss et al., 1996; Breitenmoser, 1998; Linnell et al., 2001) and therefore on the anticipation of potential human-bear conflicts. Assessment of bear habitat requirements and evaluation of human impacts on their distribution and behaviors are therefore required for a knowledge-based protection and management of this species.



A = Appenine Mountains population
 APD = Alps–Dinaric–Pindos population
 CM = Carpathian Mountains population
 CP = Central Pyrenees population
 EC = Eastern Cantabrian Mountains population
 NE = North Eastern Europe population
 RR = Rila–Rodope Mountains population
 S = Scandinavia population
 SA = Southern Alps population
 SP = Stara Planina Mountains population
 WC = Western Cantabrian Mountains population
 WP = Western Pyrenees population

Figure I: Actual distribution of brown bear in Europe, after Zedrosser (2001).

This thesis work is within the general context of habitat selection, in the disciplines of ecology and conservation biology, although I also discuss evolutionary consequences. In this **Introduction**, I clarify and discuss some of the inherent concepts of habitat selection, beginning first with the debated definition of the habitat concept. As animal movement is intimately linked to habitat selection (movement is the mechanism allowing individuals to choose their habitat in space and time), I also present a brief review of **animal movement ecology**, and especially its link to habitat selection. Then, I present detailed objectives of my work in the light of the theory I have presented.

To further discuss the choice of brown bear as model, I present the species' ecology and the biology of each studied population (Scandinavian, Cantabrian and Pyrenean) in **Material & Methods**. In the section **Main results and Discussion**, I synthesize and discuss the results reported in the scientific papers, book chapters and thesis chapters (listed above) that form this thesis and present perspectives for further research following this thesis in **Perspectives**.

THEORETICAL FRAMEWORK

Habitat selection theory

The patterns of populations' distribution in their environments are the result of processes occurring at different spatial scales. Individual choice of environmental characteristics is one of the driving forces that operates at a fine scale (Turchin, 1998). This individual choice is inherent to the concept of **habitat selection**, defined by Johnson (1980) as "the process by which an animal chooses which habitat components to use". Although this definition refers to the selection of habitat components, it can be broadened to the concept of **habitat**, which needs to be defined and clarified before developing the habitat selection concept further.

The concept of habitat

Though the concept of habitat is fundamental in ecology, it lacks a clear and consistent definition, despite numerous efforts to unify it (Whittaker, Levin & Root, 1973; Hall, Krausman & Morrison, 1997; Morris, 2003; Kearney, 2006), and its usefulness is even sometimes controversial (Mitchell, 2005). Basically, this term is often used to describe the physical environment of species, populations or individuals at different spatial scales. Habitat is sometimes considered only as a description of the physical nature of a place (abiotic and biotic) where an organism lives or potentially can live (Kearney, 2006; Morrison, Marcot & Mannan, 2006). Sometimes the definition of habitat includes the notions of species/population persistence or individual survival and reproduction (Whittaker et al., 1973; Hall et al., 1997; Morris, 2003). However, there is still a consensus toward the organism-specific property of the habitat, because it relates the presence of a species, a population, or individuals to the physical and biological characteristics of an area (Hall et al., 1997). In my opinion, the definition of this concept depends largely on the context within which it is employed. When we are talking about a species' habitat (or population or individual) in an evolutionary perspective, it is evident to me that habitat should include individual fitness or species/population persistence. In this context, the answer of the question: "What is the habitat of this species?" implicitly includes the notion of "good" habitat in which the species can persist. However, habitat selection studies rarely consider or measure any fitness component (but see McLoughlin et al., 2007), because it is difficult to relate such measures to habitat for wildlife. Indeed, researchers traditionally describe

a species' habitat by relating the presence of individuals, a population, or a species to the characteristics of an area, assuming that its presence is a good proxy for habitat quality. In this context, the concept of habitat is employed in a more spatial sense. For example, let us consider a population in a source-sink dynamic (for details see Pulliam, 1988), where the population source (for which local reproduction is higher than local mortality) lives in an area with different environmental characteristics than the the population sink (for which local reproduction fails to keep pace with local mortality). Without the population source, the population sink would not persist. Therefore, the area where the population sink lives (often referred to as "sink habitat") would not be a "habitat" of the species in the context of the persistence or performance definition.

It is probably impossible to unify this concept, so we should rather define the concept of habitat specifically before each study, according to the context. In this thesis, I did not use measurements of performance or fitness, either because it was not the focus of the analyses, or because I did not have the necessary data. I think the idea of species persistence or performance should be expressed in the underlying concept of **habitat quality**, "the ability of the environment to provide conditions appropriate for individual and population persistence" (Hall et al., 1997), which I develop more in the following section. In this context, sink habitats are still habitats, but of poor quality, inducing high mortality or low reproduction. I would therefore prefer a definition of habitat that does not include the notion of persistence, but rather physical and biological characteristics of an area where a species (or population or individual) can live. However, I prefer to borrow part of the definition provided by Whittaker (1973), who stressed the multivariate property of a habitat: "*The m variables of physical [biological] and chemical environment that form spatial gradients in a landscape or area defined as axes in a habitat hyperspace. The part of this hyperspace a given species occupies [at a particular scale of space and time] is its habitat hypervolume*". This definition is pretty close to the definition of the ecological niche (see the following section and Figure 1). We therefore try to interpret habitat choice of animals without inferring about habitat quality (except for **Paper V**, where we used the source-sink theory).

Following this definition, a **habitat patch** (or **type**) will describe a subset of the species' habitat, i.e. a particular combination of the **habitat components** (any habitat variables) constituting the species habitat. According to the question of interest, habitat variables can be referred to as environmental variables (e.g. elevation, vegetation type, weather conditions), but

also can integrate conspecifics (e.g. density of population) or other species (e.g. density of prey for a predator). The term patch often is used to describe delimited areas containing a limited quantity of resource that are aggregated in a larger resource-poor environment (Cezilly & Benhamou, 1996). These concepts can be used for different entities, such as species, populations, individuals, or even communities.

The concept of the ecological niche

This concept also suffers from the lack of a unified definition and is often confused with the concept of habitat. It was first developed by Grinnell (1917) to refer to all the environmental characteristics that allow a species to survive and reproduce (note the similarity with the aforementioned habitat definition from e.g. Hall et al., 1997). Latter on, Elton (1927) introduced the functional role of the species within its community in his new definition of the concept. Those authors are behind the past and current controversies. Should we consider the impact of the species on its environment and community or just the effect of environment on the species, i.e. the effect of the limiting factors¹ on the species? This also depends on the context. In his famous seminal paper from 1957, Hutchinson formalized the niche concept with a geometrical model. He defined the niche as the hypervolume in the multivariate space of environmental variables (the ecological space; Figure 2) where a species can persist (Figure 1). Hence, this definition does not require a mechanistic relationship between the niche dimension and the organism, but stresses the range of environmental conditions necessary for the species' persistence, i.e. the Grinnellian niche (which is similar to the concept of habitat). In this context, the ecological niche represents the entity's position in the range of environmental conditions, each dimension of the niche therefore corresponding to a subset of this range potentially or actually important for it. Hutchinson however recognized the potential role of the species in its community by describing two types of niches: the **fundamental niche** and the **realized niche**. The first term corresponds to the niche that would be occupied by a species without competition. However, the fundamental niche is rarely seen in nature, as the ecosystems are made up of species assemblages that coexist and interact with one another. Therefore, the presence of a species does not necessarily indicate the optimal habitat, but is the result of the combination between habitat quality and intra- and interspecific competition for limiting

¹ Limiting factors are “any processes [or factors] that quantifiably affect population growth” (Messier 1991), such as particular food resources, shelters, or weather conditions.

resources and interferences in resources access (Van Horne, 1983; Araujo & Guisan, 2006; Soberon, 2007). The second term takes those interactions into account and refers to the actual distribution of the species in its environment, given the presence of competitors, and therefore always is assumed to be narrower than the fundamental niche. This concept brings us to the idea of **niche partitioning**, the mechanism that allows species living in the same biotope¹ to coexist (Rosenzweig, 1981). As a result of competitive exclusion (Gause, 1934), two or more species that have similar requirements and use the same limiting factors living in the same area can modify their use of resources (at least on of the species, Gause, 1934; Rosenzweig, 1981), although this idea is controversial in the literature (Araujo & Guisan, 2006). The concepts of realized and fundamental niche are often confused in the literature (see Soberon, 2007) and the usefulness of their distinction debated (Araujo & Guisan, 2006).

I will not enter into the debate about the inclusion of the functional role of a species in the concept, but I wish to clarify the way I used it in this thesis. I used the approach of Hutchinson, because it is intimately linked to the concept of habitat (whatever the definition of habitat is, both rely upon the relationship between a species and the environmental characteristics).

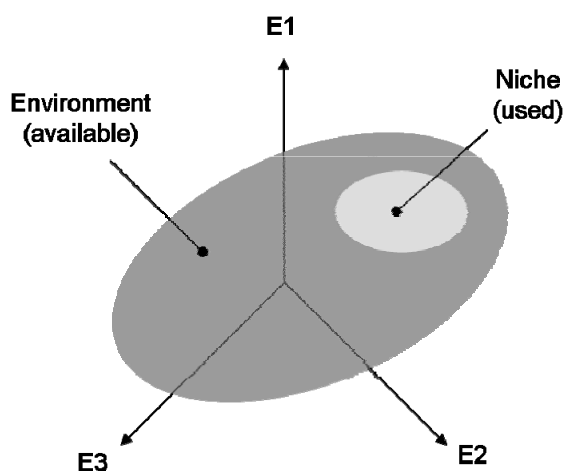


Figure 1: Schematic representation of the ecological niche. The black arrows represent environmental variables (e.g. elevation, forest cover), therefore the ecological space. The dark gray ellipse corresponds to the values of these variables that are available to the species (or population or individuals). The light gray ellipse corresponds to the range of values used by the species, i.e. its ecological niche.

Although the concepts of ecological niche and habitat are both related to ecological space, they often are related to geographical space (Figure 2.2, Calenge, 2005; Araujo & Guisan, 2006). Indeed, the study of the entity's location in its geographical space allows the identification of its

¹ A biotope is a physical area with uniform environmental conditions where a specific assemblage of plants and animals lives.

ecological properties and the association of ecological properties to spatially explicit factors leading to the potential distribution of the species (Araujo & Guisan, 2006). Several methods aiming at relating the species distribution to its environment have been developed in the framework of this concept (Hirzel et al., 2002; Calenge, Dufour & Maillard, 2005a; Basille et al., 2008; Calenge & Basille, 2008; Calenge et al., 2008). Some of these methods use two interesting niche properties: species **marginality** and **specialization**. Marginality is the position of the species in the available environmental gradients. It therefore refers to the niche eccentricity compared to the range of environmental components (Calenge et al., 2005a). Therefore, a marginal species will be located in more atypical environmental conditions (extreme values of a variable gradient), whereas nonmarginal species will use average environmental conditions. Specialization is the width of the niche, i.e. the species' degree of tolerance to the environmental gradient. The larger the niche, the more the species is tolerant; the narrower the niche, the more the species is specific to some resources. These concepts are particularly useful in describing and quantifying the relationship between a species and the environment available to it. In recent years, numerous analyses have been developed based on ecological niche estimation (Guisan & Zimmermann, 2000; Calenge & Basille, 2008). Although this concept has been developed and used at the species or population level, it can also be generalized to the individual level.

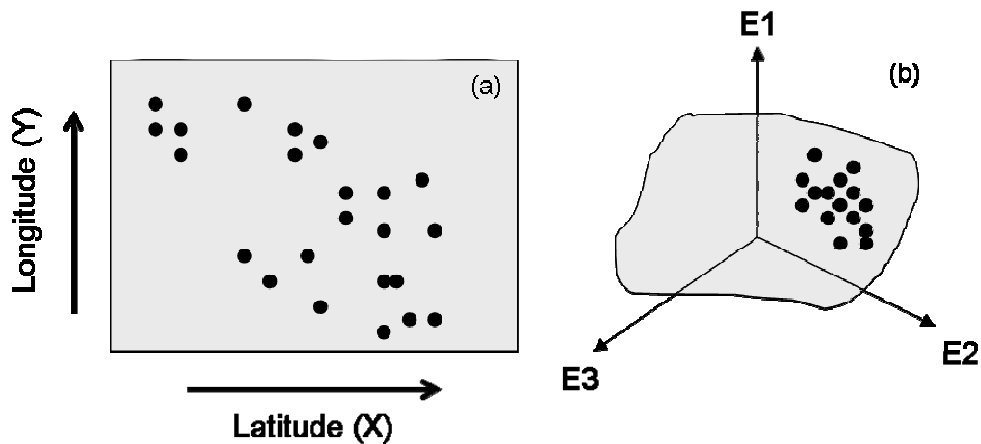


Figure 2: (a) Geographical and (b) ecological space. The location (often with two coordinates in the space: longitude and latitude) of a species often is used to analyze its ecological properties in the ecological space of environmental variables (E1 to E3). Adapted from CALENGE (2005).

Habitat selection: a hierarchical process

As stated previously, habitat selection is one of the processes that determines the distribution of species and populations across landscapes. The related theory has therefore received considerable attention (Morrison et al., 2006). Habitat selection has been defined as a hierarchical process that involves a series of decisions by individuals, innate or learned, about their habitat (Johnson 1980, Hall et al. 1997). It is well known that ecological mechanisms in general are scale dependent (Wiens, 1989; Levin, 1992) and mechanisms determining the search for resources by individuals therefore depend on the spatial and temporal scale (Orians & Wittenberger, 1991; Levin, 1992). Scales of selection are intimately linked, because fine-scale behaviors are constrained by the large-scale distribution of the population, whereas large-scale distribution patterns could result from individual behavioral processes at finer scales. To clarify these hierarchical processes, Johnson (1980) defined four orders of selection. The **first-order selection** corresponds to the geographical range of a species. The **second-order selection** is the process of home range establishment within this distributional area. The **third-order selection** is the selection of particular habitat components within individual home range, and the **fourth-order selection** is the process of food procurement within these habitat components (Figure 3).

Habitat selection processes arise from different motivations according to spatial and temporal scales and organisational levels (species, population, individuals) and are therefore not similar (see Figure 3). For example, the geographical range of a species can be ascertained by species life-history, global change of the climate and the environment, etc, which operate at large temporal scales. However, mechanisms of home range establishment are determined by annual or seasonal requirements of the individuals. At an even smaller spatial scale, habitat selection is related to individual daily cycles and states. As a consequence, habitat selection is not necessarily congruent across scales and may yield different patterns (Wiens, 1989). A thorough understanding of the species' ecology and dynamics therefore requires a multi-scale approach.

Since several authors have highlighted the importance of spatial and temporal scales in habitat selection studies (Johnson, 1980; Orians & Wittenberger, 1991), many studies investigated multi-scale habitat selection (e.g. McLoughlin & Ferguson, 2000; Rolstad, Løken & Rolstad, 2000; McLoughlin et al., 2002; McLoughlin et al., 2004; Nikula, Heikkinen & Helle, 2004; Ciarniello et al., 2007). However, there is still a lack of global theory on this hierarchical aspect of habitat selection (but see Rettie & Messier, 2000).

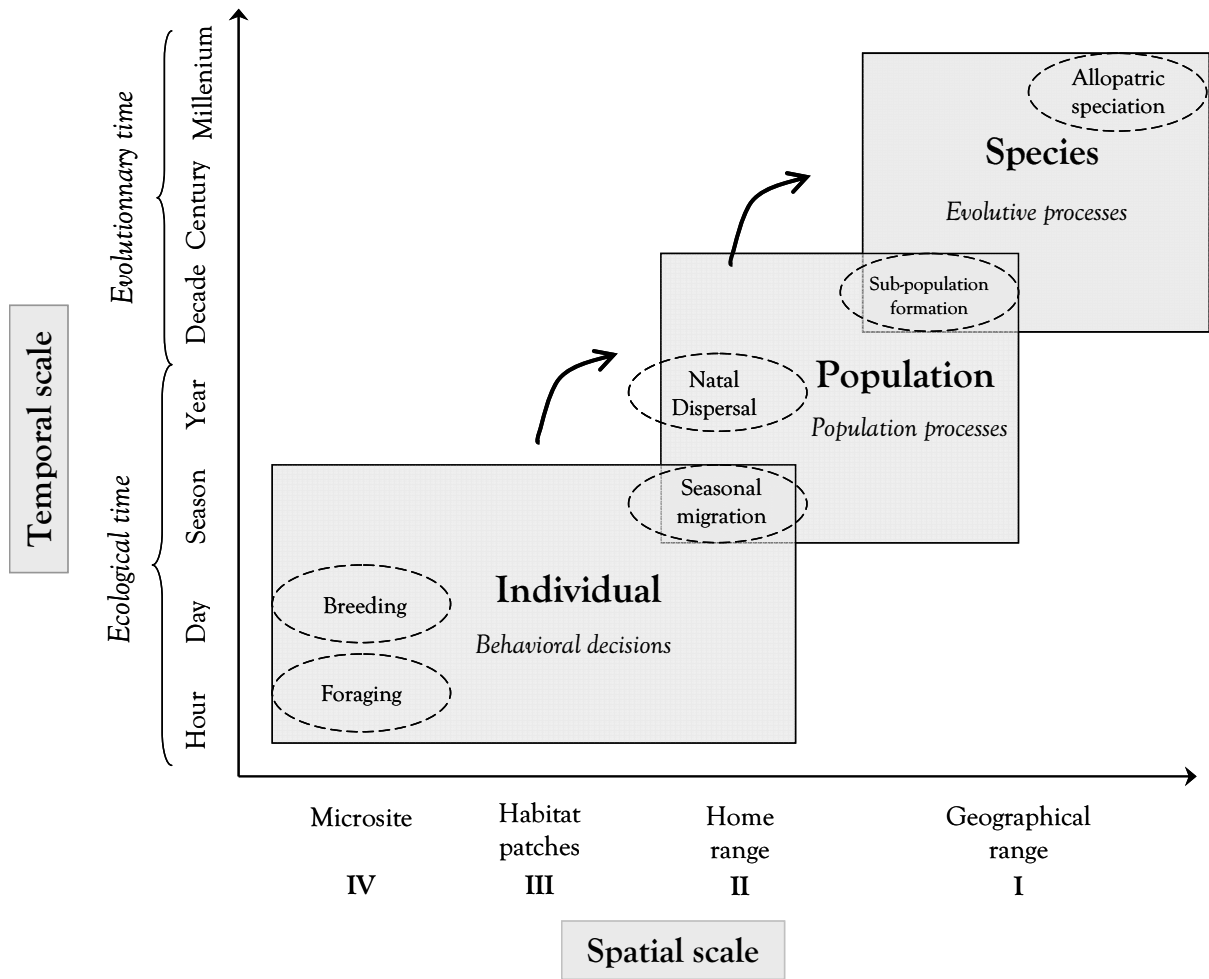


Figure 3: Relationships between spatial and temporal scales in habitat selection. Roman numbers corresponds to orders of selection defined by Johnson (1980). Dashed ellipses represent examples of processes involving habitat selection. Processes occurring at the individual level influence population process which themselves influence evolutionary processes at the species level (arrows). Adapted from George & Zack (2001) and Wallin et al. (1992).

Rettie & Messier (2000) were the first to attempt to develop a predictive theory about this hierarchical process, trying to synthesize what should be selected at each scale. They suggested that there might be a direct relationship between limiting factors and the scale of selection, with the most important limiting factor driving behavior at coarser spatial and temporal scales. Then, a limiting factor should continue to dominate selective use at successive scales until it no longer is limiting. Although this is an appealing approach, it lacks theoretical development. Several studies also have not supported this theory, finding the reverse pattern of selection across investigated scales (Morin, Berteaux & Klvan, 2005; Gustine et al., 2006). In my opinion, a weakness of this theory lies in the idea of ranking limiting factors. Rettie & Messier (2000) indeed consider that “a limiting factor should continue to dominate selective behavior at successively finer

scales until it becomes less important than the next most important limiting factor". However, several factors can act simultaneously on individual behavior and fitness, and a factor selected for or against at large spatial scale (e.g. predation risk) can still be important at finer scales, even if a new limiting factor impacts an individual (e.g. food resource). Indeed, individuals are usually in trade-off situations and habitats that provide shelter are often different from those that provide food resources. Dussault et al. (2005) reported a trade-off among three potentially limiting factors by moose (*Alces alces*), which react to them similarly at each investigated scale, so they did not find a clear correspondence between the hierarchy of limiting factors and spatial scales.

Another potential weakness of their theory is that they did not account for the variability of limiting factors, which can have strong impact on selective behaviors (Van Moorter, 2008). Despite this weakness, this is an interesting first approach that needs more investigation and theoretical development.

Habitat quality and performance

Habitat selection is the process by which individuals choose particular habitats among different available habitats at a given spatial and temporal scale. The evolutionary importance of habitat selection therefore lies in the spatial and temporal heterogeneity of the environment and in the capacity of individuals to choose the habitats that provide the necessary resources and conditions (e.g. food, shelter, mates) that allow individuals to survive and reproduce (Manly et al., 2002). In a homogenous environment, animals would not need to make particular choice concerning their habitat, because the resources would be equally distributed in the landscape. However, in heterogeneous environments, where resources are patchily distributed and of various qualities, individual choices are crucial, because they partly determine their fitness, but also the population's dynamics. Individual fitness will vary depending on habitat composition and spatial and temporal heterogeneity hence leads to variations in **habitat quality** for individuals or for a given species. The habitat quality therefore refers to the availability of resources, possibly balanced by risk (e.g. areas with predators, Cowlshaw, 1997). This notion is a relative view of habitat. For example, at the individual scale, a good habitat is a habitat in which the average fitness will be higher than the average fitness of individuals living in habitat of lower quality (Fretwell & Lucas, 1970). At the population scale, population performance (e.g. estimated by its reproductive rate λ) may also vary according to differential habitat quality.

The way animals select their habitats therefore should have been optimized by natural selection. The choices of what, when, and where to forage are among the most important choices individuals have to make. The Optimal Foraging Theory (Stephens & Krebs, 1986) has been developed in this context, to refer to the strategies employed by individuals to maximize their fitness. They should exhibit the best optimal foraging behavior, selecting the more profitable food resources (high-quality patches) under the various constraints they face, such as energetic costs of foraging, patchy distribution of resources and predation risk while foraging (Schoener, 1971).

However, social components may also affect relative habitat patch quality. Indeed, a habitat patch of high intrinsic quality may be less suitable when the density of conspecifics increases. Indeed, the presence of competitors for a limited resource may decrease the individual fitness in this patch. On the contrary, the presence of conspecifics might also have a positive influence on individual fitness (e.g. allowing easily detection of predators or catching a prey for species that hunt in groups). In evolutionary ecology, the most influential theory that relates habitat quality, fitness and conspecific density is the Ideal Free Distribution (IFD, Fretwell & Lucas, 1970). Assuming that individuals are free to move and choose any habitat type and that they have a good knowledge of their environments, this model predicts that individuals should distribute themselves among habitat patches of various quality in order to maximize their fitness. At equilibrium, all individuals should therefore have the same fitness. High-quality patches should therefore carry more individuals than less suitable patches.

However, one assumption of the IFD is seldom observed in most wild populations; individuals are rarely completely free to choose the best patches. For example, a number of species show hierarchical relationships among individuals. Often, dominants defend high-quality patches, which constrains subordinates to occupy low-quality habitat patches. In this system, defined as Ideal Despotic Distribution (IDD, Fretwell & Lucas, 1970), individual fitness is not equal among habitat patches. These hierarchical relationships among individuals are often at the core of source-sink dynamics. Another prime assumption of the IFD model is the individual omniscience concerning their environment, which remains debatable. However, we can assume that species living in home ranges or territories have a minimum familiarity of the habitat composition, although there are often stochastic spatiotemporal variations in resource distribution.

The concept of habitat quality is of high importance in an evolutionary context. Behaviors leading to the choice of high-quality habitats will be favored by natural selection. Indeed, individuals exhibiting these behaviors will leave, on average, more offspring to the next generation (Orians & Wittenberger, 1991). This is also of high interest in species conservation. As stated in the first paragraph, one of the major threats for a number of species is the reduction and fragmentation of their habitats. Understanding the relationship between species and their environment and defining which habitats are suitable for those species provides a solid basis for conservation or reintroduction programs.

However, the actual habitat quality is often difficult to assess for wildlife species. Indeed, this would require measurements of relative fitness in different habitat types. Several studies have been conducted to assess habitat quality or suitability, but few relate habitat characteristics to individual fitness in the wild (but see McLoughlin et al., 2006; McLoughlin et al., 2007). Most of the time, habitat quality is assessed by relating the spatial distribution of abundance of a species to an area, assuming that individuals choose the habitats that provide the greatest conditions for survival and reproduction (Thomas & Taylor, 2006). However, it should be noted that density might sometimes not be a good proxy of habitat quality, depending on particular environmental characteristics (e.g. strong environmental stochasticity) or species characteristics (e.g. strong dominance hierarchy, Van Horne, 1983). Density, however, remains a useful index for estimating habitat quality and habitat selection patterns are often used as a surrogate of habitat quality, although the results should be interpreted cautiously (see the discussion of source-sink dynamics above).

The pattern of habitat selection

By definition, the very nature of habitat selection is dynamic (Johnson, 1980), whatever the scale considered. For example, Van Moorter (2008) made the parallel between the natal dispersal process and the patch selection process, which both involve 3 phases: leaving the area (natal area or food patch), searching for a new area (where to establish or where there is enough food), and entering a new area (adult home range or food patch). However, most habitat selection studies focus on the pattern resulting from this process and the concept of habitat selection often refers to this resulting pattern, i.e. a “snapshot” of space occupancy. I will therefore use the term

“habitat selection” to refer to the pattern in this thesis, and the term “habitat selection process” to refer to the process.

A habitat (or habitat component) is considered to be selected when it is used disproportionately compared to its availability (Johnson, 1980). **Habitat availability** refers to the quantity of any habitat component that is accessible to animals, and should not be confused with “abundance”, which only refers to the quantity of a component in the habitat (Hall et al., 1997). Habitat availability depends mainly on spatial and temporal scales, and on the detection capacity of individuals. It should be noted that this notion is very important in habitat selection studies and has several implications which I detail in the next paragraph.

The study of habitat selection

Studies of habitat selection by wildlife are increasingly carried out in different disciplines (evolution, ecology, conservation) to identify the environmental characteristics a species select for, assuming that these characteristics have been selected because they provide the best conditions for survival and reproduction (Thomas & Taylor, 2006). Habitat selection usually is investigated using data on the space use of a given species. The habitat characteristics used by the species are then compared to those of unused areas and more commonly of areas that are considered available to the species (Thomas & Taylor, 1990; Manly et al., 2002). A habitat is selected for when the proportion used by animals is greater than the proportion available. On the contrary, a habitat is said to be “avoided” when the proportion of use is less than the proportion available. However, as stated previously interpretations resulting from these comparisons require some discretion, because they are not a direct measure of habitat quality (which would require some measure of fitness). However, although the density of individuals might be a poor indicator of the habitat quality in some conditions (as discussed before, Van Horne, 1983), most of time it is a good proxy for the suitability (i.e. quality) of a particular area.

Spatiotemporal scales of investigation

As stated previously, the very nature of habitat selection is hierarchical. Different processes act at different spatiotemporal scales, resulting in differential habitat selection according to the scale considered. The characteristics of an area where a population of a given species is distributed (first-order selection) might not be congruent with those of habitat types in individual home ranges (third-order selection), because the mechanisms involved are not the same.

The choice of scale of investigation (e.g. geographical range of the species, population establishment, individual habitat selection within home ranges, etc) is crucial, because the inference from analyses at a particular scale is limited at this scale (Pendleton et al., 1998). Moreover, the importance of a particular scale may be different according to the species under study. For generalist species, for example, larger scales (e.g. landscape scale) might be less important than finer scales (e.g. selection of habitat types or resources within the home range) than for specialist species, for which the habitat at the geographical range might be of crucial importance. However, like most ecological processes, habitat selection often occurs at more than one scale (Levin, 1992).

Thomas & Taylor (1990) proposed different study designs for comparisons of used and available (or unused) habitats to account for the organism under study (population, individuals) and the scale of investigation. **Design I** is used for population level studies (1st order selection) when individuals are not identified. Habitat use and habitat availability are measured at the population level. Data are assumed to be independent (the presence at a particular site should not influence a presence elsewhere) and resource access equal for all individuals (they should therefore follow an IFD). Indices of presence (e.g. visual observation, feces, hairs) are often used for this design.

Design II, III, and IV are used for individual level studies (2nd, 3rd and 4th orders selection). Individuals are identified (e.g. using telemetry) and use data are measured separately for each individual. In design II, habitat availability is the same for all individuals (e.g. composition of home ranges within the geographical range of the species), whereas in designs III and IV, habitat availability is measured independently for each individual. Habitat availability is constant over the study period in design III and therefore is defined by one measure (e.g. individual home range). In design IV, there is a temporal change in habitat availability for a given individual, which requires several measures of availability (one measure per individual relocation). This last design was created later by Erickson et al. (2001) to account for the increasing use of the new type of data provided by telemetry, which allows frequent relocations of animals (e.g. one relocation per 30 minutes). More discussion about this last design is provided in the **Paper II**.

What is really available and meaningful for individuals?

Measuring habitat availability requires accounting for two important aspects: choosing the biological meaningful variables for the species and the boundaries of the area we will consider available for analyses. The choice of habitat variables to integrate in analyses is a difficult task (Lennon, 1999; Guisan & Zimmermann, 2000) and should be based on a thorough knowledge of the species. Indeed, all the habitat variables that are limiting for the species should be included. However, the choice of variables often relies on logistical considerations, some variables being difficult to measure (Mitchell, 2005).

As mentioned above, the choice of scale is very important and leads to the inherent problem of defining habitat availability. In habitat selection studies, determining what is available is challenging, because only animals “know” what is truly available. In theory, researchers should define habitat availability objectively, from the species’ point of view. This is critical for the interpretation of analyses, because changing the availability will change the proportion of each habitat component, and therefore the comparison between the proportion of usage and availability of this component, especially if this component is aggregated in space (Porter & Church, 1987). In practice however, availability is often defined subjectively, because of the difficulty of assessing the species’ environmental perception. For example, an area might appear available to a given individual, whereas interspecific interactions (e.g. presence of predators) or intraspecific interactions (e.g. territory defence) might prevent its use or its access, respectively. In some cases, the definition of availability should be reduced if the question of interest refers to physical components of habitat, or variables referring to conspecifics, prey, or predators should be included.

The scales of selection defined by Johnson (1980) help to reduce this subjectivity, as they have a biological basis, but they do not completely remove this subjectivity (Erickson et al., 2001). For example, at the scale of home range establishment in the geographical distribution of a species, study area boundaries often encompass the area where the population is distributed. Home range estimators (Mohr) are often used to describe available areas for individuals.

Autocorrelation in habitat selection studies

During the last decades, telemetric tools have been increasingly used to remotely monitor relocations of wild animals. These developments have changed the nature of the data itself, as they facilitate frequent recordings of animals' positions. Especially, the Global Positioning System (GPS) has helped researchers greatly following wild fauna frequently, over large periods of time, and at any time of the day. Individuals positions recorded in this manner are not independent, resulting in sequential autocorrelation in the data, i.e. position at time t will depend on the position recorded at time $t - 1$. Sequential autocorrelation in individual habitat selection studies may pose statistical problems and is therefore often removed or ignored. The first **Paper (I)** of this thesis will be devoted to the empirical investigation of the effect of autocorrelation in individual habitat selection studies and the misinterpretation that could result from not accounting for this autocorrelation.

However, as stated earlier, although the very nature of habitat selection is dynamic, most habitat selection studies are conducted on a “snapshot” of the species' (or population's or individual's) space occupancy, i.e. a static view of habitat selection. The use of autocorrelation in individual habitat selection studies might be the cornerstone of linking movement ecology (see following paragraphs) and habitat selection, i.e. addressing the dynamic aspect of habitat selection. In **Paper II**, we provide a review of the historical use, misuse or non-use of autocorrelation in individual habitat selection studies and pursue reflections and thoughts concerning the promising use of autocorrelation in these studies.

Hindcasting vs. forecasting analyses

Two kinds of analyses can be carried out to study habitat selection: hindcasting studies and forecasting studies (Calenge, Dufour & Maillard, 2005b; Morrison et al., 2006). Hindcasting studies aim to identify the key habitat variables for populations or individuals, whereas forecasting studies aim at predicting species' habitat use. The latter type of studies are carried out to model the habitat variables influencing the species' distribution and can be used to predict species distribution on the same area (e.g. to predict the expansion of a population) or in very different areas (e.g. to predict distribution of a species in an area where no use data are available, Schadt et al., 2002). Statistical analyses used for forecasting studies (e.g. Resource Selection Function, RSF, Manly et al., 2002) preferentially include a limited number of habitat variables,

because it increases the predictive power of the model (see Calenge, 2005). As a consequence, it is assumed that the habitat variables included in the model are those of high interest for the species, requiring important *a priori* knowledge of species' requirements (Boyce & McDonald, 1999). Therefore, hindcasting studies should precede forecasting studies, as they enable the determination of habitat variables that have biological relevance for the species under study among a large set of habitat variables, because there are fewer restrictions on the number of variables that can be integrated into the model. Particularly, numerous hindcasting studies have been developed based on the concept of ecological niche formalized by Hutchinson in 1957 (Calenge, 2005). Several methods based on factorial analyses have recently been developed by Calenge (2005b; 2006; 2008).

Individual movement: the mechanism of habitat selection

It is important to link observed patterns in animal ecology to the underlying processes involved, as one pattern can be the result of different processes occurring at different spatial scales. Obtaining thorough insights into ecological patterns therefore require the study of underlying processes. A key challenge is therefore linking processes to patterns at different spatial scales (Levin, 1992).

Animal movement ecology

Most ecological and evolutionary processes involve individual movements, defined by Turchin (1998) as “the process by which individual organisms are displaced in space over time”. Although for some species movement is a passive mechanism (e.g. seed dispersal), for most animal species, movement is driven by individuals. Movement is fundamental to individual and population dynamics, as it is the mechanism allowing individuals to meet their basic requirements. Indeed, movement is the process by which individuals respond to both short-term requirements (e.g. searching for food or for mates, escaping from predator) and long-term requirements (e.g. avoidance of intra-specific competition, inbreeding). Survival and reproduction are therefore linked intimately to movement strategies, which therefore should be driven by natural selection (Fahrig, 2007).

Despite its importance in evolutionary ecology, there is a lack of a unifying theory of movement ecology, as stressed by Holyoak et al. (2008). Most of existing theories about

movement focus on a particular biological context, such as dispersal movements, foraging movements or migration movements. There are few studies investigating animal movement as a whole and over long periods of time (e.g. daily movements of individuals). This is challenging to document for wildlife, but the advances of new technology (e.g. GPS) nowadays facilitate the accurate recording of animal trajectories over time.

Also, movement studies often are isolated in sub-disciplines focusing on particular phenomena (Mueller & Fagan, 2008), such as the effect of landscape heterogeneity on movements (e.g. Morales & Ellner, 2002), navigational capacity of individuals (e.g. Benhamou, 1989; Benhamou, Bovet & Poucet, 1995), or search strategies (e.g. Bergman, 2000). As stated by Nathan et al. (2008), this lack of a cohesive framework entails overspecialization, which has led to the development of a plethora of analytical tools in each subdiscipline. Only recently, have attempts been made to develop theoretical guidelines for the study of animal movement ecology (Mueller & Fagan, 2008) or even “organismal¹ movement ecology” (Nathan et al., 2008). For example, Nathan et al. (2008) proposed a conceptual framework in an attempt to unify movement research (whatever the taxonomic group of mobile organisms). They suggested an integrated approach of movement ecology based on three basic components related to individual; internal state, motion capacity, and navigation capacity (see Nathan et al., 2008 for more details).

Individual movement and habitat selection

Animal movement is the fundamental process that allows individuals to make choices concerning the exploitation of resources (Schoener, 1971; Stephens & Krebs, 1986; Bell, 1991) at different spatial scales (e.g. dispersal, foraging) as it relates individuals to their environment. This is therefore a key process, because it will influence the fitness of mobile individuals (Schooley & Wiens, 2003; Austin, Bowen & McMillan, 2004). Indeed, in heterogeneous and variable environments, movement enables animals to change environmental conditions according to their requirements. For example, in seasonal environments, when food availability and quality as well as climatic conditions may vary, mobile animals migrate to find better weather or resources. At a small spatial scale, when food resources are patchily distributed over

¹ The authors employed the word “organismal” to refer to all taxonomic groups capable of movements (active or passive)

the landscape, animals may move from low-quality patches (e.g. after depletion of the patch) to high-quality patches. Also, the quality of a same habitat (or habitat patch) might be perceived differentially according to animal requirements. Indeed, food resources and shelters (e.g. protection from heat or predators) are often spatially disconnected, which leads animals to make trade-offs between habitat types, moving from one habitat type to another according to their activity and requirements. Animal movement and habitat selection therefore are intimately linked, movement being the key mechanism underlying the habitat selection pattern (Figure 4).

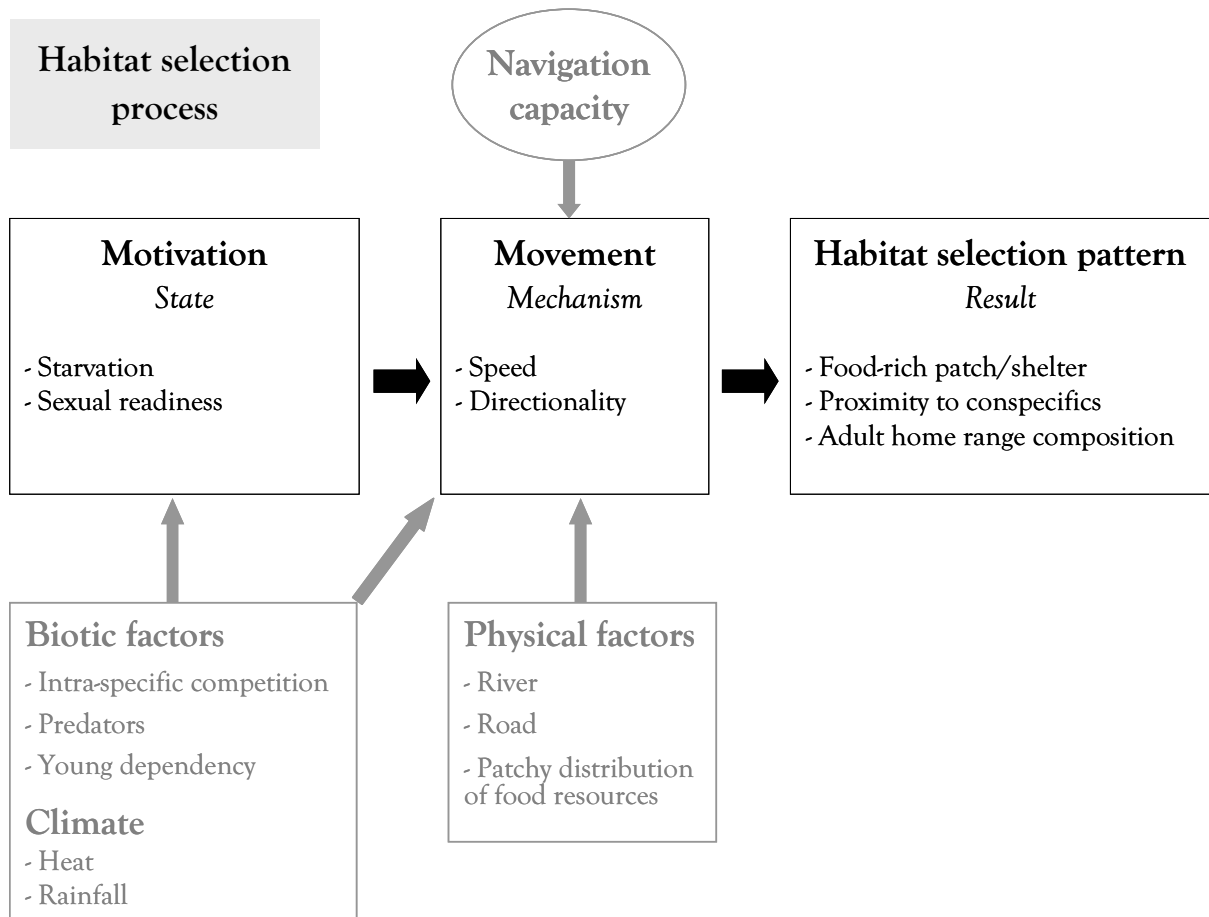


Figure 4: Conceptual scheme of the habitat selection process at the individual level. This process involves three phases that are shown in bold black, with some examples. Factors that can affect individual motivation and movement are shown in gray. Examples shown here are proximal causes of habitat selection process. However, ultimate causes, for example increasing fitness by avoiding proximity with related individuals, also induce habitat selection process, through the process of dispersal.

Individual movements and optimal search

In heterogeneous landscapes, mobile animals are able to make choices about when to move, where to move and how to move. This ability gives rise to different movement strategies, allowing individuals to increase their fitness by balancing the costs and benefits of movement. The costs and benefits of movement may differ according to different factors, such as internal state (e.g. hunger, search for reproductive partner) and external factors (e.g. habitat type, climate), and movement patterns should be under selective pressure.

As stated previously, movement is valuable when resources are distributed patchily and are depletable, because it allows access to resource patches. In this type of environment, we can distinguish two processes in search behavior: the location of patches and use of resources within patches (Bell, 1991). When searching for patches of resources, straighter and faster movements should be optimal to increase the probability to find new patches (REF). Similarly, searching for mates should be optimized by straighter and faster movement (Duvall & Schuett, 1997). The same mechanisms should occur at a larger scale, for the process of dispersal (natal dispersal or reproductive dispersal), where movements allow exchange between subpopulations, or for the process of migration, when species living in seasonal environment must find more suitable areas. In both cases, it has been reported that movement should be straighter and longer to increase search efficiency. On the contrary, animals should exhibit tortuous and slow movements in high-quality patches to stay in these patches longer.

However, movement entails two main costs for animals. First, as the time spent moving increases, the associated energetic costs increase. As such, animals with lower body conditions should exhibit slower and shorter movements. The second cost is the mortality risk due to the increasing exposure to predators or negative interactions (see Fahrig, 2007). This cost has essentially been reported in the context of dispersal (Baker & Rao, 2004), but the mechanisms should be similar at smaller scales. When searching for resources at small scales, moving across open areas (which increases the probability of being detected) or human-altered areas (e.g. roads) might increase the mortality risk. Animals should therefore balance the benefits (e.g. food access, mates) and risks (e.g. energy expended, risk of predation, time taken away from other activities) of movements (Bell, 1991).

Search efficiency depends on the species' ability to move, its knowledge of the environment, and the spatial arrangement of the landscape (Bell, 1991). Indeed, movement capacities of species can differ in various ways. First, they might exhibit different navigational abilities, namely the capacity to orient themselves in the landscape. Some species can use environmental cues to do so and the species that is better able to gather and use environmental information should exhibit more oriented movement patterns, and therefore more efficient search patterns. For example, when searching for mates, a species that is able to detect conspecifics might orient its movement toward the detected target. Second, the mobility of species might also differ and those that can move faster might find new patches of food more quickly. Third, some species might have a better knowledge and perception of their environment and might use memory (e.g. to find food resources in their home range). This memory effect should also lead to more oriented (therefore straighter) movement patterns and therefore to more efficient searching. Moreover, in heterogeneous landscapes, where patches are far from each other, species with smaller perception ranges might not detect targets easily. Therefore, instead of moving between two patches of food resources, for example, they will also have to search for the other patch. As a lower perception range also leads to higher mortality risk, these species will tend to stay in patches longer, instead of leaving the patch when it becomes less suitable, compared to a new patch (Lima & Zollner, 1996). However, it is often difficult for the researcher to assess the perception capacity of animals. The landscape also might affect movement. Habitat fragmentation might create disconnected patches of good habitat, separated by a more or less suitable matrix habitat. Animals might therefore spend more time searching for resources if resource-rich patches are scarce rather than in homogeneous habitats where resources would be evenly distributed.

In the context of OFT, animals are often assumed to have a perfect knowledge of their environment. Therefore they are supposed to direct their movement towards patches of resources efficiently. However, when animals do not have knowledge of their environment, they will exhibit random search movements.

The study of individual movements

In this section I provide a brief introduction to individual movement analyses. More details and figures are provided in **Papers IV** and **V**.

Although the very nature of animal movement is continuous, their field observations are often discrete estimations based on individual relocations taken at different times (e.g. GPS

relocations). This results in a discrete representation of the animal's **trajectory** (or **movement path**). The succession of relocations describes steps and the succession of steps forms the estimated trajectory. Several parameters can then be used to characterize such a trajectory. The most widely used parameters are the distance between relocations (d), the relative angles (θ), and the net square displacement (i.e. the total distance traveled in a straight line, noted R^2n). See **Papers I** and **II** for more details.

Several approaches have been used to analyze and model animal movements. Generally, animal trajectories are compared with null models in order to obtain insights about optimal search strategies (Viswanathan et al., 1999; Mårell, Ball & Hofgaard, 2002). Departure from theoretical models is then examined and allows extrapolation to mechanisms underlying movement behavior. However, these studies are usually carried out at a small-time scale (e.g. small movement bouts corresponding to foraging movements), because these models tend to fail when considering long-time scale movements (e.g. tracking of animals during several months). When the time lag between relocations is low, the trajectory includes all possible behaviors that affect characteristics of the movement (Firle et al., 1998; Morales & Ellner, 2002), which leads to a mixture of different movement models (Morales et al., 2004).

OBJECTIVES OF THE THESIS

Paper I and **II** are devoted to methodological considerations, particularly on the use of autocorrelation in habitat selection studies. The biological aims of this thesis cover hierarchical habitat selection, movement and conservation biology, and are presented in **Paper III to V**.

Papers I and II were dedicated to the influence of sequential autocorrelation of individual relocations in individual habitat selection studies. **Paper I** is an empirical study of the misinterpretation of results of habitat selection studies when not taking autocorrelation into account. In **Paper II**, we further discuss its use in individual habitat selection studies and the promising avenues of combining movement (through the use of autocorrelation) and habitat selection to obtain insights in behavioral processes involved in habitat selection.

The first biological aim of this thesis (**Paper III**) was to study hierarchical habitat selection in the Scandinavian brown bear population. Particularly, the objective was to assess the influence of habitat variables, including human-influence variables, at different spatial scales in the light of the theory of Rettie & Messier (2000). Are habitat variables influencing bear habitat selection in the same way across scales? We further discuss the implications of the results in terms of management of the population.

In the same population, we were interested in studying factors that drive females' movements in the light of the optimal search theory (**Paper IV**). We therefore studied internal (seasonal requirements, reproductive status) and environmental factors (such as vegetation types, human disturbance, or climate factors) that can affect females' movement strategies.

The **Paper V** covers habitat use by Pyrenean brown bears at a large spatial scale (population level) and has a more applied purpose. The first part of this paper aims to identify and model general patterns of brown bear habitat selection on two European populations: the Pyrenean population and the Cantabrian population (Spain). The second part deals with a more local habitat selection and the identification of suitable habitats in the Pyrenees with a habitat suitability map. The results serve as a tool for helping decision makers in the conservation and management of the Pyrenean population.

MATERIAL & METHODS

THE MODEL SPECIES

The brown bear is a large carnivore that uses large home ranges. It is sexually dimorphic, adult males being 1.2-2.2 times larger than females (140-320 kg for males and 100-200 kg for females, Swenson et al., 2007a). Adult males' home ranges are larger than those of females and often overlap several female home ranges. Brown bears exhibit male-biased dispersal. Females may also disperse, but they usually establish in or adjacent to their mother's home range. In Scandinavia, matrilinear assemblages occupying exclusive areas have been identified (Støen et al., 2005). Home ranges of related females often overlap, but those of unrelated females rarely do (Støen et al., 2005).

Bears are usually active from April to October. They pass through different physiological stages during the year: exhibiting 3-7 months of winter dormancy without eating, drinking, defecating, or urinating; after den emergence in the spring, they exhibit low food intake (hypophagia); then they exhibit a stage of normal activity in summer; and they show a high food intake (hyperphagia) in autumn before entering the den. They have an omnivorous diet, usually eating green vegetation, such as forbs and graminoids in spring and early summer. Ants may also be an important food, especially in spring. Bears switch to berries and fruits (soft mast) when they ripen. Later in autumn, they may consume large amounts of hard mast like acorns (*Quercus*), beechnuts (*Fagus*), and chestnuts (*Castanea*) where they are available. In northern latitudes, hard mast is lacking and bears mainly eat large amounts of berries to fatten. Bears in southern Europe make extensive use of hard masts, as well as berries and large soft mast. Bears may also hunt prey; they kill about 25% of the moose calves in central Sweden in May to early June (Swenson et al., 2007b).

The brown bear is a solitary species with a polygamous mating system. The age of primiparity varies from 4 to 6 years (McLellan 1994, Zedrosser et al. 2004). During the mating season (in spring), males may mate with several females and females may mate with several males. Multiple paternities in litters have been documented (Bellemain, Swenson & Taberlet, 2006). Implantation is delayed until late November and females give birth to 1-4 small (0.5 kg)

helpless cubs during denning in January to March. There is no paternal care; young follow their mother for 1.4 to 3.5 years (McLellan, 1994). Females do not mate until their offspring are weaned, which results in long and variable interbirth intervals. Usually, they separate from them prior to, or early in, the mating season (Dahle & Swenson, 2003a). Female bears are induced ovulators (i.e. eggs are released after behavioral, hormonal or physical stimulation). The loss of their litter during the mating season may therefore induce oestrus. The loss of their litter during the mating season may therefore induce estrus, so males may benefit from killing unrelated young to mate with the mother, a behavior termed sexually selected infanticide (SSI; Hrdy 1979).

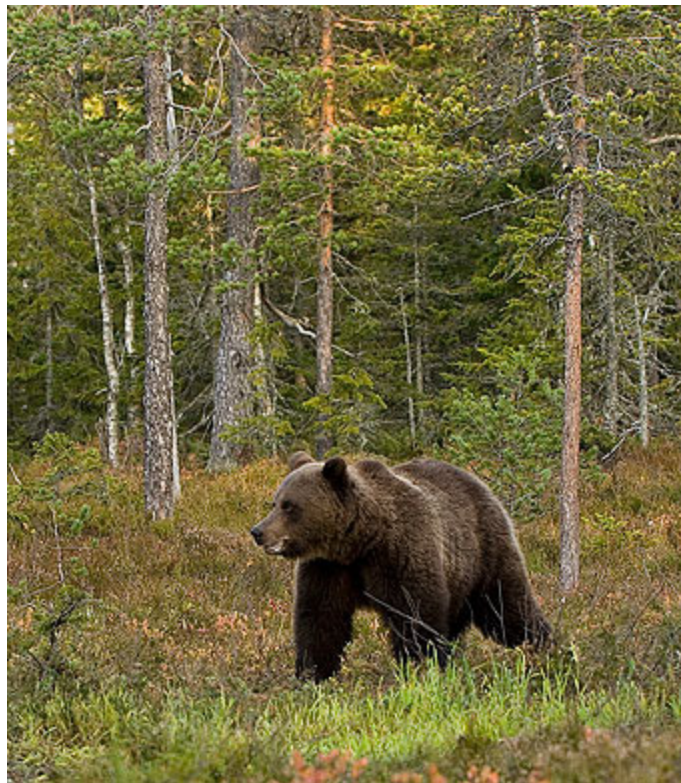


Figure 5: Scandinavian brown bear in the forest. Photo credit: Naturetrek.

STUDY POPULATIONS AND DATA COLLECTION

Scandinavian population

The Scandinavian brown bear population declined rapidly due to human persecutions (Swenson et al., 1995). By 1920, only about 130 individuals remained in four areas of Sweden. After persecution and bounties were stopped, the population started to increase and reached almost 2,900 individuals in 2008 (Kindberg & Swenson, 2008). The Scandinavian brown bear population continues to expand, both in number and geographical range. Females are present in the four core areas with little female exchange between subpopulations, contrary to males that disperse over larger areas and therefore allow genetic exchange. This population is the most productive population yet documented in the world (rate of increase of 10-15% per year). However, this population still must be monitored and there are conflicts between humans and this large carnivore.

The Scandinavian Brown Bear Research Project (SBBRP) started in 1984 to obtain better knowledge of the brown bear population using radiotelemetry. The central goal of this project is to document the ecology of brown bears using management-oriented research. This project is a Swedish-Norwegian cooperation, with international research collaborations. The project has contributed significantly to the management of brown bears in Scandinavia and Europe.

The project has two study areas located in one of the population's northern core areas (near Jokkmok) and in the southernmost core area (Hälsingland-Dalarna, Figure 5). To date, more than 450 bears have been radio-collared, some of them followed from birth to death. Another important source of data comes from bears that have been killed during hunting for which several characteristics are recorded (location of kill, weight, age, tissue samples, etc.). In 2003, the project started to equip bears with GPS-collars, with a special focus on females.

PhD and postdoctoral projects constitute the core of the research projects. The SBBRP provides scientific results on several major disciplines of ecology: life-history traits, population dynamics, genetics, space use, movements, social organization etc. An important part also focuses on bear-humans relationships (impact of hunting, human attitudes...).



Figure 6: Representation of the four brown bear core areas in Sweden (dark orange) and the Scandinavian Brown Bear Research Project (SBBRP) study areas (red areas). The light orange area corresponds to the location of males and the red strips areas to the area where the marked bears have been during the study period. Source: SBBRP.

Study area

The study was conducted in the southernmost reproductive core area of the Scandinavian brown bear population in Dalarna and Gävleborg counties, south-central Sweden (61°N, 15°E, Figure 5). The terrain is hilly and the elevation range ranges from 200 to 700 m above sea level, with a southeast-northwest gradient. The study area consists primarily of intensively managed coniferous forest (80 %) dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) and consists of patches of differently aged stands ranging from clear-cuts to 90-100-year-old forests (Swenson et al., 1999). The remaining area is mainly composed of lakes and bogs. The study area is sparsely populated by humans. Human settlements (concentrated in the north and in the south of the study area) and high-traffic roads are rare in the study area, but isolated houses and low-traffic roads are evenly distributed throughout the study area. The mean temperature in January and July are -7° and 15°, respectively. Snow cover lasts approximately from late October until early May. Average precipitation is approximately 600-1,000 mm annually (Swenson et al., 1999). Bears are intensively hunted in the study area in the fall, starting from late August and last 1-2 months.



Figure 7: Scandinavian landscape in the southern core area of the brown bear population. Top left: aerial photography of the landscape showing rolling terrain and managed forest. Bottom left: shrub layer producing berries eaten by bears. Right: under the cover of an old coniferous forest. Photo credit: Jodie Martin.

Legal harvest has been allowed in the study area and occurs in fall, from 21st of August until 15th of October. The hunting of bears is regulated by annual quotas set by the authorities. Females with litters are legally protected from harvest.

Capture, handling and data collection

Females were darted by helicopter during spring using a remote drug delivery system (Daninject®) shortly after den emergence in mid-April. The protocols for immobilization are detailed in Arnemo (2005). During immobilization, females were equipped with GPS-GSM collars (Vectronic®) scheduled to take a fix every 30 minutes (i.e. 48 relocations per day) during their entire active period from April to October (Dahle & Swenson, 2003b). Females followed by cubs of the year (hereafter referred to as female with cubs) were not captured for ethical reasons. However, some of the lone females equipped with GPS collars gave birth the following winter, which gave us the opportunity to follow these females the year of parturition. All capture and handling conformed to the current laws regulating the treatment of animals in Sweden and were approved by the appropriate Swedish ethical committee (Djuretiska nämnden i Uppsala).

Pyrenean population

The Pyrenean brown bear population is considered to be as one of the most endangered in Western Europe. After almost becoming extinct, with a population estimated to be 6 individuals (Camarra, 1999), the population has started to increase following a reinforcement program in 1996-1997 with the reintroduction of 3 adult bears from Slovenia. A second reintroduction program was conducted in 2006, when 4 adult females and 1 adult male were introduced from Slovenia. In spite of these reinforcements, the current status of the species is still precarious with an estimated population of about 20 individuals divided into 2 groups that are isolated regarding the exchange of females (Figure 8).

The Pyrenean brown is important socially it is clear that the management strategy of such a species rests on economical and social factors, in addition to ecological knowledge of the species. In the Pyrenees, the conservation of brown bears divides public opinion. For example, many, but not all, sheep farmers do not favor saving brown bears and above all the reintroduction of new individuals, because of depredation on livestock. Indeed, in the Pyrenees and particularly in central Pyrenees, there are many free-ranging sheep, which are potentially easily accessible to bears. In western Pyrenees, sheep are breed for milk, to produce cheese, and are therefore parked during the night. On the other hand, many wildlife associations promote saving brown bears in the Pyrenees.

In this complex socio-economico-political context, scientists must recommend solutions that can contribute to conserving this species. In particular, with the increase of human activity, involving destruction and fragmentation of prime habitats, it is necessary to obtain precise knowledge about habitat types that should be preserved and the best sites of release if a new reintroduction is decided. Maintaining habitats that meet the biological requirements of brown bear require the identification of suitable habitats for Pyrenean brown bears.

The “Office National de la Chasse et de la Faune Sauvage” (ONCFS) is a French agency responsible for managing wildlife and its habitats. The “Centre national d’Etude et de Recherche Appliquée” sur les “Prédateurs et Animaux Déprédateurs” (CNERA PAD) is a unit of the ONCFS responsible for scientific research on carnivores. Within this unit, the “bear technical team” is in charge of monitoring the Pyrenean brown bear population and providing knowledge on brown bear ecology, especially for conservation and management purposes. An extended network, including other state agencies (e.g. National Park of Pyrenees, PNP, the

forest management administration, Office national des Forêts, ONF) and non-governmental organisms (e.g. hunting associations, associations for nature protection), also helps the team to collect bear data on the French side of the population's distribution (Figure 8). The ONCFS is also responsible for providing expertise to determine the cause of livestock deaths. If the expert concludes that a bear was responsible, the owner receives financial compensation from the State.

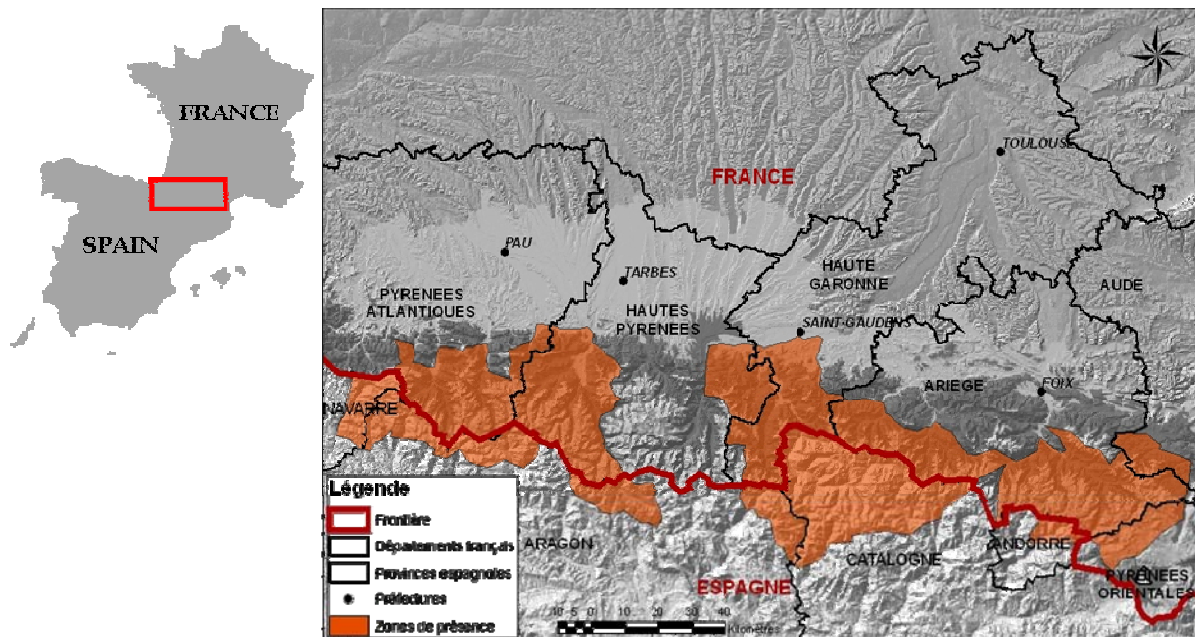


Figure 8: Distribution of brown bears in the Pyrenees (orange areas). There are 2 core areas, the central sub-population (with females) and the western sub-population where only males are remaining. Source: ETO (“bear technical team”)

The main (and difficult!) task of the “bear technical team” of the ONCFS is to unite political and scientific aspects of the management of brown bears in the Pyrenees. Several PhD students receive grants from the ONCFS to study specific scientific questions. I have been one of these students and I have been working in collaboration with the bear technical team. The main applied question I have been asked to work on was the identification of “suitable” habitats for brown bears in the Pyrenees. They asked especially to identify these areas on the French side of the Pyrenees. A pertinent analysis would at least encompass the whole area where bears are present, i.e. both sides of the Pyrenean border. Unfortunately, it has been difficult to obtain the data (especially habitat data) from the Spanish side, particularly because we had to deal with numerous people, because four separate entities are responsible for the management of bear data on the Spanish side. Dealing with several administrations is always problematic. We finally obtained the data but very late.

Study area

The Pyrenees Mountains are situated on an east-west axis between France and Spain and extend for 430 km. The study was conducted in the Pyrenees Mountains (42° 54'' N, 0° 36'' E), and the release site was near the French-Spanish border. Topography is characterized by alternating big massifs and valleys with more or less steep slopes. Elevations range from 500 to 2900 m. Over 40% of the area is forested. Forests are dominated by beech (*Fagus sylvatica*) between 800 and 1600 m, silver fir (*Abies alba*) and mixed forests of beech and fir. Other dominant deciduous tree species include oak (*Quercus robur*, *Q. pubescens*), chesnut (*Castanea sativa*), hazel (*Corylus avellana*), gean (*Prunus avium*), and common ash (*Fraxinus excelsior*) between 800 and 1600 m and common birch (*Betula pubescens*) at higher elevations. Common conifers species are mountain-pine (*Pinus uncinata*), silver pine (*Picea abies*), and Scots pine (*Pinus sylvestris*) in poorly drained areas. Above 1800 m, rhododendron (*Rhododendron ferrugineum*) and heather (*Calluna vulgaris*) dominate, with alpine pastures and rocks at the summits. Several ungulate species (*Sus scrofa*, *Cervus elaphus*, *Rupicapra pyrenaica*, *Capreolus capreolus*) are present in the reintroduction area.

Mean air temperatures were 3.6 C in January and 20 C in July. Mean annual precipitation was 115 cm, with an average of 15.9 snowy days between November and April (Meteorological Station of Fos, Météo France, Haute-Garonne, unpublished data). Snow usually persists from the middle of December to the end of March. Then, the weather was particularly mild with no snow and a mean temperature of 12.6 C between February and April, with a range of 5.9-17.3° C).

The main human activities in this area are timber harvesting and associated road building and cow and sheep farming. Between June and October livestock, mainly sheep, are grazed in summer pastures. Various forms of recreational use occur in this area during summer and fall: hunting and fishing, day hikes, backpack trips, and mushroom picking.



Figure 9: Brown bear in the Pyrenean landscape. Bottom right: wild forest of beech (*Fagus sylvatica*).

Data collection

We used indices of bear presence (e.g. scats, visual observation, tracks, hairs, etc.) for all analyses. Indices of presence are collected in two different ways: systematic collection and non-systematic collection. Systematic collection are carried out by the “bear network” and mainly consisted in walking along transects to collect indices. Photographic traps, hair traps and baiting also are methods for collecting indices systematically. Non-systematic collection consists in indices collected or reported by chance (e.g. by hikers, by members of the bear technical team during other field work, etc.)

Cantabrian population

The remnant population of Cantabrian Mountains is also considered critically endangered. In the past, the population covered the entire Iberian Peninsula (see Naves et al. 2003). As most brown bear populations, this population suffered from persecution and fragmentation of their habitat. It has been protected since 1973 and is listed as endangered (Swenson et al. 2000). Today, the relict population is fragmented into two sub-populations (Figure 10) with an estimated size of 50-65 individuals in the west, and 20-25 in the east (Clevenger, Purroy & Pelton, 1992; Wiegand et al., 1998). A population viability analysis (Wiegand et al., 1998) performed from 1982 to 1995 revealed that the population would not be viable if the mortality rate remained at the level of the last years analysis and identified survival of females to be the most important for population recovery. As for the Pyrenean population, analyses of spatial

occupancy by bears and especially the impact of humans on bear spatial behavior is required for effective conservation of the population.

Study area

The study area was located on the north-western Iberian Peninsula, adjacent to the Atlantic Sea, and covered the entire Cantabrian Mountains. These mountains run east-west along the Atlantic coast with a maximum elevation of 2648 m and average elevations and gradients of north and south facing slopes of 700 m and 34% and 1300 m and 21% slope, respectively. The eastern core area of the population is found on the south facing slopes whereas the western core area on the north facing slopes.

Forest cover is more varied on the north facing slopes, with oaks (*Quercus petraea*, *Q. pyrenaica*, and *Q. rotundifolia*), beech (*Fagus sylvatica*), birch (*Betula alba*), and chestnut (*Castanea sativa*) trees, whereas south-facing forests are dominated by deciduous durmast oaks (*Q. petraea* and *Q. pyrenaica*) and beech. Above 1,700–2,300 m subalpine shrubs (*Juniperus communis*, *Vaccinium myrtillus*, *V. uliginosum*, and *Arctostaphylos uva-ursi*) dominate.

Human densities are 12.1 and 6.1 inhabitants/km² for the western and eastern bear subpopulations, respectively (see Naves et al., 2006). Due to terrain ruggedness, density of roads is low, 0.25 km/100 km².

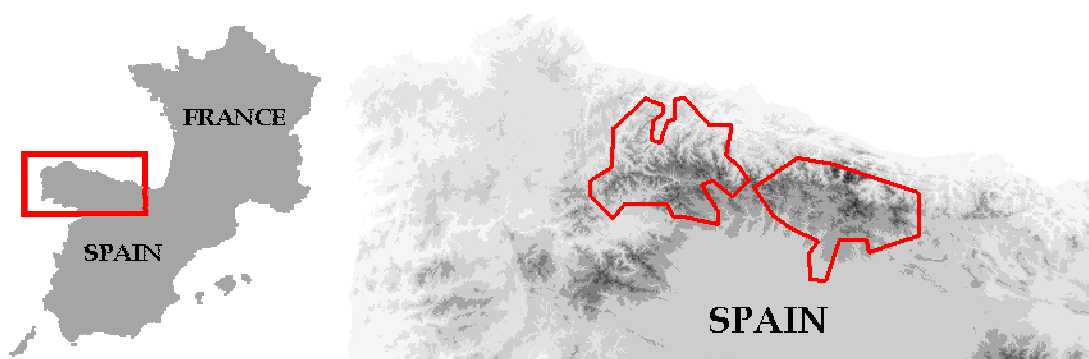


Figure 10: Distribution of brown bears in the Cantabrian Mountains (red polygons).

Data collection

We also used indices of presence of bears in Cantabrian Mountains. Indices were collected between 1982 and 1991 during systematic investigations of the distribution of brown bears in northern Spain (see, Naves et al., 2003). The observations were made by research teams and by rangers and were complimented with through interviews of local people.



Figure 11: Landscape in Cantabrian Mountains. On the right: Cantabrian brown bear.

MAIN RESULTS & DISCUSSION

In this thesis, I am interested in hierarchical habitat selection and movements of three brown bear populations located in different human-dominated landscapes. Our results provide insights into the fields of both ecology and conservation biology.

AUTOCORRELATION IN HABITAT SELECTION STUDIES: A CONCERN OR NOT? (PAPERS I AND II)

For over ten years, most habitat selection studies have been based on telemetric data (Schoener 1994). As stated in the Introduction, telemetric tools (e.g. VHF, GPS) have changed the nature of the data and brought with them new methodological considerations. Although autocorrelation among individuals has been well addressed by scientists, sequential autocorrelation of relocations issues in individual studies have been subjected to debates. Most of the statistical tools that have been developed to study individual habitat selection have been derived from second-order habitat selection (where individuals are not identified), which assumes data independence (see **Paper II**). As such, autocorrelation has often been considered as a problem and was often removed (by subsampling the data) or ignored. However, not taking this autocorrelation into account in analyses might result in a misinterpretation of tests for habitat selection (**Paper I**). Selection may appear to be stronger than it really is. Indeed, this autocorrelation in successive positions of animals is the result of high relocation frequency together with animal behaviors and their constraints. Indeed, if an animal is resting for three hours and if relocation frequency is one relocation every 30 minutes, six positions will have the same habitat attributes, although they would not correspond to real habitat selection behavior. In this case, there is therefore a positive autocorrelation between successive locations because the animal is resting. Comparing those six relocations with random independent locations would therefore lead to a very strong habitat selection (**Paper I**).

Although researchers started to take this autocorrelation into account in habitat selection studies since 1996 (Arthur et al., 1996; Hjermann, 2000; Rhodes et al., 2005), few have been interested in the nature of autocorrelation in the data, as noted by Calenge (2005). However, this autocorrelation might be an interesting proxy for behavioral processes. Recently, nevertheless, new methods have been developed to link individual states to environmental characteristics (State-space models, SSM, see Patterson et al., 2008 for a review). These types of method might provide interesting avenues to analyze habitat selection and associated behavioral processes. In particular, methods designed for segmentation of trajectories might provide valuable tools to analyze the nature of autocorrelation. They are based on the homogeneity of movement parameters (e.g. speed, turning angles). Trajectories are cut so that the resulting pieces of trajectories no longer are autocorrelated, and the corresponding animal states might then be inferred. The succession of homogenous bouts can then be fitted to mixture of movement models (e.g. Morales et al., 2004) and provide insights on behavioural processes through time and space. Each piece of trajectory (and therefore animal state) can then be related to environmental characteristics, allowing inference on behavioural processes involved in habitat selection.

HABITAT SELECTION (Paper III and V)

Scandinavia

Habitat selection is a hierarchical process occurring at different spatial and temporal scales (Johnson, 1980; Orians & Wittenberger, 1991). A thorough understanding of specie's ecological requirements therefore involves investigations of habitat selection at different spatial and temporal scales. This is particularly true for human-sensitive species with large spatial requirements living in human-dominated landscapes such as brown bears in Europe. Few studies have investigated the spatial dependence of habitat selection by brown bears, and all of them have been conducted in North America (McLoughlin et al., 2002; Nielsen, Boyce & Stenhouse, 2004a; Ciarniello et al., 2007), in very different landscapes compared to Scandinavia.

Rettie & Messier (2000) proposed that the most limiting factors should be avoided (or selected) at larger scales. Then, avoidance or selection for the next limiting factors should occur at finer scales. They suggested that a limiting factor should be avoided or selected until it

becomes less limiting than another limiting factor, which implies a ranking of these limiting factors. Our results support (1) the utility of such a hierarchical approach, Scandinavian brown bears show differential habitat selection according to scales of investigation (**Paper III**) and (2) broadly support the idea of Rettie & Messier (2000) on the relationship between spatial scale and importance of limiting factors.

Bears (like most carnivores) have low reproductive rates and are sensitive to high mortality rates. Humans are well known to be the main cause of brown bear mortality (Wiegand et al., 1998). As such, human density and infrastructures should be the factor that limits brown bear populations most, and should thereby be avoided at larger scales. Then, bears should select for food-rich habitats. Previous studies and this thesis documented a selection for forested areas with low human densities at the scale of population establishment in Scandinavia (Katajisto, 2006) and a negative effect of roads, human density and agricultural areas in the Cantabrian Mountains and in the Pyrenees (**Paper V**). These studies are hence partly in accordance with Rettie & Messier's (2000) hypothesis. However, it should be noted that at this scale, Scandinavian brown bears also select for forested areas, which provide food resources. There was no common pattern of habitat selection at the scale of home range establishment at the fringe of the southern core area of the Scandinavian population (**Paper III**). This result could be explained by three factors. (1) The philopatric behavior exhibited by female brown bears (Støen et al., 2005) might be the main driving force of female settlements near their mother. Støen et al. (2005) identified matrilineal groups that form multigenerational assemblages of related females occupying exclusive areas. One of the potential benefits of females being philopatric is the familiarity with the local area and neighbours (Støen et al., 2006). Although philopatric behavior of females might entail delayed primiparity, it may increase cub survival (Støen et al., 2006). Hence, benefits resulting from settling within part of their mother's home range might override the habitat composition of home range. (2) Another explanation would be a dominance hierarchy among females or even among matrilineal assemblages. Dominant females or matrilineal groups might force subdominant females to occupy less suitable areas (in our case, with few regenerating forests and high degree of human influence). Benhamou (1998) pointed out the role of social relationships in spatial organization of home ranges in mammals. In the case of Scandinavian brown bears, social structure might supplant the choice of home range habitat composition. Finally, this scale of investigation might be irrelevant regarding the ecological requirements of brown bear. Indeed, habitat may not be particularly limiting for

females at this scale and may be globally suitable. When there is no strong environmental variability, it can be difficult to demonstrate habitat selection (Aberg et al., 2000).

In Scandinavia, brown bear selection might therefore occur at a larger scale (establishment of the population) and at a very fine scale (selection of habitat within their home range) as demonstrated in **Paper III**. There, we documented a common selection pattern for slopes and regenerating forests within individual home ranges. Regenerating forests are known to favor several food components of bear diet (see **Paper III**) and slopes might provide more secure areas. As Hebblewhite & Merrill (2008) pointed out, the indirect influence of human is seldom investigated. They found a spatio-temporal avoidance of human activity by wolves (*Canis lupus*) during daylight. Our results on hourly variation in selection for slopes and disturbed areas also suggested a temporal avoidance of human infrastructures (settlements, isolated houses, high and low traffic roads). Indeed, bears were located in areas far from human infrastructures and in slopes during the daylight hours, which correspond to important human activity. When considering this fine temporal scale, humans appeared to be avoided. Human influence therefore affects bears at different spatio-temporal scales. If we had not investigated this temporal scale, we would have failed to detect this influence.

We also highlighted a functional response of females in response to disturbance. Females located in home ranges with a higher proportion of human influence tended to select for slopes and regenerating forests even more (**Paper III**). This result corroborates those from the temporal analysis of human influence on bears. At fine spatial and temporal scales, as well as the landscape scale, females perceive anthropogenic structures as disturbance and adapt their behaviors according to the degree of this disturbance.

Rettie and Messier (2000) pointed out the discrete property of selection orders defined by Johnson (1980), stating that they correspond to “*several spatial scales that can best be regarded as points on a continuum*” and the fact that patterns of habitat selection across scales should reflect the hierarchy among limiting factors. Dussault et al. (2005), however, pointed out the weak point of these suggestions. Their study investigating limiting factors of moose across scales revealed trade-offs between limiting factors that make their hierarchy unclear. Moose tended to avoid predation at the landscape scale, using areas unused by wolf packs and within areas receiving higher rainfall (wolf being less adapted than moose to deep snow). However, at a finer scale (home range scale), they documented a trade-off between food resources and avoidance of snow. Our results also suggested that a hierarchy between avoidance of human influence and

selection for food resources was not that clear. Scandinavian brown bears avoided disturbance and selected for areas that provide food resources at the landscape scale (Katajisto, 2006). At the intermediate scale, social organization might be the driving force that organize home range establishment (**Paper III**), and bears again showed a strong habitat selection within home ranges, mainly toward secure areas (slopes) and habitats with abundant food resources (regenerating forests, **Paper III**). They also exhibited temporal avoidance of disturbance at the fine temporal scale. Our results therefore confirm the weakness of establishing a hierarchy among limiting factors, though we did not document trade-offs between limiting factors for bears because forested areas with important connectivity at large scales are also areas with lower human density.

Cantabrian Mountains and Pyrenees

Large-scale habitat selection was similar for brown bears in the Pyrenees and in Cantabrian Mountains (**Paper V**) underlined the similarity of habitat selection behaviour between the two populations. We carried out habitat selection analyses using different resolution (pixels of $5\text{ km} \times 5\text{ km}$ using large-scale habitat variables for the global-scale model; $200\text{ m} \times 200\text{ m}$ pixels using finer habitat variables for the local-scale model in the Pyrenees only). The global-scale model that was built using data from Cantabrian Mountains fitted in the Pyrenees well. Both populations therefore selected for forests that produce hard mast, areas with forest connectivity at a large scale (15 km), greater shrub cover, low road and human densities, and low proportion of agricultural areas. This global-scale analysis was carried out within the framework developed by Naves et al. (2003), which is based on two important demographic parameters for bears: survival and reproduction. Their idea is to build separate models for each demographic parameter and then to combine the models to divide the habitat into demographic categories according to the framework of source-sink theory (Pulliam, 1988). We could therefore classify habitat in five different classes within each study area: source-like habitat (safe habitats good for reproduction), attractive-like habitats (good for reproduction but high mortality risk), refuge habitats (safe habitat with low quality for reproduction), sink-like habitats (risky and poor habitat for reproduction) and matrix habitat (non-habitat areas). Linking species spatial occupancy and demography is of prime interest for conservation purposes (Naves et al., 2003; Nielsen, Stenhouse & Boyce, 2006), because it may allow the identification of habitats that can

have negative effects on survival (attractive sinks), therefore impacting population dynamics of species with low reproductive rates such as brown bears.

At a local scale, Pyrenean brown bears were located preferentially close to forests (especially mixed and coniferous forests) and further from agricultural areas and regenerating forests, compared to what was available in average. Moreover, they seemed to be specialized on a medium range of elevations, not because elevation is limiting in itself, but because of a trade-off between low disturbance (at higher elevations) and high forest productivity (at lower elevations).

Contrary to our study on individual habitat selection of Scandinavian females, showing a strong selection for regenerating forests (**Paper III**), Pyrenean brown bears seemed to avoid this type of vegetation (**Paper V**). Although the studies were not conducted at the same spatial scale, it should be noted, that regenerating forests might not have the same influence and importance for these two populations. Indeed, hard mast (an important component of Pyrenean brown bear diet) is negatively impacted by timber harvesting, and are therefore less available in regenerating forests (Reynolds-Hogland, Pacifici & Mitchell, 2007). On the contrary, the availability of soft mast (an important component of Scandinavian brown bear diet), increases in young successions following tree harvesting (Mallik, 2003). Hard-mast availability might therefore be more limiting for Pyrenean brown bears, whereas soft mast might be more limiting for Scandinavian brown bears. As a consequence, effects of forestry might have opposite effects on the two populations.

MOVEMENT ECOLOGY (PAPER IV)

As stated in the Introduction, movement is the mechanism allowing animals to make choices concerning their habitat. Understanding the processes of habitat selection at the scale of behavioral decisions requires an integrated analysis of movement ecology, especially identifying factors that drive movements.

We studied daily movements by Scandinavian brown bears over the entire period of activity (from April to October), investigating both internal and external correlates, using GPS relocations. More precisely, we studied the influence of changing requirements between seasons, reproductive status, and age (internal correlates) and the influence of daylight, weather, vegetation type, and human disturbance (external correlates) on daily movement patterns. Our

results provided insights into the three basic components related to the individual (influence of internal state, motion capacity and navigational capacity) and influence external factors, as defined in the framework developed by Nathan et al. (2008). As internal state and motion capacity are intimately related, we discussed these two aspects of movement together.

Internal state and motion capacity

We documented a circadian rhythm in daily movement pattern, with two peaks of movements at twilight and a main resting period during daylight (**Paper IV**), which is consistent with previous studies on activity patterns of European brown bears (Gervasi, Brunberg & Swenson, 2006; Kaczensky et al., 2006; Moe et al., 2007). We reported an important variability of this rhythm, as well as in intensity and linearity of movements according to seasons and reproductive status. After den emergence, females with cubs-of-the-year (hereafter cubs) showed peaks of movement only during daylight, probably because cubs are more active during this period. During the mating season, which occurs in May-June, they established a bimodal movement pattern, with peaks of movements occurring during daylight, contrary to lone females. Switching activity to daylight may be a counterstrategy to SSI, by avoiding males when they are active. Indeed, low-movement capacity of cubs is not the reason for restricting their movements during this period (Dahle & Swenson, 2003b). Although we did not have data on movement patterns of males, we can expect them to synchronize their movement with lone females during the mating season to increase the encounter probability (Dahle & Swenson, 2003b). Having cubs therefore entails important changes in movement rhythm and mobility. Moreover, females with cubs tend to have very convoluted movements during the period after den emergence and during the mating season. However, linear movement have been reported to be more efficient for locating new patches of resources (Bell, 1991; Fahrig, 2007). There is therefore an important trade-off between search efficiently for food resources (which is crucial for lactating females that have additional energetic demand, Hamel & Cote, 2008) and protection of cubs from SSI. Females with cubs showed patterns similar to those of lone females during the following seasons, when cubs were larger and when there was no risk of SSI.

As stated in the Material & Methods, brown bears pass through very different physiological stages during their activity period, i.e. through seasons. After den emergence, their body condition is low (in average 62 kg lost compare to autumn, Swenson et al., 2007a) and exhibit hypophagia. We documented a very low movement rate during this period, which may be

explained by the balance between costs and benefits of movement, i.e. in our case, finding food resources and saving energy, respectively. During the mating season, lone females have a normal food intake, but roam to find mates (Dahle & Swenson, 2003b), and therefore increase their movement rate and the linearity of movement. Linear movements have been shown to be more efficient in locating resource patches or mates (Duvall & Schuett, 1997; Fahrig, 2007). Females increased the intensity and linearity of their movements the following seasons as they became less limited by movement costs and needed to find abundant food resources to prepare for the denning period.

Navigational capacity

We did not investigate navigational capacity *per se*. However, our results regarding the effect of age on movement provided some interesting insights. Older females tended to move more slowly (and therefore less) than younger females, irrespective of the reproductive category. This result is in accordance with our hypothesis on memory effect (see above). Indeed, older females might be more familiar with the habitat composition of their home range, which may allow them to use environmental cues better and therefore to orient their movement better, hence moving less (Bell, 1991).

External factors

We also documented the influence of external factors on bear movements. Daylight was an important factor affecting bear movement. As for numerous species, daylight is a major determinant of circadian rhythm. The timing of movement peaks was correlated with sunrise and sunset. As daylight duration varies greatly in Scandinavia, bears showed important variation in the timing of movements among seasons.

Temperature also affects bear movements. They tended to be globally more active during the hottest days, but they actually shifted toward more nocturnal movement patterns, increasing the duration of their diurnal resting period, and moving more at night. This pattern has also been reported in several ungulates populations (Dussault et al., 2004; Maloney et al., 2005; Aublet et al., 2009).

Bears also changed their movements according to the vegetation type they were in. In open habitat with low food resources (bogs), they increased the speed and linearity of movement, whereas they had slower and more convoluted movements in resource-rich vegetation types (young forests and coniferous forests). Open bogs might also represent risky habitats for bears,

as they increase the probability to be detected. Bears therefore spent more time in secure and resource-rich habitats by reducing their movement rate and showing convoluted movements.

We also investigated the potential effect of human disturbance on bear movements. The influence of anthropogenic structures was the highest after den emergence for both reproductive statuses, probably because of their low body condition, and during the mating season for females with cubs. When located in disturbed areas, movements were faster and more linear, which is known to be a strategy to avoid predation risk (Fahrig, 2007). In addition, there was a strong effect of slope on movement patterns. Irrespective of the reproductive category, females had slower movements on slopes during the summer and autumn. These periods correspond to the bear hunting season and also when humans pick berries in the forest. Together with the results of **Paper III**, documenting a higher selection for slopes during daylight, this pattern could be explained as an avoidance of human contacts by resting in secure areas during periods of higher human activity, especially periods of higher human activity in the forest. These results are consistent with the study of Ordiz, Støen & Swenson (Submitted) which reported that bears selected for secure areas when resting during daylight (further from human settlements and in dense vegetation), especially during seasons with higher human activity in the forest and the hunting season.

A limitation of this work is the lack of interactions between external factors and hours in our Generalized Additive Mixed Models (GAMM) to facilitate interpretation of already complex models. However, the temporal avoidance of disturbed areas and selection for slopes that we documented (**Paper III**) suggest such interactions. In addition to the environmental variability that could affect movements and habitat selection, internal state, which varies throughout the day, also has an influence on these processes. However, our goal was to document movement ecology of bears, and it opened new areas of inquiry.

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT OF BROWN BEAR

It is often difficult to determine the spatial scale at which to conduct investigations for conservation purpose, because animals may not have the same perception of habitat for a given scale as biologists. Habitat selection studies addressing conservation purposes are often conducted at large spatial scale, as recommended by some authors (Noss et al., 1996). Indeed, conservation actions are often based on the basis of costs and benefits, large-scale studies being generally considered less expensive than fine scale analyses that require data at a higher resolution (Corsi et al., 2000). However, large-spatial scale studies only may not be sufficient. Our results documented well the complementarities of multiple-scale analyses and their importance in conservation or management guidelines (**Paper III**). At a large spatial scale, bears are located in forested areas with low human density. At a finer spatial scale, bears strongly selected for regenerating forests, because of the abundance of food resources they provide. Regarding only large spatial scales, conservation actions would perhaps focus on natural forested areas, areas with low forestry or even propose a reduction in forestry. However, logging creates new habitats that can substitute the loss of meadow and pasture (Rolstad et al., 2000), which favor biodiversity and in our case, food items for bears (Nielsen et al., 2004b). Nevertheless, forestry entails increasing road networks and increasing access to the forest. Anthropogenic structures, such as roads, houses and small human settlements found within bear home ranges, impact bears' movements and habitat selection negatively at a fine spatial and temporal scale (**Papers III and IV**). Our results therefore suggested that the present forestry management in Sweden, which can affect brown bear habitat positively though the potential benefit to food plants, might be at the cost of an increased human disturbance through the development of a large road network. Management of the Scandinavian population therefore should focus on transportation and resorts planning (**Paper III**, Nellemann et al., 2007). Forestry might be positive for bears, as it opens habitats which may favor food resources, but this positive effect may only be beneficial in areas with low human density and where soft-mast production is more abundant than hard-mast production, as in Scandinavia, and contrary to the Pyrenees (**Paper V**).

Our results also provide insights into the perception of habitat connectivity by bears. Bears seem to favor forest connectivity at large scales (15 km, **Paper III**, Katajisto, 2006). However, as

documented for Scandinavian bears (**Paper I**), at the home range scale, they prefer mosaics of habitats made up of old forests and young/open forests, therefore, apparent fragmentation from a human perception. This result is in accordance with previous studies showing a preference for mixture of forest structural stages (Waller & Mace, 1997; McLellan & Hovey, 2001; Nielsen et al., 2004a).

Assessment of wildlife-habitat relationship is important for conservation planning. As stated earlier, carnivore conservation in multiple-use landscapes is a difficult task that requires both scientific knowledge of ecological requirements, but also considerations of the social, political and economical contexts. Human-carnivore relationships are complex and require thorough investigations of spatial organisation and behaviors. For example, Hebblewhite & Merrill (2008) showed a functional response of wolves at a fine spatial scale. They found that wolves' habitat selection was not related to the proximity of humans in areas of low human activity, whereas they selected for areas closer to humans when human density increased. However, they showed a spatio-temporal avoidance of human activity during daylight, which is consistent with our results on Scandinavian brown bears (**Paper III**).

PERSPECTIVES

HABITAT SELECTION AND EVOLUTION

During this thesis, I have mainly focused on ecological aspects of habitat selection. However, by the end of the “thesis process”, I felt the need to further investigate of the relationship between habitat selection and evolutionary processes. In this section, I will therefore provide some research perspectives that would naturally follow this thesis work, with more emphasis on the evolutionary consequences of habitat selection.

Our results showed that habitat selection did not occur at the scale of home range establishment in the Scandinavian brown bear population (**Paper III**). This result deserves more investigation, especially focusing on the variability between females. Indeed, it would be worth relating females' biological parameters (e.g. body mass, reproductive success, social status) to home range composition, including both physical habitat and the proportion of overlapping home range with their mother. Also, as a complementary approach, investigating movement optimality among females would provide insights into the benefits of remaining close to their mothers. Indeed, young females that settle within part of their mother's home range might have a better knowledge of the composition of their home range (Støen et al., 2006). As a consequence, we can hypothesis that they would have more oriented movements and therefore more efficient search behavior than young dispersing females which should show more random movements.

Our results on movement patterns of females brown bears (**paper IV**) documented common patterns of movement in accordance with ecological requirements of females, and differences between lone females and female with cubs, which do not have the same requirements and constraints. However, we did not investigate the movement variability of females. We showed that age of females might have an effect on movement patterns, older females moving less than younger females, probably because they have a better knowledge of their home range or a better risk perception (**Paper III**). Investigating these variations more deeply, as well as variation among females with different body mass, would provide insights into the optimality of movements and search behaviors.

Sexually selected infanticide has been reported in the Scandinavian brown bear population and is one of the main causes of cubs' mortality in the southern core area of the population (Swenson et al., 1997). We found that females with cubs-of-the-year had different movement patterns than lone females, especially during the premating and mating seasons. One of the hypotheses we suggested to explain this variability is a temporal avoidance of males. However, this suggestion is based on lone female behavior only, and we suppose they synchronize their movements with males to increase encounter probabilities. Dahle & Swenson (2003b) documented that females with cubs restricted their home range during the mating season, apparently as a spatial avoidance of males. Investigating temporal avoidance by studying movement patterns of these females would provide insights into adaptive behaviors involved in preventing infanticide.

HABITAT SELECTION AND ECOLOGY

The **Paper V** is a preliminary analysis on the similarities of habitat selection of two European populations: the Cantabrian Mountains population and the Pyrenean population. Because of time constraints, I have not been able to integrate the Scandinavian population into the analysis. However, testing our model in Scandinavia would provide useful knowledge on the process of habitat selection of brown bear at the continental scale. Indeed, the Scandinavian landscape, where brown bears evolved, is quite different from those of south-western Europe. Nevertheless, we might expect that large-scale processes of habitat selection should remain quite similar among bear populations. Then, we could explore the ecological niche of each population independently as we did in Pyrenees (local-scale model, **Paper V**) to identify local differences and local adaptations of bears in various environments.

As stated earlier, human-carnivore relationships may be complex. To complete our analyses on habitat selection of the Pyrenean brown bear population, individual level analyses are required. Especially, they might provide additional insights into the perception of human influence by bears at different spatial and temporal scales.

HABITAT SELECTION AND MOVEMENT

During my thesis, I have been working with statisticians on segmentation techniques for cutting trajectories into homogeneous bouts. Until now, attempts to cut bear trajectories were not very successful. These segmentation methods have been developed on animals that show clear patterns of movements such as migratory and encamped movements of moose (Morales et al., 2004), or by simulations (Barraquand & Benhamou, 2008, Calenge, Gueguen, Royer-Carenzi and Dray, in prep). These methods were designed for large and clear movement processes (e.g. migration versus stationary). However, for real data covering all possible behaviors, including foraging, resting, dispersing, etc., the output may be unclear (Martin, unpublished data). Our analyses of brown bear movement patterns helped us to identify factors influencing bear movement, which may facilitate the segmentation procedure. As the methods have been published only recently or are still in development, a future comparative analysis of the outputs of the different methods applied on real data may provide more robust biological results and would be helpful in identifying potential weakness of each method. The resulting movement bouts could then be related to habitat, and therefore help to link behavioral processes to habitat selection.

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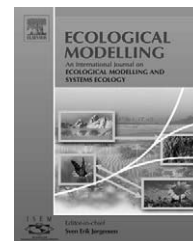
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PAPERS AND MANUSCRIPTS

Paper I

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Importance of movement constraints in habitat selection studies

Jodie Martin^{a,b,*}, Clément Calenge^a, Pierre-Yves Quenette^c,
Dominique Allainé^a

^a Université de Lyon, Université Claude Bernard Lyon1, UMR CNRS 5558, Laboratoire de Biométrie et Biologie évolutive, 43 bd du 11 novembre 1918, F-69622 Villeurbanne Cedex, France

^b Department of Ecology and Natural Resource Management, Norwegian University of Life Science, P.O. Box 5003, NO-1432 Ås, Norway

^c Office National de la Chasse et de la Faune sauvage, F-31800 Villeneuve de Rivière, France

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ABSTRACT

The aim of this study is to empirically illustrate the importance of taking movement constraints into account when testing for habitat selection with telemetry data. Global Positioning System relocations of two Scandinavian brown bears were used to compare the results of two different tests of habitat selection by the bears within their home range. Both relied on the comparison of observed dataset with datasets simulated under the hypothesis of random habitat use. The first analysis did not take movement constraints into account (simulations were carried out by randomly distributing a set of points in the home range) whereas the second analysis accounted for these constraints (simulations were carried out by building random trajectories in the home range). The results for the two analyses showed contrasted results. Therefore, not accounting for movement constraints in analyses may result in a misleading biological interpretation. Autocorrelation between relocations is not undesirable: it contains information about ecological processes that should be integrated in habitat selection analyses.

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1. Introduction

During the last decade, the Global Positioning System (GPS) has been used increasingly by biologists to study the habitat selection by animals. The study of habitat selection with this kind of data implies a comparison between the habitat used by this animal and a null model describing the habitat that would have been used under the hypothesis that no habitat selection occurs (random habitat use, Boyce et al., 2002).

The simplest and the most widely used null model considers that, assuming random habitat use, the habitat used

by the animal would be similar to the habitat composition of an area considered available to the animal (usually its home range, Aebischer et al., 1993). The use of this null model strongly relies on the assumption of independence between animal relocations which implies that the animal could be found anywhere within its home range at any time of the study period. In other words, this model supposes that patterns observed in the relocations of the animal (e.g. areas of higher relocations density) are only due to the animal's habitat choices. In many instances, this is often a reasonable assumption. However, this might not be the case in

* Corresponding author at: Université de Lyon, Université Claude Bernard Lyon1, UMR CNRS 5558, Laboratoire de Biométrie et Biologie évolutive, 43 bd du 11 novembre 1918, F-69622 Villeurbanne Cedex, France. Tel.: +33 4 72 43 35 84; fax: +33 4 72 43 13 88.

E-mail address: martin@biomserv.univ-lyon1.fr (J. Martin).

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studies relying on GPS data. Due to automated positioning using GPS, these data are often characterized by short time intervals between relocations, which causes serial autocorrelation in the position of successive locations (Swihart and Slade, 1985). Thus, the position of an animal at time t is constrained by its movement capabilities between $t-1$ and t .

Ignoring this autocorrelation may result in misleading conclusions concerning the animal habitat selection. Several authors have noted that autocorrelation may result in an increased probability of type I errors (Legendre, 1993). It is therefore necessary to use an appropriate null model incorporating these movement constraints for the description of random habitat use. On the other hand, it is difficult to dissociate the effect of the movement constraints from that of habitat choice behaviour when building the null model under the hypothesis of habitat selection. We advocate that the null model used in habitat selection studies should depend both on the biological knowledge and on the available data for the studied individuals (species, sex, age, season of monitoring, study area, etc.). We therefore challenge the idea that some statistical methods can be used systematically to test for habitat selection, as no automatic method allows the design of such context specific null model. In this paper, we illustrate this approach by comparing the results of two “automatic” methods to test for habitat selection by two female brown bears (*Ursus arctos*) monitored using GPS. Our aim is not to draw conclusions about habitat selection by brown bears, but rather to illustrate the potential different conclusions regarding the strength of habitat selection depending on which approach is used. In the first analysis, we did not take movement constraints into account, and we assumed the spatial distribution of relocations to be explained exclusively by the habitat (i.e. a model without constraints, which is the simplest null model as described above). In the second analysis (i.e. a model with constraints), the null model accounted for patterns of the animal's trajectory to test the habitat selection: random habitat use was thus simulated preserving the shape of the observed trajectory.

2. Materials and methods

2.1. Data

We used GPS data from two Scandinavian female brown bears (ID numbers: W0208 and W0410) followed in central Sweden (Fig. 1): one female was alone whereas a second one was followed by cubs of the year. Relocations were collected every 30 min, from mid-April until the end of July 2006 (a total of 2309 and 2812 were available for the lone and the followed female bear, respectively).

We used raster maps of bear home ranges to describe the habitat, with a resolution of 200 m $\times$ 200 m. The maps included nine variables: elevation, slope, aspect, vegetation, distance to private and to public roads, distance to streams, distance to settlements and distance to houses. Each pixel of the resulting map thus contains geographic coordinates and the value for each variable. This environmental information is stored in a table X containing N rows (the N pixels of the home range) and P columns (the P environmental variables). This table has been centred and scaled, so that each habitat variable has a mean of 0 and a variance of 1. Each row of this table contains the coordinates of a point in the P -dimensional space defined by habitat variables (Fig. 2). The proportion of relocations in each pixel of the map is a utilization weight of the pixel (Fig. 2). The set of points in the available space for which the utilization weights are greater than 0 define the niche of the animal.

2.2. Habitat selection measurements

To study the strength of habitat selection, we used the concept of ecological niche formalized by Hutchinson (1957) (Fig. 2); a species niche is the hypervolume in the multidimensional space of environmental variables where the species can maintain a viable population. In this study, we extrapolated this definition to the third-order selection on Johnson's (1980) scale of selection, i.e. preferred habitat within the home range. We thus considered each home range, estimated by the Minimum

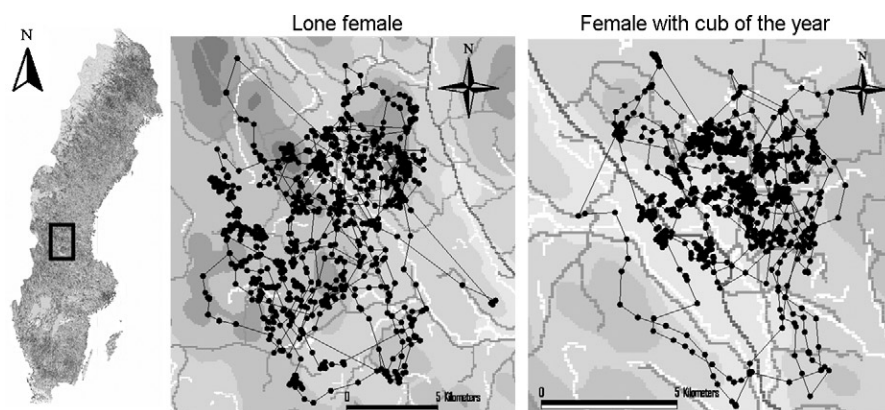


Fig. 1 – On the left: study area in central Sweden. On the right: trajectories (in black) of the two female brown bears on an elevation map. Grey lines are private roads and white lines are streams.

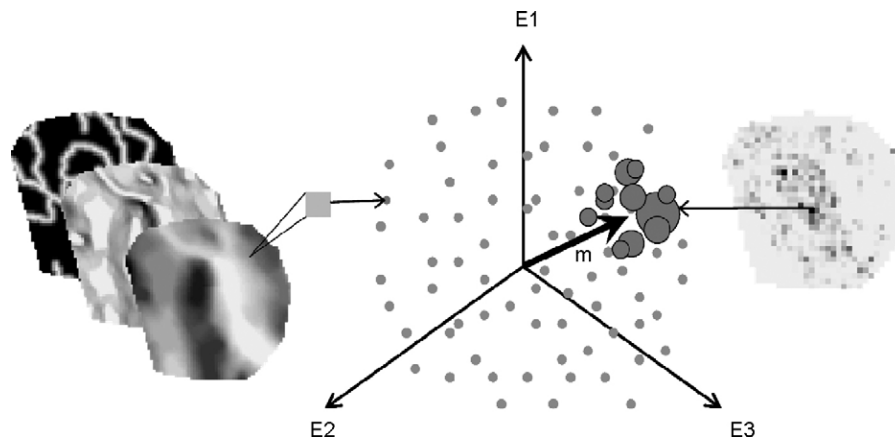


Fig. 2 – The use of the niche concept for study of habitat selection using GPS data. For a given animal, P maps of its home range are available (left). Each one of the P mapped variables defines one dimension in a multidimensional space, the ecological space (centre). Each pixel of the home range takes a value for each variable, so that each pixel corresponds to an available point in this space. On the other hand, the number of relocations of the animal in each pixel of the home range corresponds to a “utilization weight” (UW) of this pixel (right). These utilization weights are represented by grey circles in the middle figure (with a diameter proportional to the weight). The niche of the animal in the ecological space is defined by the set of points having an UW greater than 0. As the cloud of available points is centred (the origin of the space corresponds to the average available habitat conditions), the vector M , connecting the origin of the space and the average used habitat conditions, is the marginality vector.

Convex Polygon method (MCP; Mohr, 1947), as the available physical space.

Two complementary parameters can be used to characterize the niche: marginality (an index of the eccentricity of the niche relative to the average available habitat conditions) and tolerance (an index of the volume of the niche in the space of environmental variables) (Doledec et al., 2000; Hirzel et al., 2002). Marginality corresponds to the squared distance between the average habitat conditions used by the animal and those available to it:

$$m^2 = \sum_{j=1}^P (u_j - a_j)^2$$

with u_j the average use of the variable j and a_j the average availability of the variable j .

Tolerance is the sum, over all habitat variables, of the variances of the used pixels:

$$t^2 = \sum_{i=1}^N \sum_{j=1}^P p_i (x_{ij} - u_j)^2$$

with p_i the utilization weight of the pixel i and x_{ij} the value of the variable j in the pixel i . Note that the variables are centred and scaled, i.e.

$$\frac{1}{N} \sum_{i=1}^N (x_{ij} - u_j)^2 = 1$$

for all j .

These parameters have already been used by several authors to measure habitat selection (Doledec et al., 2000; Hirzel et al., 2002).

2.3. Habitat selection analysis

For each female, we tested the strength of selection behaviour using randomization tests of marginality and tolerance for the two models. In other words, we tested whether the marginality and the tolerance of their niche were significantly different from those obtained under the hypothesis of no selection, i.e. random use of the habitat, which we measured in two different ways.

In the model “without constraints”, we distributed 1000 samples of N random points within the home range of each bear, N being the number of actual relocations of the corresponding bear. In this model, any pixel in the home range is considered to be available at any time, and each set of points corresponds to a simulation of random habitat use.

In the model “with constraints”, we kept the shape of the animals’ trajectory unchanged, to account for the autocorrelation between relocations. We performed 1000 rotations of the observed trajectory for each of the female around the centroid of the respective observed trajectories (Fig. 3). Each random rotation of the trajectory corresponded to a simulation of random habitat use by the animal taking into account the movement constraints on the trajectory.

For each model, marginality and tolerance were computed on simulated datasets. These values were then compared with observed values of marginality and tolerance to test for the strength of habitat selection in the two models.

Analyses were carried out using the package “adehabitat” (Calenge, 2006) for the R software (Ihaka and Gentleman, 1996).

3. Results

For each female, the range of simulated values of marginality and tolerance for the model “with constraints” was much

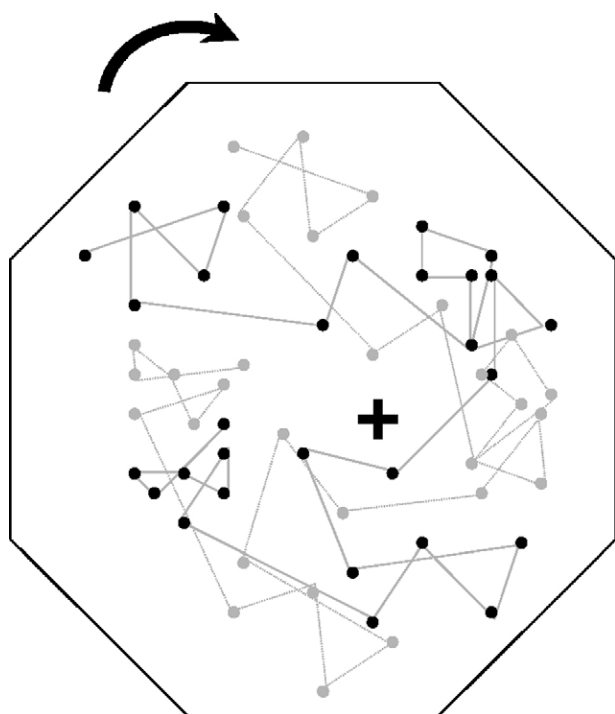


Fig. 3 – Trajectory simulation procedure for the model with constraints. The polygon represents the individual home range. Simulated trajectory (dashed grey line) were generated by a clockwise rotation (arrow) of the observed trajectory (black line) around its centroid (black cross).

broader than that for the model “without constraints” (Fig. 4). This result can be explained by the fact that habitat availability is restricted when simulating trajectories. Indeed, due to constraints of speed and orientation (turning angles between successive moves) the probability is higher for the next relocation to be located in a pixel close to the previous one. Therefore, the probability of remaining in a similar habitat type is high, resulting in a less homogeneous distribution of

these simulated “used” points in the home range. This results in larger differences between the simulated “used” pixels and the pixels of the whole home range, and therefore larger values of marginality.

Note that for the lone female, the observed habitat use (observed marginality and tolerance) is far from the distribution of simulated values obtained by randomly sampling points in the home range. This null model was therefore rejected, which suggested a strong habitat selection. On the other hand, the observed habitat use was located on the border of the distribution of values obtained by randomly rotating the trajectories. This other null model was accepted, which suggests a very weak habitat selection. We obtained the same results for the female with cubs, except that the observed used point is in the centre of the distribution of values estimated using simulated trajectories.

4. Discussion

We compared two extreme approaches to test for the habitat selection by two female brown bears monitored using GPS. For both bears, the results depended on the approach used to perform this test. When we tested habitat selection using a null model that did not account for movement constraints (the most common in the literature), we found a strong habitat selection by both bears. However, ignoring movement constraints might lead to an overestimation of the strength of this selection, because not considering these constraints artificially reduces the marginality and the tolerance under the assumption of random habitat use. Indeed, this model relies on the assumption that the individual not only has the capacity to move everywhere in its home range at any time, but also that it has no intrinsic constraints (due to feeding or resting requirements, restriction on movements because of cubs, etc.). When we tested for habitat selection accounting for movement constraints, using random rotations of the trajectories, we found no significant habitat selection for either bear. Actually, the shape of the trajectory, which is kept

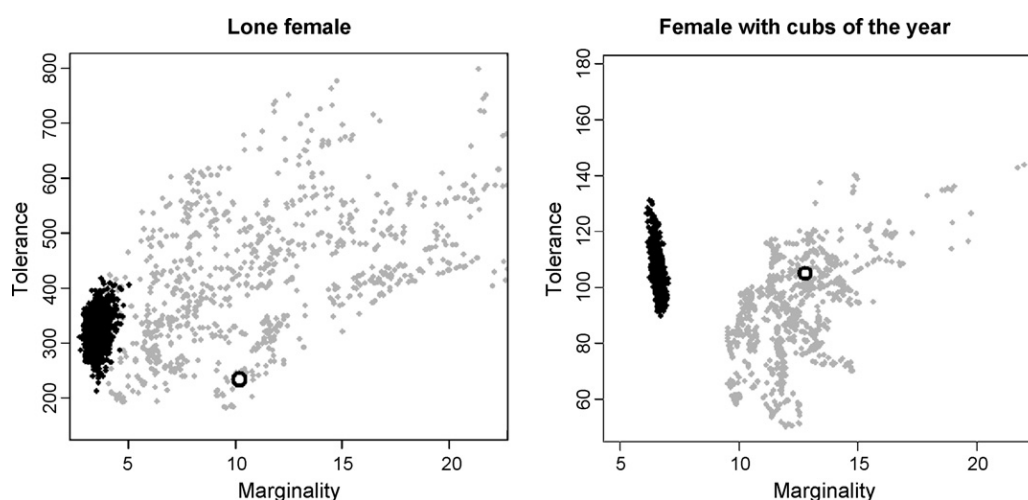


Fig. 4 – Joint distribution of the marginality and the tolerance for each female brown bear according to the two tested models of absence of habitat selection. Black points: simulations “without movement constraints” model; grey points: simulations “with movement constraints” model. The white point indicates observed data.

unchanged in our rotations, is also partly the result of habitat selection. For example, animals move less in some periods perhaps because they search intensively for food in specific habitat, indicating habitat selection. Keeping the shape of the trajectories unchanged in this test may have been too conservative and underestimated the strength of habitat selection. For the female with cubs, the difference between the simulations computed with random points and random trajectories was more pronounced than for the lone female. This can be explained by the difference in trajectories structure between the two females (see Fig. 1). The female with cubs was constrained to move in a more “patchy” way, probably because small cubs are not capable of large movements in spring, and the female may be avoiding potential infanticide (Bellemain et al., 2006). Thus, she was restricted to small areas that she used in a more intensive and homogeneous manner. It is important to stress that the observed distribution of an animal's positions is the result of several effects: (i) intrinsic constraints (depending on the status and activity rhythm of the individual), (ii) extrinsic constraints (environmental or artificial barriers), and (iii) the actual habitat selection. However, most of habitat analyses inside home range ignore intrinsic and extrinsic constraints. A few biologists praise accounting for autocorrelation in their models (Arthur et al., 1996; Fortin et al., 2005; Rhodes et al., 2005), but the nature of the dependence between relocations within the whole trajectory is seldom analysed, as noted by Calenge (2005). Indeed, the so called design IV (Thomas and Taylor, 2006) is increasingly used to compare position of relocations at time t and $t - 1$, but this procedure only considers trajectories as a first order Markovian process and deems the successive steps (displacement between two relocations) independent whereas they may be themselves autocorrelated. Indeed, when an animal changes its behaviour during the monitoring period, the mathematical properties of the steps (e.g. their length) may change accordingly (e.g. shorter step length when the animal forages than when it flees from a predator). This non-stationarity in the animal behaviour often results in autocorrelation of the trajectory property (Calenge et al., unpublished).

A possible solution to this problem would be to study the spatial structure of the trajectory to identify patterns of movement before relating these patterns to habitat structure. This is a similar approach to indirect ordination in community ecology (Okland, 1996) which has met a large success in relating the environmental variable to pattern of vegetation composition. Starting with identifying patterns in the data, and then relating them to the environment, is an approach that has been widely used in community ecology because of its strong efficiency. As noted by Morales (2002), *the main challenge of scaling up movement resides in the complexities of individual behaviour rather than in the spatial structure of the landscape*. Such an approach would allow identifying the role of both the environment and the animal behaviour on animal movements.

This knowledge would be essential in most fields of ecology, wildlife management, and conservation. In particular, the recent field of complex adaptive systems would benefit from this statistical approach. Indeed, more and more models in this framework presently tend to integrate movement behaviour to predict population dynamics (Railsback et al., 1999; Railsback, 2001). Such models are of the utmost inter-

est to manage a population, as the framework to which they belong is used to predict emerging properties of population dynamic (population growth, survival, reproduction...) using computer programs simulating a biological population composed of interacting individuals with a behaviour defined by the modeller (Clark and Rose, 1997; Van Winkle et al., 1998; Breckling et al., 2005). These individual-based models heavily rely on the definition of the individual behaviour of the animals in relation to the environment. In particular, many of these models attempt to include the moving behaviour of the animals in relation with both the internal state of the animals (e.g. current energy reserves) and the environment (e.g. see Clark and Rose, 1997; Railsback, 2001). As noted by Railsback (2001), *movement rules are critical to realistic simulation of how individuals, and therefore population, respond to changes in habitat and population density*. Considering seriously autocorrelation in studies of GPS data will increase our knowledge into animal moving behaviour, and thereby allow a more efficient modelling of population dynamic.

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Paper II

ON THE USE OF TELEMETRY IN HABITAT SELECTION STUDIES

***Jodie Martin^{1,2,3*}, Vincent Tolon^{1,3,4}, Bram Van Moorter¹, Mathieu
Basille^{1,5} and Clément Calenge³***

¹ Université de Lyon, F-69000, Lyon ; Université Lyon 1 ; CNRS, UMR5558,
Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France.

² Department of Ecology and Natural Resource Management, Norwegian University of
Life Science, P.O. Box 5003, NO-1432 Ås, Norway

³ Office National de la Chasse et de la Faune Sauvage, 85 bis avenue de Wagram, BP
236, F-75822 Paris Cedex 17, France

⁴ Laboratoire d'Ecologie Alpine CNRS UMR5553, Université de Savoie, Bâtiment
Belledonne, F-73376 Le Bourget-du-Lac, France.

⁵ Centre for Conservation Biology, Department of Biology; Norwegian University of
Science and Technology; NO-7491 Trondheim, Norway

ABSTRACT

Understanding the relationships between organisms and their habitat is a central question in ecology. The study of habitat selection often refers to the *static* description of the pattern resulting from the selection process. However the very nature of this habitat selection process is *dynamic*, as it relies on individual movements, which are affected by both internal components (i.e. related to the animal itself, such as its behavior; foraging, resting, etc.) and external components (i.e. related to the composition of the environment). Coupling habitat selection and movement analyses should thus provide new insights into the proximal mechanisms and evolutionary causes of animals' space use.

To achieve this, the introduction of GPS technology in the early 1990s showed great promise, as it facilitates tracking of animals with high fix frequency over long time periods. From a statistical point of view, this led to an increased temporal *autocorrelation* in the positions of successive locations. Whereas classic approaches of habitat selection often relied on the assumption of statistical independence between relocations, the

* Corresponding author e-mail address : martin@biomserv.univ-lyon1.fr, jodiem@free.fr

development of newer methods has made possible the use of autocorrelation for more dynamic approaches. As several statistical tools are now available for researchers, autocorrelation can be incorporated successfully into the analysis, instead of being removed or even ignored. We emphasize the need to integrate individual behavioral mechanisms in habitat selection studies.

The use of GPS technology in wildlife management issues is, however, often motivated by its technological advantage to produce large amounts of data, rather than biological questions. We warn users of GPS devices about the statistical and conceptual changes induced by this technology used for studying habitat selection. We encourage a solid biological reflection about the ecological characteristics of studied species and spatial and temporal scales considered, before deciding on which sampling protocol and which telemetry technology to use in accordance with the biological question of interest.

INTRODUCTION

Understanding the relationships between organisms and their habitat is a central question in ecology. The habitat defines the available range of resources and living conditions for a species (Hall et al., 1997). Thus, the habitat potentially has an important impact on vital rates, such as survival and reproduction, which are directly related to population dynamics and evolution (Caswell, 2000). It is therefore crucial to study the mechanisms of habitat selection, i.e. the process by which animals actually choose specific habitat components within their environment. This process is recognized to be highly scale dependent; habitat selection at a given scale can be seen as the result of individual behavioral processes at finer scales (like movements), while at the same time it will be constrained by larger scale processes (like the geographical range of a species). In order to clarify the study of habitat selection, Johnson (1980) distinguished four levels or orders of selection, from the species' geographical range to the selection of food items, through individual home range establishment and patch selection within the home range. The higher levels, like the species' range, are governed mainly by population processes, whereas at lower levels individual choices are more important. To understand animal space use, ecologists have to investigate these multiple scales, often simultaneously (Johnson, 2002).

It has been recognized that both spatial and temporal scales are positively correlated (Holling, 1992). For example, distributional ranges of populations are necessarily defined at large spatial scales and the study of factors affecting large scale distribution of a given population requires knowledge of long-term population dynamics at large temporal scales. On the contrary, individual movement processes at fine spatial scales (e.g. within a home range) are considerably faster than population processes, and therefore need to be studied at much finer temporal resolutions.

Although “habitat selection” has been defined as a process, the study of habitat selection often refers to the *static* description of the pattern resulting from this process, i.e. “space occupancy”. For example, many individual-level studies dealt with the characteristics of the environment within home ranges (e.g. Mc Loughlin 2002 and 2004; Mitchell and Powell 2007). However, the very nature of the habitat selection process is *dynamic*, as it relies on individual movements, which are affected by internal and external components (such as individual state or vegetation types). Hence, habitat selection and movement processes are intimately related, because movement partly is driven by habitat selection, whereas habitat

selection is a consequence of movements. Coupling habitat selection and movement analyses should thus provide new insights into the proximal mechanisms and evolutionary causes of animals' space use.

To study the mechanistic aspects of individual habitat selection, it is therefore advisable to obtain and use detailed information on movements of individuals, based on a high frequency of relocations. The transition from a static to a more dynamic approach to habitat selection therefore can be achieved by increasing serial (or temporal) *autocorrelation* in the positions of successive locations (Swihart and Slade, 1985). The level of serial autocorrelation in datasets describes the importance of temporal structure in individual movements. In a dynamic approach of habitat selection, the spatio-temporal structure of relocations arising from more or less complex movements should be considered and studied (Frair et al. 2005), whereas in the static approach all relocations are considered to be temporally independent (Otis and White 1999). The choice to analyze habitat selection from a static or a dynamic point of view should be motivated by the biological questions of interest. Commonly, when studying habitat selection in a static way, autocorrelation is considered a nuisance that should be overcome (Morrison et al. 1998). The use of autocorrelation in habitat selection studies reflects a shift from the more classic static approach to a dynamic approach of habitat selection.

To study mechanisms of individual habitat selection, one possibility is to record movements by directly observing animals in their environment (e.g. Shine et al. 2004; Klaassen et al. 2006). However, this method of tracking animals requires many hours spent in the field, and cannot be done for elusive species, which are difficult to observe in their natural environment. Since its appearance in the early 1960s (Figure 1), VHF technology facilitated tracking of wildlife by providing researchers with a new tool to remotely detect individuals and then directly measure their location (consisting of a set of coordinates in the form of latitude x , longitude y , and time t) by homing or triangulation. This technology has been used successfully on elusive species. However, using this technology to estimate individual small-scale movements still requires a great deal of field effort (in terms of field work) to allow the collection of frequent relocations, and therefore often results in short-duration tracking (e.g. 1 location every 10 minutes for a couple of days, Nicholls and Racey 2006).

The introduction of GPS technology in the early 1990s, and its generalization at the turn of the century (Figure 1), showed great promise for studying processes of habitat selection. Thousands of relocations can now be stored on-board or even directly transmitted to the user, without relying on much human intervention after an animal is equipped with the tracking device. GPS technology, therefore, facilitates fine-scale tracking (relocations can be delivered up to every second, Fritz et al. 2003) of animals over longer time periods (e.g. 1 location every 3 hours for a whole year, Johnson et al. 2002). Although the accuracy of individual relocations obtained by GPS does not equal direct observations and measurements in the field, the accuracy obtained with recent GPS remains acceptable for most research purposes (around 20 meters). Hence, GPS technology facilitates the study of animal movement both at small and large spatial scales during long periods.

The purpose of this chapter is twofold. The first part is dedicated to the role of autocorrelation in habitat selection studies from the past till now. We demonstrate that, whereas temporal autocorrelation was first considered as a problem when studying habitat selection in a static way, the progressive combination of habitat selection and movement concepts have led to an increased use and interest in autocorrelation.

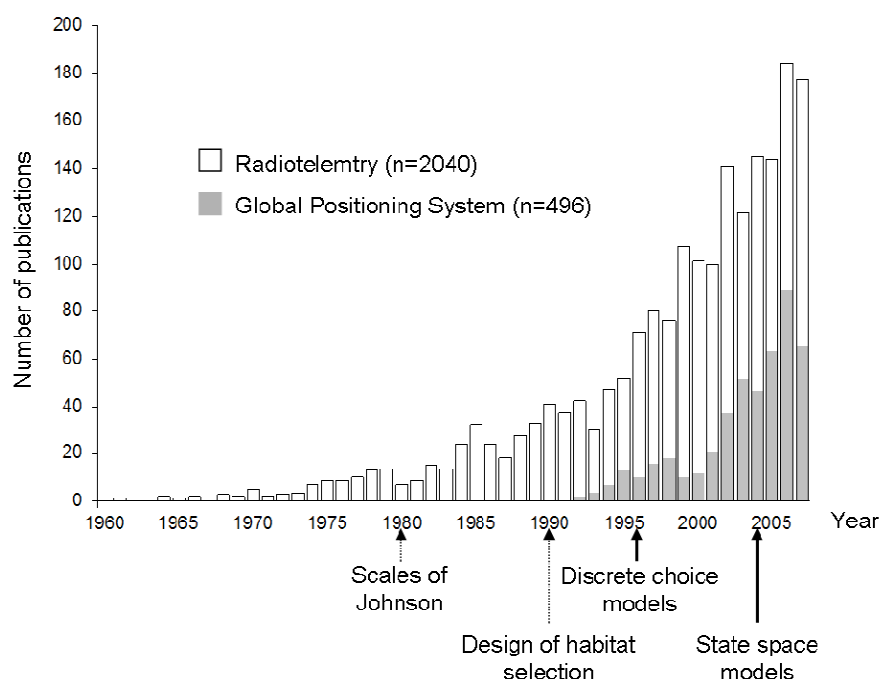


Figure 1. Trend in the number of publication including « radio telemetry » and « global positioning system ». The review was performed using the ISI Web of Knowledge with all data bases and was restricted to zoology, biodiversity and conservation, evolutionary biology and behavioral sciences. Dashed arrows represent the appearance of important concepts in habitat selection studies and black arrows the appearance of analytical methods.

As several statistical tools are now available for researchers, autocorrelation can be incorporated successfully in the analysis, instead of being removed or even ignored. We emphasize the need to integrate individual behavioral mechanisms into habitat selection studies. In the second part, we stress the importance of thorough reflections about biological questions before heading out into the field to deploy GPS collars. We provide some guidelines for the choice of monitoring technology in the context of habitat selection, regarding considerations of biological questions, spatio-temporal scales, and research costs.

1. TOWARDS THE USE OF AUTOCORRELATION IN INDIVIDUAL HABITAT SELECTION STUDIES

Johnson (1980) defined the selection of a habitat component as “*the process in which an animal actually chooses that component*”. Thus, tests of nonrandom habitat selection by individual animals usually compare used habitat components (the relocations of individuals, i.e. their actual habitat choice) with a null model describing the habitat components that could have been used alternatively by the individuals under the hypothesis of absence of habitat selection (i.e. random habitat use; Pendleton 1998, Millspaugh and Marzluff 2001, Boyce et

al. 2002). The latter components are called “available” components (Manly 2002). Rejection of this null model for the observed pattern allows the conclusion that a nonrandom process generated the observed data. At the scale of individual habitat selection, it is therefore crucial to define precisely what is available to animals, because the null model will depend directly on it.

Availability can be defined differently depending on whether the animals are identified or not (see Thomas and Taylor 1990, 2006, for an overview of the different study designs). In the case of identified animals (typically the case with telemetry), availability can be related to the selection order of concern: for second-order selection availability is defined at a population level, whereas for third-order selection availability is defined at an individual level (Aebischer et al. 1993). Several other factors may further affect availability. For example, movement capacity of animals is a factor that can restrict availability (Martin et al. 2008). The behavioral state of an animal is also a potential factor that can limit access to a particular area (e.g. resting animals). These factors therefore should be taken into account when determining which habitat components are available for use.

Classic statistical methods used to test habitat selection (e.g. logistic regression, log-linear regression, χ^2) assume independence between locations of a given individual (Johnson 1980, Thomas and Taylor 1990, Swihart and Slade 1997, Aebischer et al 1993, Alldredge and Ratti 1992, Pendleton et al 1998). In other words, individual relocations must not be spatially or temporally correlated. Dependency between relocations produces more similar values than expected by chance; as such, positive autocorrelation should result in underestimating the true variance. This induces an increased probability of type I error by inflating the number of degrees of freedom (Legendre 1993, Lennon 1999, Diniz-Filho et al. 2003, Martin et al. 2008), i.e. the null hypothesis (random habitat use) is rejected too frequently. The independence between relocations is often ensured by adopting a sufficiently large time lag between successive relocations, which circumvents the problem of autocorrelation. However, the growing use of GPS technology has led to a decrease in time intervals, and resulted in an increased serial autocorrelation.

1.1. From the Past. The Null Model as Random Locations: Autocorrelation as a Problem

Few statistical tools have been developed for individual data analyses; most of them being adapted from methods developed for second-order selection by unidentified individuals (Calenge 2005). For example, Manly et al. (2002) recommended estimating a Resource Selection Function (RSF) for each animal and then combining the results to infer conclusions at the population level. Means and variances for each individual are therefore estimated without considering autocorrelation between relocations and then averaged across animals to estimate population level selection parameters (Thomas and Taylor 2006). As a matter of fact, several authors considered autocorrelation not to be a concern if the statistical unit is the animal and not the animal's relocations (Alldredge and Ratti 1992, Aebischer 1993, Otis and White 1999). Indeed, there are several ways to deal with pseudo-replication when pooling a collection of relocations from several animals in analyses. However, temporal autocorrelation between individual relocations still remains a problem. When using relocations as sampling units, autocorrelation in the data makes variances and hypothesis tests no longer valid.

Therefore, tools that have been developed to test habitat selection at the population level still assume independence between relocations, i.e. a comparison of independent use points and independent available points (that is, randomly sampled in the study area; Figure 4a).

This problem is critically important in third-order selection, where the null model commonly is built using points randomly sampled within what is considered to be available. This will result, when important autocorrelation exists in the animal's relocations, in the comparison of used locations containing this autocorrelation structure with random available locations lacking such structure. Therefore, comparing autocorrelated data with uncorrelated data is not valid (Martin et al. 2008). An empirical demonstration of the effects of not considering autocorrelation in habitat selection studies has been conducted by Martin et al. (2008) on brown bears (*Ursus arctos*). They compared two extreme approaches to test third-order selection by individuals with autocorrelated data. Both approaches relied on the comparison of two datasets; an observed dataset of habitat used by individuals (through individual trajectories) and a simulated dataset (with the same number of relocations as the observed dataset) under the hypothesis of random habitat use. For each dataset, they estimated marginality (an index of the eccentricity of the used environmental conditions relative to the average available environmental conditions) and tolerance (an index of the range of used environmental condition compared to the range of available conditions), two measures of the strength of habitat selection (Doledec et al. 2000). In the first approach, simulated datasets did not take into account movement constraints affecting individuals, i.e. random relocations where points are randomly and independently sampled in the home range (corresponding to the classic approach). In the second approach, simulated datasets accounted for the observed shape of individual trajectories, i.e. simulations were carried out by randomly rotating the observed trajectories within the home range. The results obtained from the two approaches differed dramatically (Figure 2). The second approach (with unchanged trajectory shape) led to the conclusion that bears showed no selection of the variables considered in the analysis (i.e. the marginality of the observed dataset was not different from marginalities estimated from simulated datasets). On the contrary, the classic approach concluded that there was strong habitat selection (i.e. marginality of the observed dataset was significantly different from marginalities estimated using random locations from the home range) (see Figure 2). However, as noted by the authors, both approaches have their limitations, because neither of them took into account the nature of the autocorrelation between relocations. Indeed, the first one did not take any movement constraints into account and the second one kept the shape of the trajectory unchanged; in this later case both movement constraints and some actual habitat selection were included in the null model, which results in a too conservative testing of habitat selection. Therefore, this study highlights the risk of not accounting for autocorrelation in animal relocations by comparing them with an inappropriate null model.

As autocorrelation affects our ability to perform standard statistical procedures (Legendre 1993), it has often been advised to avoid autocorrelation in individual relocations (Morrison et al. 1998). Swihart and Slade (1985) developed a framework for analyzing independence between successive relocations in order to determine the time interval necessary to achieve statistical independence. They proposed using Schoener's (1981) ratio statistic (t^2/r^2 ; where t is the average distance between successive observations and r the average distance to the center of activity) to estimate the Time To Independence (TTI), i.e. the smallest time lag necessary to consider successive relocations as independent.

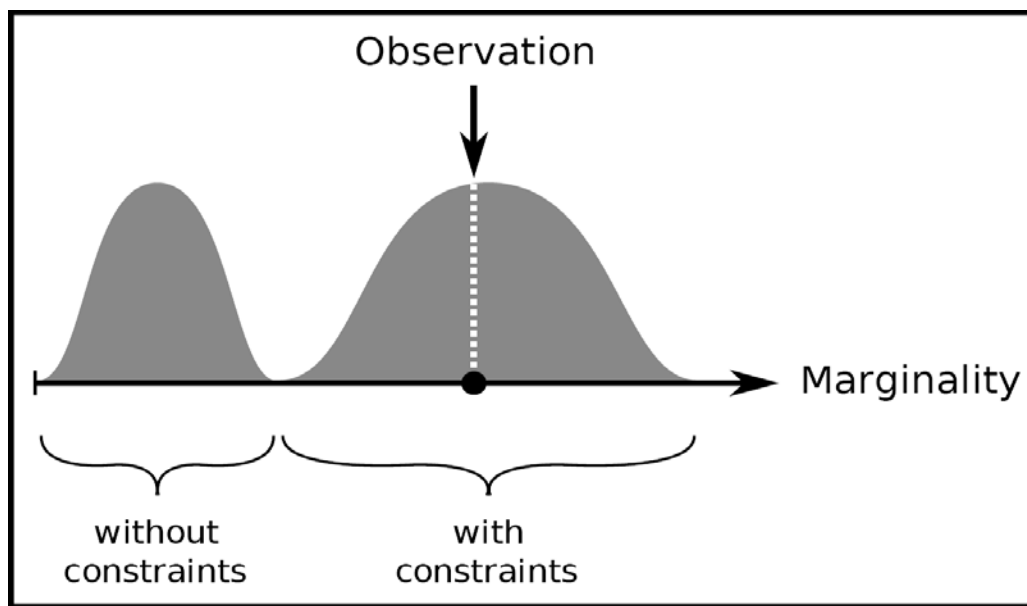


Figure 2. Martin et al. (2008) tested the marginality (deviation from the average conditions in the area) in habitat selection of female brown bears, following two tests. Both relied on the comparison of the observed dataset with datasets simulated under the hypothesis of random habitat use. The first analysis did not take movement constraints into account (simulations were carried out by randomly distributing a set of points in the home range), whereas the second analysis accounted for these constraints (simulations were carried out by building random trajectories within the home range). In the first case, the observation is out of the range of the simulations and would be considered significant, whereas it is not the case while taking into account constraints (after Martin et al. 2008).

Often, the TTI between consecutive fixes is considered as the time lag required by an animal to cross its entire home range (Swihart and Slade 1985, White and Garrot 1990). The problem of autocorrelation can then be effectively circumvented by sub-sampling data (Boyce et al. 2002) or adopting a sampling regime that uses the TTI as a criterion for independence between relocations. Unfortunately, subsampling data (which is not a problem in itself, because it only removes redundancy) inherently brings with it the loss of data which are, as every field biologist knows, expensive to collect. Moreover, several authors have shown that attempting to obtain independent data is not always possible and can lead to a loss of biological meaning (Rooney et al. 1998, De Solla et al. 1999).

Serial autocorrelation is linked intimately with the definition of availability for individuals. Hence, independence between individual relocations assumes that animals are free to move between two relocations across the area that the researcher considered available, meaning that this whole area (often the home range) is available at each step. But even if the time lag between two relocations is long enough for the animal to cross this area, behavioral constraints (e.g. need for rest, need for foraging, movement constraints) result in the fact that animals are not free to move everywhere every time in this area. An extreme example illustrates this; an animal never wakes up at the other side of its home range! Therefore, even if we statistically reach the TTI, we seldom reach the biological independence between relocations with telemetry data. Moreover, when there is no stable home range, there is no TTI, or the TTI might become very large, in which case subsampling will not provide a

solution to the problem. There is thus a need to create a statistical framework that allows taking into account spatio-temporal structures of individual relocations, i.e. explicitly incorporating autocorrelation into models (Legendre 1993). Today, with the increased use of intensive sampling protocols, we can no longer consider fixes as independent relocations, but instead should consider them as trajectories. Analyses of animal movements are therefore needed in order to proceed with habitat selection.

1.2. The Present. The Null Model is a Random Walk: Accounting for Serial Autocorrelation

1.2.1. Analyses of Animal Movement

An animal's movement is a continuous path in space and time, but a discrete representation of the path facilitates its analysis (Figure 3a; Turchin 1998). Often, relocations are recorded with a fixed time interval and the straight-line moves between consecutive fixes are referred to as steps. The sequence of steps then provides the basic units for further analysis of the path (Turchin 1998). Several descriptors then can be used to describe the step series; most frequently used are step lengths and turning angles (see Figure 3b) and their distributions can be used to characterize animal movement paths. Accordingly, movement types can be identified based on these distributions. For example, intensive search movements can be characterized by short steps and low directionality of the turning angles, whereas exploratory movement steps will be long and have a high directionality in their turning angles.

The statistical framework for animal movement path analyses is based on the comparison of empirical data with a theoretical null model. Several theoretical movement models have been developed that could be used as reference. Each of these models has different statistical properties, and often different assumptions about the independence (i.e. absence of serial autocorrelation) of specific movement descriptors (like step length or relative turning angles). The observed movement characteristics are then compared with the theoretical ones and departure from these models allows inference of biological conclusions about animal behavior (Franke et al. 2004, see below). The mere random walk (RW) is the simplest null model of movement which can be used to model animal movement through a homogeneous environment (Turchin 1998; Figure 4b). It relies on the independence of all descriptors, and thus it assumes the absence of serial correlation between successive steps. Therefore a random walk does not take into account the natural tendency of animals to go forward and is therefore not very accurate to represent most of animal movement, especially at short time intervals (Turchin, 1998; Bovet and Benhamou, 1988). Today, the most widely used theoretical model is the correlated random walk (CRW), which differs from the RW in that absolute angles are generally dependent, whereas the relative or turning angles are assumed to be independent (Turchin 1998; Bovet and Benhamou, 1988). The distribution of turning angles is centered on 0, resulting in a forward persistence in the direction of movements. The direction of the previous step thus influences the direction of the following step.

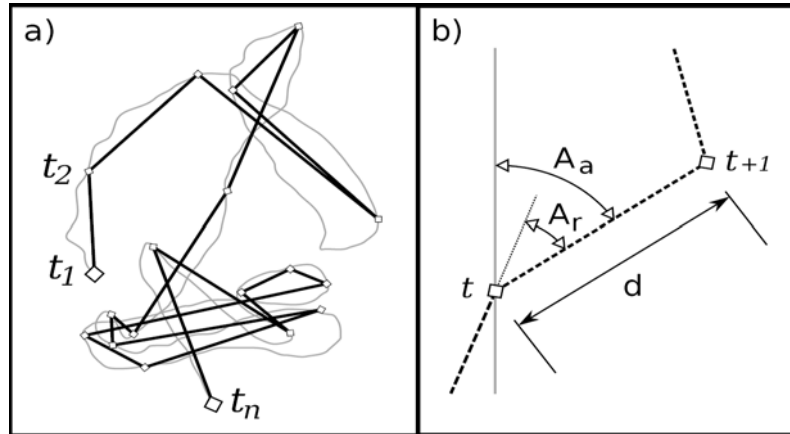


Figure 3: a) Representation of a movement path. In gray: actual path; in black: discrete representation of the path. A movement path is defined by a set of successive relocations, characterized by their position (generally latitude and longitude). Each movement between two successive relocations (i.e. between time t and $t+1$) describes steps. b) Examples of movement path descriptors: d is the distance between 2 relocations; A_r is the turning angle (or relative angle), i.e. the angle between the direction of the previous step (small dashed line) and the actual one; A_a is the absolute angle, i.e. the angle between a given direction (gray line) and the direction of the actual step.

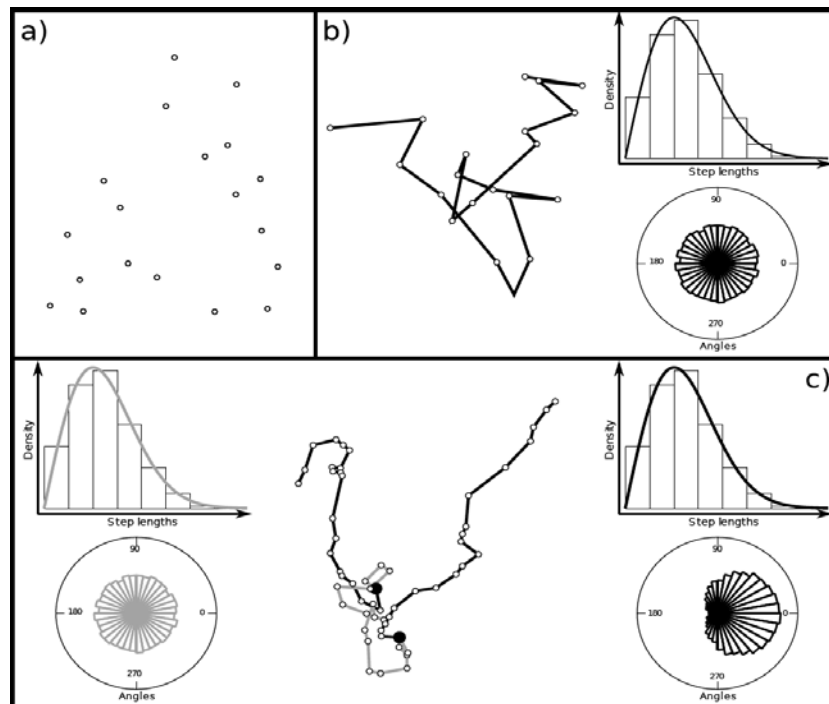


Figure 4: a) The null model as a set of locations randomly sampled in the study area; b) The null model as a random walk, where the whole trajectory can be characterized by step length distribution (top right) and turning angle distribution (lower right); c) The null model as a mixture of two random walks. In gray, a mere random walk, characterized by a uniform distribution of turning angles and normally distributed step lengths; in black a correlated random walk characterized by a distribution of turning angles centered around 0 (forward persistence) and normally distributed step length.

1.2.2. Discrete-Choice Models

Some authors have started to take serial autocorrelation into account by defining habitat availability separately for each relocation in the so-called “discrete-choice models” framework (Arthur et al. 1996, Hjermmann 2000, Fortin et al. 2005, Rhodes et al. 2005). The test for nonrandom habitat selection is derived from a comparison of random locations from this fix-specific availability with the actual chosen locations. In this case, the null model consists of random locations with serial autocorrelation, similar to the class of random walk models. Different authors have used different methods to determine availability, corresponding to different types of random walks. The simplest approach involves determining a circle around a fix of available locations (e.g. the availability radius of Arthur 1996); in this case there is no directional persistence. Alternatively, the observed distributions of step lengths and turning angles have been used to define availability. Even more complex relationships are possible with a dependence of availability on the time interval between fixes or habitat characteristics (Hjermmann 2000).

It is therefore assumed that for a given time lag between two relocations, the animal has access only to areas close to the current position, and not to its complete home range (Arthur et al. 1996). In the same perspective, Cooper and Millspaugh (1999) adopted a statistical technique derived from the field of economics that allows researchers to define availability separately for each animal observation. At each relocation, a unique set of habitat or resources is available, called the “choice set”. Fortin et al. (2005) also developed a simple statistical approach that incorporates movement into a logistic regression framework. This method, called Step Selection Function, considers steps (displacement between two relocations) as sampling units, each of them being contrasted with n random steps, which are defined using the observed distributions of step lengths and turning angles.

This approach partially resolves the statistical and biological issues of serial autocorrelation of relocation data. Indeed, this procedure only considers first-order autocorrelation, i.e. dependence between relocations at time t and $t-1$ only, and deems the successive steps as independent (Martin et al. 2008). However, the nature of the dependence between all the relocations making up the whole trajectory is seldom analyzed, as noted by Calenge (2005). Martin et al. (2008) stressed that positions of individuals are the results of three effects: (i) intrinsic constraints (e.g. movement capacity, activity patterns, internal state), (ii) extrinsic constraints (e.g. environmental or artificial barrier) and (iii) habitat selection behavior (the animal is in a particular habitat because it is “suitable” for it at this moment). Therefore, testing differences between used and available points suppose knowledge of the processes that generate data without any habitat selection, i.e. null model under the hypothesis of no habitat selection, by taking into account the internal constraints of animals that partly shape the trajectory. However, habitat selection analyses rarely take into account intrinsic and extrinsic constraints (Martin et al. 2008; see Matthiopoulos (2003) for an example accounting for movement and extrinsic constraints). In general, researchers aggregate data from different behavioral states and, therefore, their conclusions on habitat selection result from the joint selection of both activity and habitat components (Cooper and Millspaugh 2001). As habitat selection and animal behavior are closely related, there is need for a statistical approach that includes spatio-temporal aspects of individual behavior (Thomas and Taylor 2006, Martin et al. 2008).

1.3. Into the Future. The Null Model is a Mixture of Random Walks: Autocorrelation as a Paradigm

1.3.1. Nonstationarity, an Interesting Property of Many Animal Trajectories

As movements and activities are closely related, movement processes tend to be different according to the animal's behavioral state. For instance, during foraging activity an animal may have shorter and more sinuous movements than during transitions between patches of resources, where it should have directed and faster movements. As an illustration, consider a bee foraging on a patch of flowers. Movements between flowers will be short and sinuous compared with movement between patches of flowers or between the patch and the hive. Franke et al. (2004) used differences in movement characteristics to differentiate behavioral states of woodland caribou; they distinguished bedding, feeding and displacements. Indeed, for given spatial and temporal scales, we can consider most animal trajectories as a succession of different types of movement corresponding to specific activities, each of them being characterized by its own statistical properties (Figure 4c). However, trajectories can remain unchanged for different activities defined at very fine temporal scales (animals can switch quickly between foraging and vigilance while keeping the same type of movement). But at longer temporal scales, major activities, such as foraging, exploring, or resting, often correspond to specific movement types.

A statistical process is said to be nonstationary if the statistical properties of the process generating the trajectory change over time. Therefore, a trajectory composed of different movement types may be considered to have been generated by a nonstationary process. This implies that the definition of availability should be different according to the state of the individual. Indeed, an animal that is foraging or resting does not have the same available habitat as when it is searching for mates or patrolling its territory. Therefore, this nonstationarity is of major interest, because it provides information on animal behavior and activities. This nonstationarity of the process is often the cause of the autocorrelation in the data.

1.3.2. Building Movement Models as Mixtures of Random Walks

Each movement type trajectory potentially can be represented by a different theoretical model based on its properties. The trajectory can then be modeled as a succession of these movement models (Figure 4c). It is therefore important to partition the whole trajectory into different pieces of stationary paths, with stable mathematical properties. Typically, each of these stationary paths corresponds to a certain type of behavior. To date, several methods have been developed and used for this partitioning of trajectories, for instance First Passage Time (Fauchald and Tveraa 2003), fractal dimension (Nams and Bourgeois 2004), and State Space Modeling (Patterson et al., 2007). First Passage Time, for instance, has been used as a method to detect Area-Restricted Search (ARS) behaviors, which can occur when an animal encounters a food-rich resource patch. More recently, state-space models based on hidden Markov models have become more popular for extraction of behavioral states from movement paths (reviewed by Patterson et al. 2007). For example, Morales et al. (2004) employed state-space models to highlight a biphasic movement for elk (*Cervus elaphus*); the

“encamped” movement with small movements and sharp turns and the “exploratory” movements with longer directed movements. They modeled elk movement by fitting a mixture of random walk models with different properties, each model corresponding to a different behavioral state. However, these approaches often assume a constant probability of animal behavior changes (“switching probability”), or at least assume prior knowledge of factors that could potentially affect this switching probability (e.g. constraints on hourly activity patterns or environmental features, Morales et al. 2004). Such methods therefore require prior exploratory analyses of factors potentially influencing the shape structure of the trajectory.

1.3.3. Some Recommendations

In order to test third-order habitat selection with highly autocorrelated data, we stress that an in-depth analysis of the characteristics of individual trajectories is an important step towards a more accurate analysis of habitat selection process. Autocorrelation between relocations should not be removed or avoided, but rather integrated into a statistical framework. Discrete-choice models are a first step toward this integration, but only consider the first degree of autocorrelation to create the null model. Therefore, they do not take into account the behavioral state of individuals, which potentially may affect habitat selection behavior. We emphasize the need to analyze the rules of animal movement using partitioning methods based on the division of the whole trajectory into homogeneous movement bouts. Each of these movement bouts can then be characterized by a probability distribution for each descriptor (e.g. step length, turning angles). Then, for each relocation belonging to a particular behavioral state, availability can be estimated more precisely using the corresponding movement characteristics for this state. These state-movement analyses are required to build more realistic null models of random habitat selection that take into account behavioral constraints.

2. GPS TECHNOLOGY: A DOUBLE-EDGED SWORD

The appearance of new technologies has resulted in important advances in many scientific fields, as it offers new opportunities to answer more questions. Since the early 1990s, GPS technology has facilitated the measure of fine-scale movements of elusive animals in their natural environments over long time periods. Especially, it aids in our understanding of the link between fine-scale behavioral movement mechanisms and the actual distributions of animals. However, scientists, wildlife managers, and conservationists should be careful before adopting this technology. Even though GPS technology is appealing, the choice of the monitoring tool should be the consequence of a well-defined biological question. Such careful planning could aid the avoidance of mismatches between the question of interest and the type of data collected using a particular tool. Compared to older technologies (especially VHF) the use of GPS technology offers many advantages, but also induces different constraints and is not necessarily the adequate tool for every question about animal movements or distributions. Above all, the choice of the appropriate tool to record an

animal's locations should be directly dependent on the sampling protocol defined itself by the question of interest. Irrespective of the biological question or sampling protocol, it is an accepted fact that the number of equipped individuals should be as large as possible in order to increase the generality of the findings. Two other parameters can then vary according to the question of interest: the time lag between relocations and the study period. In the following, we will discuss the relationships between biological question, sampling protocols, and choice of the adequate tool to record animal locations.

2.1. Individual Variability

The ecological characteristics of the focus species and especially the ratio of inter/intra-individual variability in habitat selection can help determine the best sampling protocol and therefore the right tool to track animals in their environment. Girard et al. (2006) showed in their study that the number of animals is more important to assess habitat selection than is the number of fixes per animal. They obtained accurate habitat selection by moose with fix frequencies of only 1-7 per week, whereas often more than 15 individuals were needed to generalize the findings over the population. This suggests that, for generalist species with high inter-individual variability, it is important to obtain data from many individuals to assess habitat selection. On the contrary, if there is a strong intra-individual variability, the number of relocations obtained for each individual can become as important as the number of tracked individuals. Thus, knowledge about the biology of the species will influence the choice of sampling protocol (number of samples per individual versus number of sampled individuals) and, by consequence, the monitoring technology.

2.2. A Matter of Scale

The fix frequency of a telemetry protocol and the study period are generally a direct consequence of the scale of the study: questions regarding small-scale movements require high fix frequency (e.g. 1 point every second for a fractal analysis of albatrosses' movements, Fritz et al. 2003). In the beginning of this chapter we discussed the interest to combine fine-scale movement analyses with habitat selection studies. In this context, increased fix frequency may facilitate a more profound investigation of animal behavior. Moreover, the study duration may be long enough to explore the link between fine-scale behaviors and habitat selection at longer time scales.

However, many questions in ecology do not rely directly on fine-scale behaviors of animals. Large-scale distributional questions can be answered with a lower fix frequency (e.g. 1 point every 3 weeks for an analysis of home range composition and habitat use, McLoughlin et al. 2005). Important in the context of conservation and population dynamics in general is the linkage between habitat and animal performance (McLoughlin et al. 2005), for example to identify critical habitats for population viability in conservation biology (e.g. Akçakaya 1995). Mere occurrence has been shown to be misleading in some situations. For instance, an attractive sink is a habitat that is selected despite the lower performance experienced by the animals occupying it (Delibes et al. 2001). It can, therefore, be argued that to assess the existence of such attractive sinks, the measurement of performance is critical.

Performance of animals, e.g. lifetime reproductive success, however is defined over quite long time scales and often is related to large-scale distribution patterns (e.g. habitat use, Conradt et al. 1999, home range composition, McLoughling et al. 2007). These measures of space occupancy do not require fine-scale measures of animals' movements. Instead, a high number of individuals is often needed to highlight relationships between their performance and habitat. In this context it might be more interesting to invest less in fix frequency and more in number of tracked individuals.

2.3. Main Costs and Benefits of GPS Technologies

Tools and sampling protocols are intimately related, they often involve trade-offs between costs and perfect match. Prior to the selection of a telemetry technology, researchers should think about the associated costs and benefits (in terms of correspondence with the defined protocol) of the use of different tools within the biological context of the question. In theory, any study using VHF tracking by triangulation could be done with GPS tracking instead. That is, GPS collars potentially can deliver the exact same data (regarding frequency and time-lag) as VHF collars, whereas the reverse is not necessarily true over a long period. That being said, a study using telemetry will cover three main budget compartments; capture, equipment, and operation costs. We will consider only the case of nonlimiting captures, as it potentially involves limiting equipment and operating costs directly related to the monitoring technology to be chosen.

The cost of equipment to monitor one animal is considerably higher with GPS technology than with VHF technology; GPS-tracking devices are approximately 10 times more expensive than VHF devices. However, with GPS devices the collection of data is automated, whereas VHF devices require human intervention to be effective; relocations are usually collected by triangulation of the signal, which implies a relatively high time and financial investment in the field. This results in limited operation costs of GPS technology (even with the use of a GSM device to download the data) as compared to VHF technology, especially for high fix frequencies. At a fixed cost, GPS technology, therefore, leads to an increase in sampling intensity compared to VHF technology. However, when the budget of the study is limited, this is often at the cost of lower numbers of individuals monitored (Figure 5). It is thus important to take into account these considerations of costs before deciding upon the adequate tool to choose for the sampling protocol.

2.4. Some Recommendations

When a large number of relocations per animal must be collected, GPS technology can provide adequate data, thanks to the automation of the process. This technology is particularly useful when fine-scale movements of animals need to be recorded, especially over long periods of time. This tool is, therefore, most appropriate to study dynamic aspects of habitat selection, as reported in this chapter. However, when the number of individuals is critical (as for generalist species, see above), and no intensive tracking is required, other tools can be more appropriate (e.g. VHF). For example, when ecologists must link habitat selection and animal performance on long time scales, it is better to invest in more individuals, tracking

duration, and field personnel to obtain the essential animal performance measures (source of mortality, breeding, litter size, etc.). The GPS technology does not seem to be the best tool for this task and VHF tools combined with direct observations can provide sufficient locations per animals to estimate their habitat selection at a large spatio-temporal scale. In this case, the savings made on equipment can be used to increase the number of tracked individuals. In general, at constant costs, what is gained in sampling intensity with GPS technology, on one hand is lost in generality on the other hand.

It should be noted, however, that the increased fix frequency obtained by using GPS-tracking might prove useful in determining animal performance using their movement patterns. GPS-tracking can be used to assess foraging success in particular cases. For instance, it is now commonly used to determine kill sites by large predators (e.g. cougar (*Felis concolor*), Anderson and Lindzey 2003; wolf (*Canis lupus*), Sand et al. 2005). These applications require previous calibration and validation of the models on the field. These examples are likely only the top of the proverbial iceberg of potential applications; we can expect more applications with our increasing knowledge of how movement patterns change with specific factors, like the presence of offspring etc.

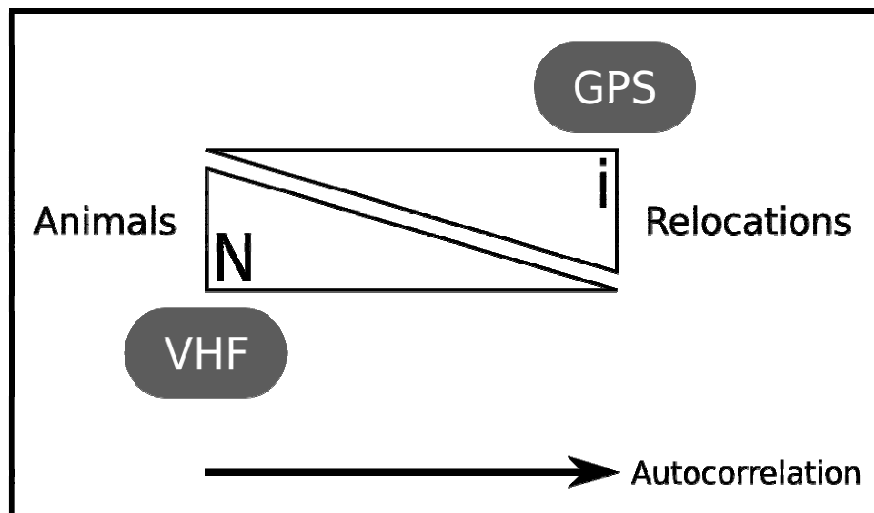


Figure 5. The sampling strategy, at a fixed cost, is the result of a trade-off between the number of individuals marked (N) and the number of relocations per individual (i). Typically, VHF monitoring allows a large number of individuals with fewer relocations per individual (thus no autocorrelation), whereas GPS monitoring allows fewer individuals with more relocations (thus autocorrelation).

CONCLUSION

Despite some budget limitations, GPS technology offers interesting avenues for our understanding of the habitat selection process. The shorter time intervals between relocations allow for the study of more rapidly changing decisions of habitat selection at small spatio-temporal scales. The increased temporal autocorrelation also allows the detailed investigation of different behavioral states with different movement characteristics. Whereas *static* approaches of habitat selection often rely on the assumption of statistical independence of

relocations, the development of newer methods, driven by the collection of relocations with a shorter time lag, now allow the use of autocorrelation for more *dynamic* approaches. We expect such dynamic habitat selection studies to become even more common in the near future, as ecologists become more familiar with the use of methods from time-series analysis like state-space models (Patterson et al. 2008). Coupling habitat selection and movement analyses should provide new perspective to understand how individuals react to environmental heterogeneity during their lifetime.

The use of GPS technology in wildlife management or conservation issues, however, often is motivated by technological advantage rather than biological questions. The appealing nature of GPS data (through higher precision and frequency, as well as automation of the data collection) often results in sampling strategies targeting large amounts of data. This often leads afterwards to data-dredging that can cause mismatches between the scale of the monitoring and the scale of the biological processes of interest. We warn every user of GPS devices about the statistical and conceptual changes induced by this technology used for studying habitat selection (Figure 5). In answer to the potential increase in autocorrelation due to higher fix frequency following technological developments in telemetry, we call for a paradigmatic shift in the study of animal habitat selection from static patterns towards dynamic processes. Especially with critical management or conservation issues, we stress that every ecologist should take care to start from the biological question at hand in making his choice of the most appropriate monitoring technology.

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Paper III

SCALE-DEPENDENT EFFECTS OF HUMAN DISTURBANCE ON LARGE MAMMALS: BROWN BEARS IN SCANDINAVIA

Jodie MARTIN^{1,2,3*}, Mathieu BASILLE^{1,4}, Jonas KINDBERG⁵, Bram VAN MOORTER⁴, Dominique ALLAINÉ¹ & Jon E. SWENSON^{2,6}

¹ Université de Lyon, F-69000, Lyon ; Université Lyon 1 ; CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France.

² Department of Ecology and Natural Resource Management, Norwegian University of Life Science, P.O. Box 5003, NO-1432 Ås, Norway

³ Office National de la Chasse et de la Faune Sauvage, 85 bis avenue de Wagram, BP 236, F-75822 Paris Cedex 17, France

⁴ Centre for Conservation Biology, Department of Biology; Norwegian University of Science and Technology; NO-7491 Trondheim, Norway

⁵ Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden

⁶ Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

ABSTRACT

Habitat selection is a complex process occurring at different spatio-temporal scales. Studies on habitat selection should consider effects of spatial scale and temporal variability. Failing to do so may reduce considerably the power to detect important fine-scale habitat selection behaviours, as is illustrated by our analyses. In this study, we investigated habitat selection of Scandinavian female brown bears *Ursus arctos* at two spatial scales: (1) establishment of home ranges and (2) use of habitat within home ranges, using Global Positioning System (GPS) data and K-select analyses. Previous research has suggested that most important limiting factors should be selected for at coarser scales. Our hypothesis, that females should avoid human disturbance (to improve their survival) when they establish their home range, was rejected. Low environmental heterogeneity and social constraints in bear populations may limit the opportunity for home-range selection. Our hypothesis that females should select habitats within their home range that provide ample food resources and minimize human-caused disturbance was supported, demonstrating important habitat selection at this fine spatial scale. In addition, our temporal analysis of habitat selection in relation to changing environmental conditions revealed an avoidance of disturbed areas and a selection of rugged terrain by bears during periods of highest human disturbance. Our study clearly demonstrates the importance of considering the temporal changes in the animal's environment for the process of habitat selection, especially at fine spatial scales.

Keywords: Hierarchical; Brown bear; *Ursus arctos*; Spatial scale; Temporal scale

* Correspondence : martin@biomserv.univ-lyon1.fr, Tel : + 33 04 72 43 35 84, Fax: +33 04 72 43 13 88

INTRODUCTION

Habitat selection is a hierarchical process that is not necessarily consistent across scales (e.g. Boyce, et al. 2003, McLoughlin, et al. 2002, McLoughlin, et al. 2004, Schaefer and Messier 1995). Indeed, different key factors may be involved according to the scale considered (Orians and Wittenberger 1991), therefore, it is important to determine the differences at multiple scales (Boyce, et al. 2003, Thomas and Taylor 1990). Johnson (1980) distinguished four orders of selection through spatial scales from geographical distribution of the species, over home range selection and patch selection within the home range to the selection of individual items (e.g. food items or bedding sites) within habitat patches composing individual home ranges.

Rettie and Messier (2000) suggested that the most important limiting factors should be selected at coarser scales. According to these authors, a limiting factor dominating at a large scale should dominate selective behaviour until it becomes less important than the next most important limiting factor. Often, decisions at large scales reveal avoidance of predation or disturbance, whereas occurrence of food resources drives selection at finer scales (see e.g. May, et al. 2006, Rettie and Messier 2000). A complete understanding of the relationship between animals and their environment only can be appreciated after analysis at multiple spatial scales (Bowyer and Kie 2006), which could also greatly improve the effectiveness of management or conservation strategies.

Although the influence of large-scale changes in environment (e.g. seasonal variation) on individual space occupancy has been well studied, short-term changes in environment (e.g. daily variations) that may influence animal behaviour at fine scale have been rarely investigated (however, Paukert and Willis 2002). For species living in human-dominated landscape, human influence is an important component of habitat. Typically, human activity varies along the day, being high during daylight and lower during the night. For species sensitive to human disturbance, these variations may provide important temporal changes in habitat selection behaviour. However, studies aiming at assessing hierarchical aspect of habitat selection often consider spatial component only. Failure to detect selection for a particular habitat component at a fine scale may result from temporal changes in the habitat selection process due to either changing environmental conditions or changing internal states (Moe et al. 2007).

After almost having become extinct by the end of the 19th century due to overharvesting and habitat exploitation by humans, the Scandinavian brown bear *Ursus arctos* population

started to recover in the early 1900s as bounties were removed and protection policies were adopted (Linnell, et al. 2001, Swenson, et al. 1994, Swenson, et al. 1995, Swenson, et al. 1998). Today, the population has grown to a substantial size (2000-3000 individuals throughout Scandinavia, Kindberg, et al. 2006) and the still increasing population size is accompanied by an expanding distributional range. Consequently, bears are colonizing more human-dominated landscapes, with large networks of roads, higher human densities, and concentrations of recreational cabins (Statistics Sweden 2003). Bear mortality is widely recognized to be mainly induced by humans (Wiegand, et al. 1998, Woodroffe and Ginsberg 1998). Moreover, the Scandinavian brown bear population is hunted (Bischof, et al. 2008). Reproduction, however, is limited by both food resources (Hilderbrand, et al. 2000) and male infanticide (Swenson, et al. 1997). For long-lived species with low reproductive rates, it has been shown that survival is the most critical demographic parameter influencing population dynamics (see Gaillard et al., 2005). Following the hypothesis of Rettie and Messier (2000), bears should therefore avoid human disturbance at larger spatial scales, whereas food resources should be selected at finer scales. Previous studies of bear distribution in Scandinavia demonstrated the avoidance of high human density and infrastructures and a selection of forested areas and rugged terrain (Katajisto 2006, Nellemann, et al. 2007). Thus, the results from these studies are in agreement with the assertions of Rettie and Messier (2000) concerning selection of the most limiting factor at larger spatial scale, i.e. human influence. However, selection for forested areas not only indicates an avoidance of human presence, but also a selection for areas that provide food resources. In this study, we further explored habitat selection of Scandinavian female brown bears at the individual level to evaluate the influence of habitat variables across different spatial scales. We used a hierarchical approach to investigate factors affecting (1) the position of the home range location within the southern range of the population (Figure 1), and (2) the habitats used within the home range, corresponding to home-range and patch selection, respectively. We hypothesized that (i) bears should avoid human disturbance when establishing their home range and (ii) decisions regarding use of space at a finer scale should correspond to habitat components providing abundant food resources (Dahle, et al. 1998). Several important food items in the Scandinavian brown bears' diet occur in regenerating forests. These forest stands harbour numerous species of ants (Rolstad, et al. 1998, Rolstad, et al. 2000), more diverse and abundant herbaceous materials (Apps, et al. 2004, Nielsen, et al. 2004), and promote grasses, herbs and crowberries *Empetrum spp* (Mallik 2003, Rolstad, et al. 2000). In addition, moose *Alces alces*, whose calves are predated by bears, forage preferably in regenerating forest

stands and clear-cuts (Cassing, et al. 2006, Edenius, et al. 2002, Nikula, et al. 2004). We therefore expected bears to select for these forest stands within their home range. We also investigated (3) fine-scale habitat selection on a daily basis. Humans should disturb bears at fine spatial and temporal scales. We thus expect that (iii) bears should escape human influence during period of high human activity, which takes place during daylight. Specifically, we investigated whether bears avoided human disturbance and selected for habitat features offering improved security. Notably, slopes can provide increase security for bears (Apps, et al. 2004, Nellemann, et al. 2007) by increasing the detection range due to increased visibility and more olfactory information delivered by the wind (S. Brunberg, Pers. Com.), therefore, we expect selection of steeper slopes during daylight hours.

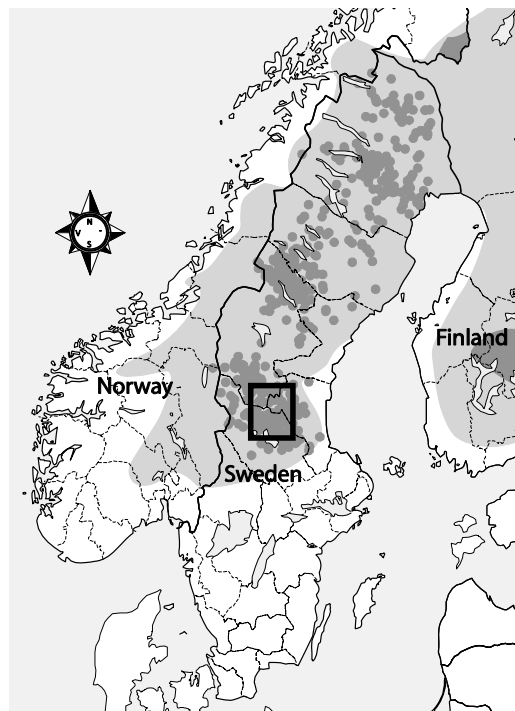


Figure 1: Distribution of bears (light grey) and locations of shot female brown bears (grey dots) in Scandinavia. The black rectangle represents the study area.

MATERIAL AND METHODS

Data

Study area

The study was conducted in the southernmost reproductive core area of the Scandinavian brown bear population in Dalarna and Gävleborg counties, south-central Sweden (61°N, 15°E, Figure 1). The study area consists primarily of intensively managed coniferous forest (80 %) in patches of different age stands, ranging from recent clearcuts to 90-100 years old trees (Swenson, et al. 1999). The other main land cover types are lakes and bogs. The terrain is hilly and the altitudinal gradient increases gradual from 175 m in the southeast to 725 m in the northwest. Human settlements are concentrated in the north and south with only few high-traffic roads crossing the study area. However, isolated houses and both paved and gravel roads with low traffic volumes are distributed throughout the whole study area.

Individual tracking data

We used relocations of 23 solitary adult female brown bears (3 to 14 years old) from May to August in 2006 (2 females), 2007 (9 females) and 2008 (12 females). Females were darted from a helicopter using a remote drug delivery system (Dan-inject®) shortly after den emergence in mid-April. For more details on drug protocols, see Arnemo (2005). During immobilization, females were equipped with GPS-GSM collars (Vectronic®) scheduled to take a fix every 30 minutes (i.e. 48 relocations per day). Location errors are inherent with this kind of data, which can potentially induce bias in habitat analysis. We therefore eliminated potentially large location errors by data screening based on two-dimensional (2D) and three-dimensional (3D) fixes in relation to the positional dilution of precision (PDOP) (Lewis, et al. 2007); 3D positions having a PDOP > 15 and 2D positions having a PDOP > 5 were removed. Due to missing data and large error positions, we obtained 80% of the theoretical number of fixes in average. As we used a resolution of 200 m × 200 m, the remnant GPS error became negligible.

Environmental data

The environmental data for the study area were available with a resolution of 200 m × 200 m square pixels; each pixel was characterized by 7 variables related to topography, vegetation and human disturbance (Table 1). A Digital Elevation Model was available for the whole

study area (GSD–Höjddkurvor, 25m ekvidistans Lantmäteriet, Sweden) and used to derive slope. The CORINE Land Cover map (CLC00) was used to define six vegetation types and then distances to each type. Maps of distances to anthropogenic structures (low- and high-traffic roads, houses and settlements) were derived from digital data of Sweden (GSD-Översiktskartan, Lantmäteriet, Sweden).

To assess the potential influence of human disturbance on habitat selection during the day, we computed an index of human disturbance, based on distances to anthropogenic structures (low- and high-traffic roads, houses and settlements). We computed a Principal Component Analysis (PCA) on the four variables and used the first axis of the analysis as synthetic index of human disturbance. ArcView version 3.2a (ESRI Inc., Redlands, California, USA) was used for preliminary preparation of environmental data.

Table 1: Description, proportion and label of the different habitat variables used in the analyses of habitat selection of female brown bears in south-central Sweden.

Habitat variables	Description	Label
Distance to vegetation type	Coniferous forest (66%)	Mainly Scot pines (<i>Pinus sylvestris</i>) and Norway Spruce (<i>Picea abies</i>) D_Conif
	Regenerating forest (19%)	Young aged stands forests from clear-cut to young forest D_Reg_for
	Wetlands (7%)	Mainly peat bogs (99.5%) D_Wet
	Water (5%)	Mainly water bodies (98%) D_Lake
Elevation	Digital elevation data in meter	Elev
Slope	Slope in degrees, derived from Digital Elevation model	Slope
Distance to high-traffic roads	Linear distance to public roads in km	D_high_traffic
Distance to low-traffic roads	Linear distance to private roads in km	D_low_traffic
Distance to houses	Linear distance to houses in km	D_houses
Distance to settlements	Linear distance to human settlements (small villages) in km	D_settle

Data analyses

Hierarchical habitat selection

We used a factorial analysis, the K-select, (Figure 2, Calenge, et al. 2005) to study home-range and within home-range habitat selection by female brown bears. For each animal, the strength of habitat selection was assessed using marginality, i.e. the difference between the mean environmental conditions used by each individual and the mean environmental conditions available to them. For the selection of the home range, the whole study area was considered to be available to all animals and the home ranges (estimated using the classical method of Minimum Convex Polygon (Mohr 1947) with the 5% outermost relocations excluded) represented the utilisation, whereas for the within home-range selection, the home range itself was considered available and the utilisation was measured using the relocations directly. A Principal Component Analysis (PCA) was then run on the marginality vectors and returned a linear combination of the environmental variables that maximised the mean marginality, and thus extracted most of the habitat selection. If all animals have the same pattern of habitat requirements, all their marginality vectors will be oriented in the same direction and the mean marginality explained by the first axis will be high. The marginality explained by the first axis decreases as the variability in individuals' habitat use increases. See Calenge et al. (2005) for details on mathematical procedures of K-select. All analyses were carried out using R (R Development Core Team 2007) and the package “adehabitat” (Calenge 2006).

Time and home-range effects on small-scale habitat selection

As discussed above, we expect small-scale habitat selection to depend on the changes in the environment. Some environmental variables, like human disturbance, show marked diurnal changes, therefore we investigated changes throughout the day of small-scale selection of the disturbance effect.

The results from our previous analysis suggested further analysis of the interaction between selection of the home range and selection within the home range. Therefore, we analysed the relationship between the structuring variables of home range selection and those within the home range.

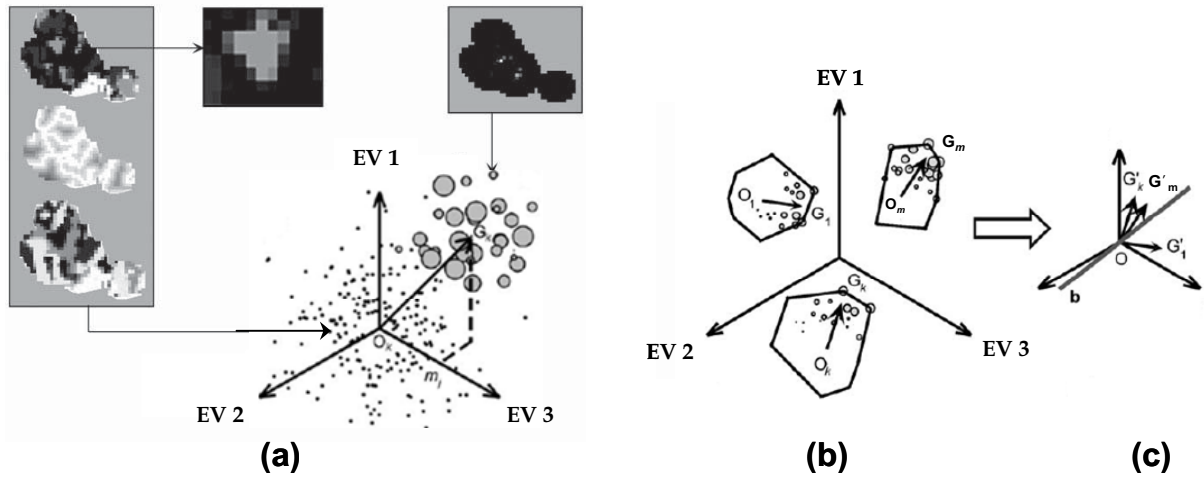


Figure 2: Principle of K-select analysis. (a) Case of a single animal. The set of available pixels that compose the home range define a j -dimensional space of environmental variables (here, EV 1 to EV 3) where j is the number of EV. The origin of this space (O_k) defines the barycentre of the space, namely the average environmental conditions available to this animal. The relative frequency of use of the pixels as determined by the relocations forms the ecological niche of the individual in its home range (gray circles). The diameters of the circles are proportional to the frequency of use of the pixels. The barycentre of the niche (G_k) corresponds to the average environmental conditions used by this animal. The vector $O_k G_k$ therefore corresponds to the marginality of the niche. (b) Case of 3 individuals. For each animals a vector of marginality is computed ($O_k G_k$). (c) K-select applies a translation of marginality vectors so that they all have a common origin and an eigenanalysis is performed on the translated vectors OG'_k so that the successive components of the K-select maximize averaged marginality. Adapted from Calenge et al. (2005).

RESULTS

Establishment of individual home ranges

The two first axes of the K-select accounted for 71% (i.e. $41.5 + 29.5$) of the individuals' marginality — i.e. the strength of habitat selection — (Fig. 3a) and were retained in the analysis. The third axis still explained 14.2 % of the variation; however, the biological meaning of this axis is unclear (see Table 2). Major anthropogenic structures (distances to high traffic roads and disturbance index) contributed most to the first axis, whereas the second axis was explained primarily by an elevational gradient and distance to lakes, but also distance to settlements (Fig.3 b; Table 2). These results mirrored the structure of the study area itself (elevational gradient, isolated high traffic roads and settlements). No common pattern of habitat selection by individuals was apparent (Fig. 3c).

The landscape composition regarding vegetation types was quite homogeneous, with coniferous forests and regenerating forests covering 67% and 19% of the study area, respectively. Therefore, variation in vegetation composition among the individual home ranges was limited. However, the average distance to each vegetation type differed ranging

form a minimum average distance to regenerating forest of 143 m (W0422) to 980 m (W0826). Isolated houses and private roads were found equally in each home range. At this scale, the bears did not show a strong avoidance of high-traffic roads and settlements, while high variation existed between home ranges.

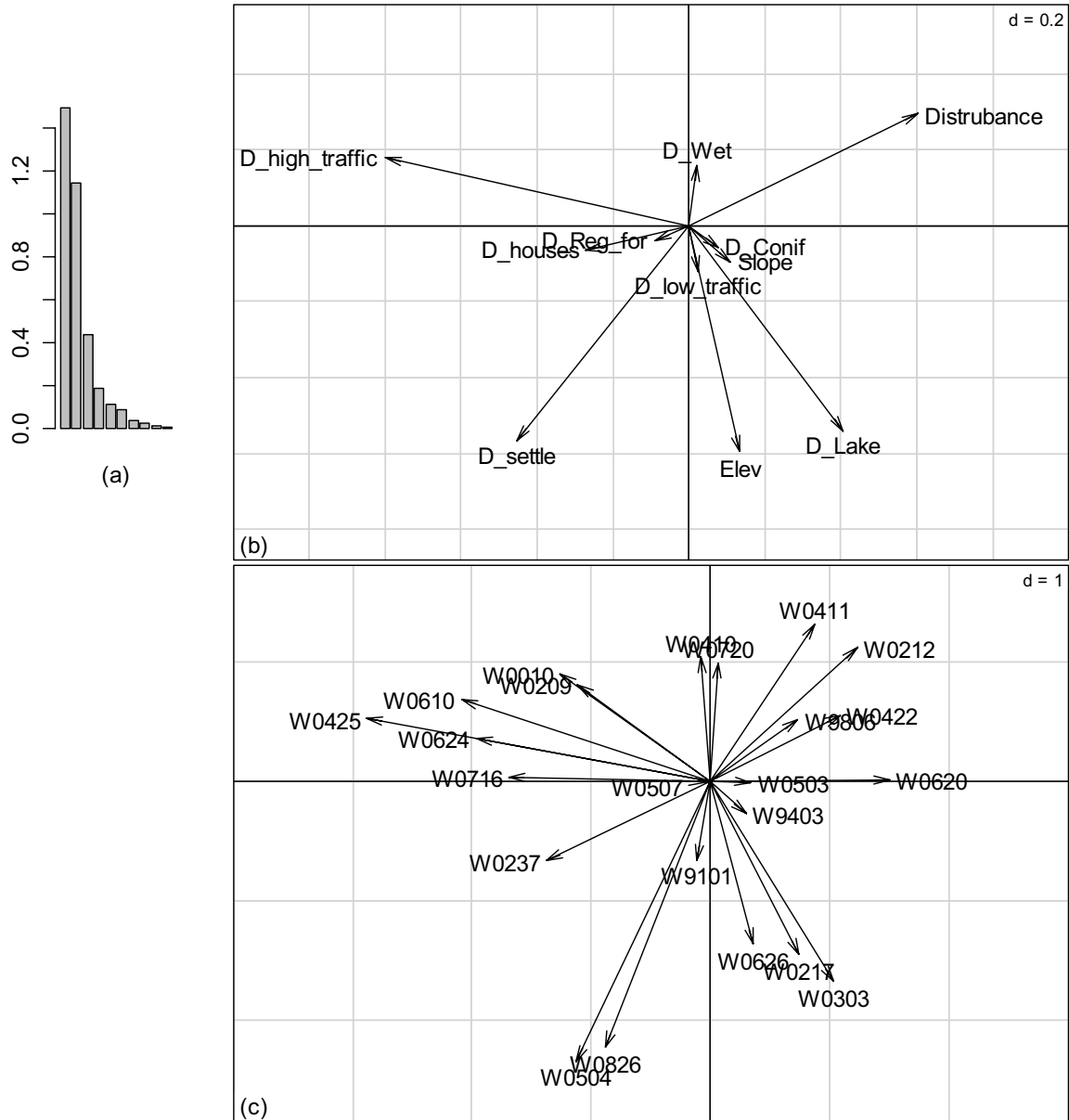


Figure 3: Habitat selection of female brown bears in south-central Sweden at the 2nd order of selection. (a) Bar chart of the eigenvalues of the K-select, measuring the mean marginality explained by each factorial axis. (b) Variable loadings on the two first factorial axes. The projection of the variables on the factorial axes gives a representation of their contribution to these axes. (c) The individuals' marginality vectors on the first factorial plane. The projection of individuals on the factorial plan allows the interpretation of the habitat selection by these individuals; the longer the arrow, the stronger the marginality. As availability is the same for all animals, the arrows are centered on the origin of the factorial plane.

Table 2: Scores of variables on the three first axes of the K-select analyses regarding habitat selection of female brown bears in south-central Sweden. The higher the absolute value, the higher the contribution of the variable on the axis.

Habitat variables	2 nd order			3 rd order		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Elevation	0.133	-0.595	-0.263	-0.102	0.011	-0.027
Slope	-0.110	-0.095	-0.094	-0.345	0.037	-0.088
D_Conif	0.077	-0.057	-0.052	0.007	-0.001	0.056
D_Reg_for	-0.089	-0.041	-0.025	0.191	-0.022	-0.156
D_Wet	0.021	0.158	-0.010	-0.056	-0.064	0.053
D_lake	0.406	-0.540	0.513	-0.070	-0.016	-0.020
Disturbance	0.903	0.295	0.014	0.027	-0.151	-0.008
D_High_traffic	-0.799	0.178	0.254	-0.002	-0.037	0.009
D_low_traffic	0.026	-0.119	-0.154	-0.007	-0.130	-0.065
D_houses	-0.271	-0.066	-0.021	-0.055	-0.193	0.019
D_settle	-0.453	-0.565	-0.071	-0.003	-0.008	0.038

Use of habitats within home ranges

The two first axes accounted for 61% of the individuals' marginality (Fig. 4a) and were retained in the analysis. In contrast to the level of home range establishment, there was a common pattern of habitat selection within home ranges; all females selected steeper slopes and shorter distances to young forests (as revealed on the first axis, Fig. 4 c, d). However, a high variability in habitat selection in relation to anthropogenic structures (distance to houses and distance to low-traffic roads) was found on the second axis; W0624, W0826, W0411 and W0504 selected areas particularly close to houses and private roads, whereas W9403, W0425, W0209, W0720 and W0610 selected areas further from houses and low-traffic roads.

It is important to note that there was no correlation between slope and regenerating forest in the overall study area ($r = -0.06$), nor between coniferous forest and slope ($r = -0.14$). Additionally, there was no correlation between slope and these vegetation types ($r = -0.11$ and $r = -0.02$ for young forests and coniferous forests, respectively) in the bear relocations. Thus, female bears did not seem to select steeper slopes when they were in regenerating forest compared to older forest.

There was a strong variability in the use of disturbed areas and rugged terrain during the day (Fig. 5). Females were located on steeper slopes and in less disturbed areas during the main periods of human activity (i.e. during daylight hours).

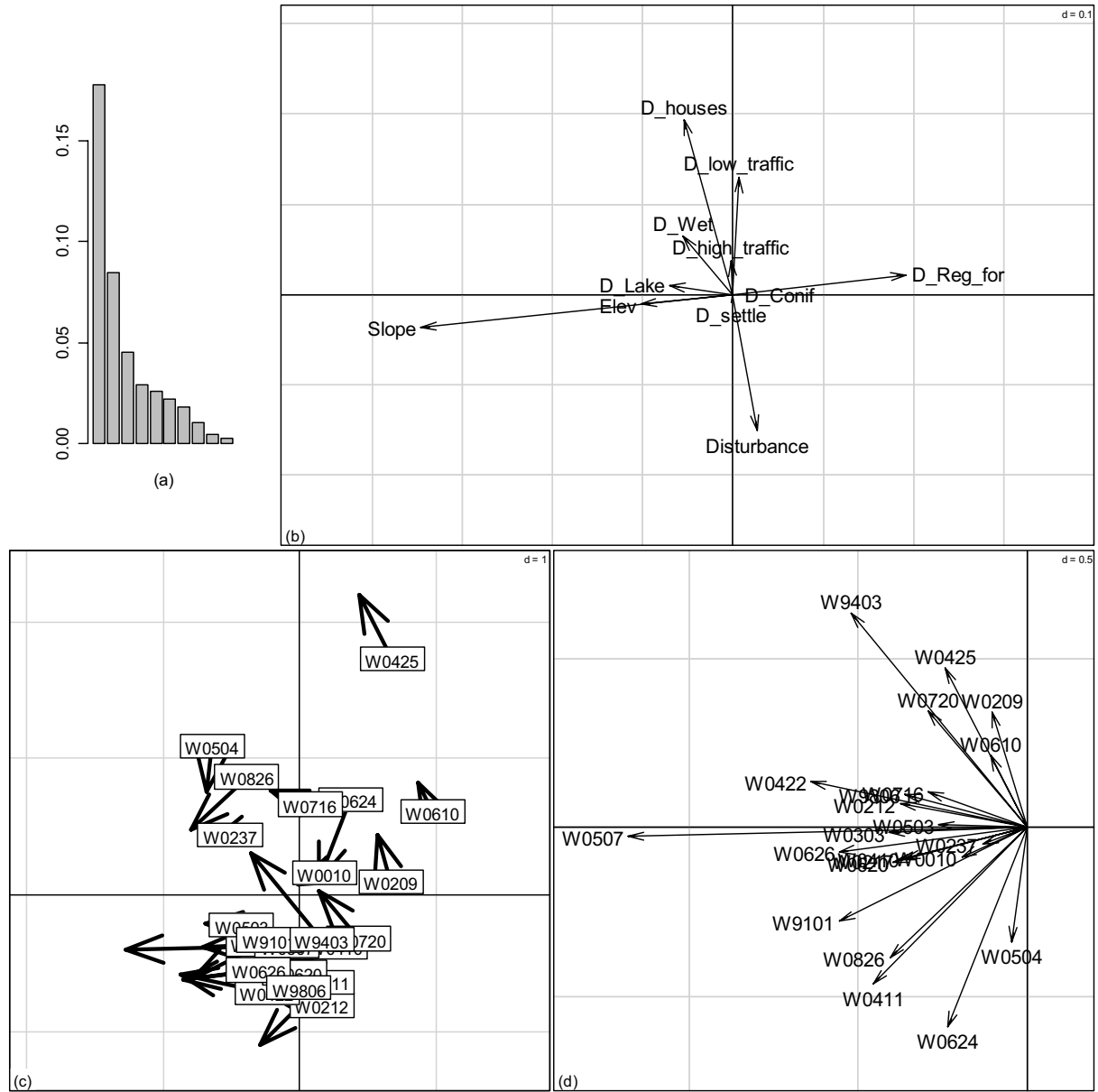


Figure 4: Habitat selection of female brown bears in south-central Sweden at the 3rd order of selection. (a) Bar chart of the eigenvalues of the K-select, measuring the mean marginality explained by each factorial axis. (b) Variable loadings on the two first factorial axes. (c) The individuals' marginality vectors on the first factorial plane, labels corresponding to the average habitat availability. (d) The individuals' marginality vectors after re-centering each individual habitat availability.

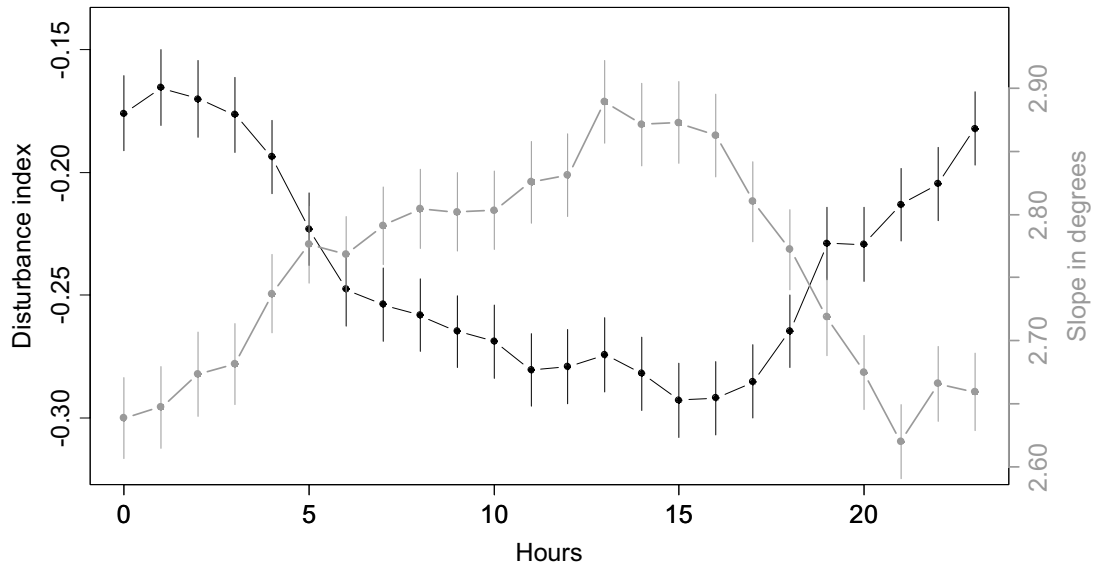


Figure 5: Variability in the use of slopes and disturbed areas by 23 Scandinavian female brown bears during the day (mean $\pm$ se for each hour of the day).

In addition, females in home ranges with a higher disturbance (the left-hand side of Fig. 4c) seemed to show a stronger selection for slopes and shorter distance to regenerating forests (longer arrows parallel to first axis, Fig. 4c). We therefore investigated the influence of home range composition in terms of anthropogenic variables (coordinates on the second axis of the home-range establishment K-select) on the strength of selection (length of the marginality vectors on the first axis of the within-home-range selection K-select). Although two individuals had extreme values, we highlighted a positive correlation using a non-parametric regression curve (LOWESS, Cleveland 1993), meaning that females with more human disturbance in their home range tended to show greater selection for steeper slopes and regenerating forests (Fig. 6).

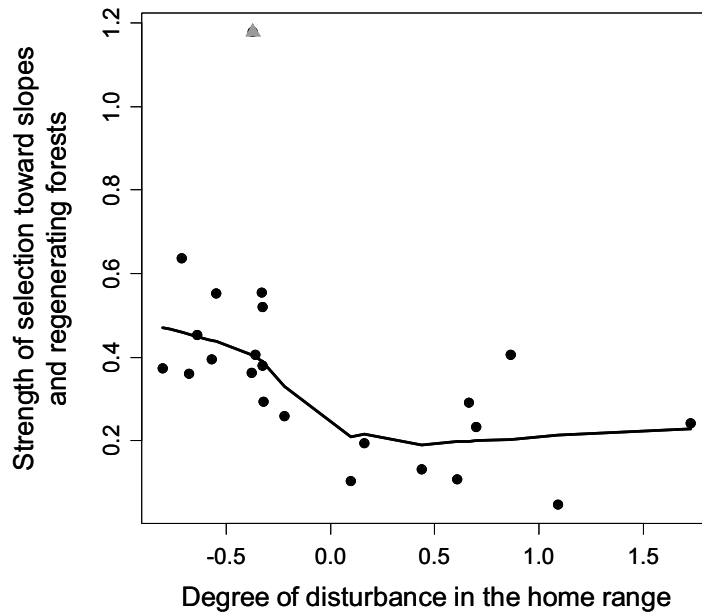


Figure 6: Relationship between the composition of Scandinavian female brown bear home ranges regarding anthropogenic structures (x) and the strength of selection for slopes and regenerating forest. The composition of home ranges regarding anthropogenic structures is estimated by the position of each individual on the second axis; the strength of selection for slopes and regenerating forest is estimated by the length of marginality vectors on the first axis. On this figure, individuals with many houses and low-traffic roads in their home ranges are associated with higher value of selection toward slopes and regenerating forests. Gray triangles are individuals with extreme values. For visualizations of this association, we fitted a non-parametric regression curve (LOWESS, Cleveland 1993) to the data points.

DISCUSSION

Our hypotheses were that bears should (i) select undisturbed areas while establishing their home range, (ii) select habitats providing food items inside their home range, and (iii) show temporal avoidance of human anthropogenic structures at a daily scale. Our first hypothesis clearly was rejected, whereas the second and the third hypotheses were supported. Rettie and Messier (2000) suggested that limiting factors that potentially can reduce individual fitness should drive selection at coarser scales. They proposed a direct relationship between these limiting factors and the selection level of individuals, suggesting a continuum of scales at which these factors should impact individual fitness differentially. Our results do not support this hypothesis completely. Indeed, female brown bears do exhibit an avoidance of human structures at the landscape scale (Katajisto 2006, Nellemann, et al. 2007) and at a fine scale (within home ranges), but there seems to be no particular pattern of avoidance of these structures at an intermediate scale, that of home range establishment. Our results also showed

that bears avoided disturbed areas and selected steeper slopes during daylight hours, supporting our third hypothesis.

At the level of home range establishment, the bears showed no general pattern of habitat selection of the variables considered and did not particularly avoid anthropogenic structures, such as high-traffic roads or human settlements. Instead, individual home ranges seemed to be distributed randomly throughout the study area and were composed of various distances to habitat types. This pattern can be explained by the fact that our study site as a whole was well suited for bears. Aberg et al. (2000) also reported the difficulty to demonstrate habitat selection in the absence of strong environmental variability in suitability.

In addition to the relative spatial homogeneity in suitability, also the social organisation of female brown bears probably contributed to the apparent lack of home-range selection. Indeed, Benhamnou (1998) commented on the importance of social relationships for the spatial organisation of home ranges. In our case, the home ranges of unrelated females show little overlap (Støen, et al. 2005), suggesting a form of territorial behaviour. Beckmann & Berger (2003) also found an ideal-despotic distribution of black bears *Ursus americanus*, with larger males precluding females and smaller males from areas with abundant food resources. The same mechanism may occur among female brown bears, subordinate females being forced to establish in lower quality habitats by dominant females, for instance in more disturbed areas. This phenomenon has been demonstrated in social species like wild chimpanzees *Pan troglodytes*, where dominant females compete with subordinates, forcing them to settle in lower quality areas (Murray, et al. 2007). In addition, female brown bears are often philopatric (Støen, et al. 2005), settling close to or within their mother's home range, although subdominant siblings are sometimes forced to disperse due to competition for philopatry (Zedrosser, et al. 2007), but do not move far from their natal area (27 km on average; Støen et al. 2006). Philopatry could provide benefits for females establishing matrilineal assemblages (e.g. "silver spoon"-effects), which can partly replace habitat-driven home-range selection behaviour. Mothers often let their daughters have pieces of their own home ranges (Støen, et al. 2005). As such, daughters may have better knowledge of their environment, particularly the locations of food resources within parts of their home range, contrary to those that settle in completely new home ranges. Therefore, the proportion of the mother's home ranges within a female home ranges may be an important "habitat" variable. The concurrent study of matrilineages and habitat selection would allow a fuller investigation of the choice of home ranges.

Although no selection occurred at the level of the home range, within the home range a common pattern arose of selection for steep slopes and regenerating forests. In agreement with our hypothesis, females selected for areas providing food resources (regenerating forests) within their home range. However, we also found a strong selection for steep slopes, which demonstrated that they selected for areas providing higher relative security, although no particular avoidance of human disturbance was demonstrated by the analysis. However, the analysis of temporal selection of disturbed areas during the day revealed an avoidance of these areas during hours of higher human activity. In addition, bears also selected steeper slopes during that same period of the day.

Our results suggested a functional response by bears to human disturbance. Although all bears seemed to select slopes and regenerating forests, the strength of this selection varied greatly according to the degree of human disturbance in the home range (Fig. 6). Bears used steeper slopes when their home range was located in an area with higher human disturbance, probably due to the need for increased security (Nielsen, et al. 2004). Thus, females that may not have the possibility to establish their home range in less disturbed areas may compensate for this by adjusting their habitat selection at a finer spatial scale, showing greater selection for steeper slopes than females located in less disturbed areas.

In this context, it is important to note that, at the individual scale, the reason older forests seemed not to be particularly selected was because of their high availability throughout the study area and thus in home ranges. However, these forests probably are important, as they provide security and thermoregulation during resting periods (REF). Old forests also provide some important food items, like blueberries *Vaccinium myrtillus*, which are negatively affected by clear-cutting (Kind 2001).

CONCLUSIONS

Habitat selection is a complex process occurring at different spatio-temporal scales. Our results demonstrated that limiting factors for bears were not consistent across spatial scales. In agreement with the hypothesis of Rettie and Messier (2000), bears avoided the most limiting factor (human influence) at the largest scale (landscape scale, Katajisto 2006) and selected food resources at the finest scale (within their home range). However, although human influence did not appear to be avoided at this fine scale, our results showed a temporal avoidance of disturbed areas and a differential selection of secure areas (slopes); bears were located in rugged terrain and less disturbed areas during the main period of human activity. At

the intermediate scale (home range establishment), our study did not reveal any common pattern of habitat selection, indicating that either the social structure of females is the most important factor driving females' home range establishment (i.e. this scale may not be biologically relevant for bears' habitat selection) or dominant females or matriline might force subdominant females to occupy less suitable areas (with few regenerating forests and high degree of human influence), resulting in home ranges with high and low habitat quality.

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Paper IV

MOVING ALONG SEASONS: CHANGING ENVIRONMENT AND REQUIREMENTS AFFECT BROWN BEAR MOVEMENT PATTERNS

Jodie MARTIN^{1,2†}, Bram VAN MOORTER¹, Stéphane DRAY¹, Pierre-Yves QUENETTE³, Dominique ALLAIN¹ & Jon E. SWENSON²

¹ Université de Lyon, F-69000, Lyon ; Université Lyon 1 ; CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France.

² Department of Ecology and Natural Resource Management, Norwegian University of Life Science, P.O. Box 5003, NO-1432 Ås, Norway

³ Office National de la Chasse et de la Faune Sauvage, 85 bis avenue de Wagram, BP 236, F-75822 Paris Cedex 17, France

ABSTRACT

Movement patterns should reflect interactions between individual requirements and temporal variability in resource availability. In seasonal environments and under various internal conditions, animals should therefore exhibit spatial and temporal variability in their movement patterns. Brown bears (*Ursus arctos*) undergo different changes in their internal states during the year (hypo- and hyperphagia) and therefore their requirements change according to season. In addition, reproductive status entails additional energetic demands and constraints. As expected, we found important differences across seasons and according to reproductive status in bear movement patterns. Moreover, external factors such as climate, vegetation types or degree of disturbance affected speed and sinuosity of movement differentially throughout the year. To our knowledge, few studies investigated simultaneously the effect of internal state and environmental variables on daily movement patterns of animals through the entire year.

Keywords: Daily movement pattern, Brown bear, *Ursus arctos*, search behaviour, internal state, external correlates

[†] Correspondence : martin@biomserv.univ-lyon1.fr, Tel : + 33 04 72 43 35 84, Fax: +33 04 72 43 13 88

INTRODUCTION

In heterogeneous landscapes, animal movements reveal the strategies that individuals have adopted to meet their requirements (Bergman 2000, Austin et al. 2004), such as choices concerning the type of resources to use, the location of resources, and how they distribute the use of resources among time periods (Schoener 1971, Stephens & Krebs 1986, Bell 1991). In theory, animals should balance the potential benefits (e.g. resource access) and costs (e.g. energetic costs, risk of predation) of movement (Bell 1991). Several factors may influence these individual movements including both internal state (e.g. reproductive status, body condition, seasonal requirements) and external factors (e.g. food distribution, climatic conditions, disturbance) (Stephens & Krebs 1986). In seasonal environments and under various internal conditions, animals should therefore exhibit spatial and temporal variability in their movement patterns.

To our knowledge, there are few studies that simultaneously have investigated how both internal states and external factors affect animal movement to obtain an integrated understanding of their combined influence. Moreover, movement studies usually focus on particular types of movements (mainly foraging and dispersal movements) and seldom on variation of daily movements (including all individual activities) over the year. However, studying daily movement patterns can provide insights on both daily activity patterns (because of the close connection between activity and movement; Schmidt 1999) and resource search behaviour (Bell 1991). The main activity of most animals being the search for resources (mainly foraging, but also search for mates), we can therefore link movements to search behaviour (and particularly optimal foraging), and investigate questions regarding when, where and how an individual should move (or search for resources).

Activity patterns should optimize energy intake while minimizing costs associated with foraging (Charnov 1976). Foraging time should therefore be optimized to exploit resources efficiently (Schoener 1971, Stephens & Krebs 1986). Most animals show a rhythmic behaviour called the “circadian rhythm”, which depends mostly on physiological states (Sollberger, 1965), but also can be affected by environmental variables (Aschoff 1966). Therefore, the daily movement pattern should vary according to both external correlates and internal factors (Sollberger, 1965) and hence exhibit variability, especially for species that undergo marked seasonal changes in their habitat and requirements.

In addition to this expected great variability in daily movement patterns, animal movement rates may vary according to individual requirements (which vary for example during the year and with reproductive status) and the environment in which they move (e.g. habitat types, terrain ruggedness, risky habitat). When resources are patchily distributed, movements should be slower and more convoluted in high-quality patches, to keep individuals in these good habitats (Zollner & Lima 1999, Fahrig 2007, Snider & Gilliam 2008; e.g. Marell et al. 2002). The same type of movement should be exhibited by animals with low body condition, because of the energetic costs of movements (faster movements leading to higher energetic costs). When animals are searching for new resources patches however, movement should be faster and more directed because it leads to higher search efficiency, as it increases the probability of finding new patches and reduces the number of patches revisited (Stephens & Krebs 1986, Wolf & Hainsworth 1990, Zollner & Lima 1999). Also, faster and linear movements reduce the time spent in risky habitat (Zollner & Lima 1999, Chapman et al. 2007). Climate (especially temperature) might influence movement and daily activity patterns as well. For example, ungulates change their behaviour to avoid thermoregulation costs by resting during periods of high temperature and waiting for cooler temperatures before moving (Dussault et al. 2004, Maloney et al. 2005, Aublet et al. 2009). Therefore, individuals constantly have to balance efficient search and energetic costs associated with movements.

The factors that drive movement patterns of large animals remain poorly understood, because of their large spatial requirements and their elusive behaviour (Noss et al. 1996, Austin et al. 2004). New technologies, such as Global Positioning Systems (GPS), enable researchers to estimate individual movements by remotely recording individual relocation with high frequency. In this paper, we investigate daily movement patterns of GPS-collared female brown bears (*Ursus arctos*) over a whole year of activity (from April to September). In particular, we investigate how movement patterns vary under the joint influence of seasonal change of environment and biological requirements of bears. Our goal therefore is to characterize the influence of both internal factors (reproductive status, energetic requirements) and external factors (weather, habitat type, human influence) on movement speed and turning angles between relocations. Studying these two movement parameters allows us to investigate movement according to bear requirements and under the various constraints experienced by individuals.

Several studies of bears have revealed a bimodal daily pattern, with activity peaks around dawn and dusk (Gervasi et al. 2006, Kaczensky et al. 2006, Moe et al. 2007). We therefore

expected a strong variability of movement during the day, due to this circadian rhythm. We expected to find an alternation of fast and slow movements, as well as sinuous and straighter movements corresponding to necessary activities, such as feeding or moving, but also resting behaviour, shown by very slow and convoluted movements due to GPS error (Calenge et al. 2009). We also expected to find an effect of daylight duration, which has been shown to be the major factor determining circadian circles (Sollberger 1965).

Bears' requirements vary greatly throughout the year (e.g. post-denning period, the breeding season, pre-denning period of hyperphagia), as does the availability of resources. We therefore expect bears to adapt their movements according to seasons. Particularly, bears should move slower after den emergence because of their low body condition during this period (weight difference between autumn and spring averages 62 kg; Swenson et al. 2007a). On the contrary, during the breeding season where females have gained body mass, they should increase their movement to increase the probability to find mates. Similarly, during pre-denning season, females should increase their speed and the directionality of their movement to search efficiently for food resources, necessary to meet their energetic demands to prepare hibernation period. Females followed by cubs of the year should have additional energetic requirements (e.g. lactation; Loudon 1985), especially after exit of the den, but the low movement capacity of their pups might constrain their movements. Moreover, they should have slow movements on limited areas (convoluted movements) during mating season to avoid encountering infanticidal males (Ebensperger 1998, Dahle & Swenson 2003), which has been reported to be an important cause of cub mortality on our study area (Swenson et al. 1997).

Generally, we expect bears to move faster in less secure areas (e.g. open habitat, areas close to human structures) than in resource-rich habitats (regenerating forests; Martin et al. unpublished) or secure habitats (slopes, coniferous forests; Martin et al. unpublished).

We also hypothesize an influence of climate variables (rainfall and temperature) on bear movements. Particularly, we expect that bears decrease their movements during days with higher temperatures. Due to behavioural thermoregulation, we expect less intensive movements when temperature is high during the warm season and that rainfall should promote movements during the warm season. During cooler seasons (e.g. after exiting the den) however, temperature should have a positive influence on movements.

MATERIALS AND METHODS

Study area and species

We conducted the study in the southern-most reproductive area of the Scandinavian brown bear population, located in the counties of Dalarna and Gävleborg, in south-central Sweden (61°N, 15°E). The terrain is hilly and the elevation ranges from 200 to 700 m above sea level. The area consists mainly of highly managed productive forest (80%), bogs and lakes (together 20%). The forest is dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) and consists of patches of differently aged stands ranging from clear-cuts to 90-100-year-old forests (Swenson et al., 1999). Human settlements and high-traffic roads are rare in the study area, but isolated houses and low-traffic roads are evenly distributed throughout the study area. The mean temperature in January and July are -7° and 15°, respectively. Snow cover lasts approximately from late October until early May. Average precipitation is approximately 600-1,000 mm annually (Swenson et al. 1999). Bears are intensively hunted in the study area in the fall, starting from late August and last 1-2 months.

The brown bear is a solitary species that is active on average about 7-8 months annually, from April to November. It is omnivorous and the diet varies among populations. In Scandinavia, bear diet varies greatly across seasons and is mainly composed of graminoids, forbs, berries, ants and ungulates. (Dahle et al. 1998, Persson et al. 2001)

The year was divided in 4 biological seasons, each corresponding to particular foraging behaviours (related to food availability) and reproductive status (Dahle et al. 1998, Dahle & Swenson 2003b, Zedrosser et al. 2007). The pre-mating season (15 April – 8 May) corresponds to the emergence from winter hibernation. During this period bear diet is mainly composed of herbaceous vegetation and ants, but also on old berries (Dahle et al. 1998, Persson et al. 2001). The mating season (9 May – 22 June) corresponds to the period where females are in oestrus (Dahle & Swenson 2003b). During this period, brown bears become more carnivorous, mainly hunting moose calves (Swenson et al. 2007b). Both males and females roam to mate during this period (Dahle & Swenson 2003a). Because the implantation of the foetus is delayed until November, females give birth during the following winter, generally in January. There is no paternal care; the young follow their mother during 1.5 to 4.5 years. Females that separate from dependent cubs before or during mating season become receptive within 2–4 days after separation (Bellemain et al. 2006). Infanticide (the killing of

dependent young by conspecifics) by males has been reported in this population and is considered the most important factor influencing cub survival (Swenson et al. 1997, 2001).

During the post-mating season (23 June - 31 July), bears mainly eat ants and forbs (Dahle et al. 1998, Persson et al. 2001, Swenson et al. 1999). The last biological season we defined (1 August - den entrance) corresponds to the period of hyperphagia, when bears consume mainly berries rich in carbohydrates (Dahle et al. 1998) to fatten before entering the winter den.

Data collection

We analysed relocation data of female brown bears over 3 years (2005, 2006 and 2007). Twenty females were darted from a helicopter using a remote drug delivery system (Dan-Inject, Børkop, Denmark) and equipped with GPS-transmitter collars (GPS-plus-3; VECTRONIC Aerospace GmbH, Berlin, Germany). Due to the high battery capacity of the collars, some females were followed 2 or 3 consecutive years (8 and 1 females, respectively), resulting in 30 periods of bear activity. Females followed by cubs of the year (hereafter referred to as female with cubs) were not captured for ethical reasons. However, some of the lone females equipped with GPS collars gave birth the following winter, which gave us the opportunity to follow these females the year of parturition. As a result, 6 of the 30 periods of bear activity were from females accompanied by cubs of the year. GPS collars were programmed to record relocation with a fixed frequency of 30 minutes (i.e. 48 daily relocations).

Movement parameters

To estimate daily movement patterns, we used speed between successive locations as a measure of movement rate. For each female, movements were characterized independently by discrete segments connecting successive relocations. Speed between relocations was estimated by dividing segment lengths (or distances between each relocation) with time lags separating relocations (i.e. 30 minutes). As a measure of sinuosity, we also calculated cosines of relative angles (or turning angles; Turchin 1998).

To avoid any bias that could result from missing data, we removed estimates of speed and cosines of relative angles that were obtained from 2 relocations separated by one or more missing data points. It is important to note that when animals are resting, apparent movement due to GPS error creates apparent sinuosity of movement (Calenge et al. 2009). We therefore considered sinuous and very slow “movements” to be resting behaviour. Analyses were

carried out using R (R Development Core Team, 2007) and the package “adehabitat” (Calenge, 2006).

Habitat and environmental variables

The study area was divided into a grid of square pixels (200 x 200 m), which were characterized for three variables: slope, vegetation, and human disturbance. We derived slope from a Digital Elevation Model available for the whole study area (GSD - Höjddkurvor, 25m ekvidistans Lantmäteriet, Sweden). The CORINE Land Cover map (CLC00) was used to define 5 vegetation types: bogs, coniferous forests (mainly Scots pine and Norway spruce), lake, mixed forests (mix of coniferous forest and deciduous forest which are mainly composed by common birch *Betula pubescens*), and regenerating forests (young-aged forests stands from clear-cut to young forest).

An index of human presence was computed, based on 4 anthropogenic variables: distances to public and private roads, to isolated houses, and to human settlements, each derived from digital data of Sweden (GSD-Översiktskartan, Lantmäteriet, Sweden). As the influence of distances to these structures on bears may not be linear, we assumed that the potential influence was the same above a given threshold. Although bears express a relative tolerance for human-caused disturbance, a review by Linnell et al. (2000) revealed an avoidance of human activity at 1-2 km. Moreover, Swenson et al. (1996) found that brown bears prefer den sites >3 km from villages. We therefore chose a maximum threshold value of 2000 m for distances to roads and houses, and 3000 m for distances to settlements. Above these thresholds, distance values were equal, meaning that the potential influence was the same. We added all the distance maps to create the human influence index. The resulting map provided an index ranging from 200 to 9000, with low values corresponding to high human influence. For reading convenience, we standardized the index, dividing it by the maximum value (9000), and inverted it so that a low index corresponded to low disturbance.

ArcView version 3.2a (ESRI Inc., Redlands, California, USA) was used for preliminary preparation of spatial data and the package “adehabitat” (Calenge, 2006) for R for the computation of the index.

We used average daily temperature (in degrees) and daily accumulated precipitations (in mm) from weather data obtained from Särna and Sveg weather stations. We averaged climatic data values from the two stations, as the study area is located between them.

We estimated daylight duration (in minutes) by calculating the time between sunrise and sunset. Time of sunrise and sunset were available at <http://www.cactus2000.de>. We used the data from Östersund (63.18°N, 14.65°E).

Statistical analyses

We used multiple regressions to assess the influence of daytime (in hours), vegetation type (coniferous forest, mixed forests, young forest, bogs), slope (in degrees), human influence (standardized index, see above), temperature (in degrees Celsius), precipitation (mm per day), age (in years), and length of daylight (in minutes) on movement parameters (speed in km/h and cosine of relative angles). Due to the strong effect of daytime found in previous research on bear activity (Kaczensky et al. 2006, Moe et al. 2007) and in preliminary analyses of mobility in our data (Figure 1), a null model without daytime would not make biological sense. Hence, we included daytime in all our models. A total of 128 models were evaluated, corresponding to all potential combinations of the aforementioned variables.

We expected a strong influence of reproductive status and season on movement patterns and to avoid too much interactions in the models, we chose to model movement patterns for reproductive categories (lone females and females with cubs of the year) and seasons (pre-mating, mating, post-mating and hyperphagia) separately (2 reproductive status * 4 seasons * 128 models). In addition, this choice reduced model complexity and facilitated interpretation.

We used Generalized Additive Models (GAM; Hastie and Tibshirani, 1990) to account for non-linear effects of daytime on mobility (Figure 1 and Kaczensky et al. 2006; Moe et al. 2007). A GAM is a flexible semi-parametric method to model non-linear relationships between a response variable and its explanatory variables. This non-linear relationship is modelled by a smooth function of these explanatory variables. We used a cyclic cubic spline smoother to model the non-linear and cyclic effect of daytime (this smoother is available in the R package “mgcv”; Wood 2006). In this cubic spline the point at the end of the day is constrained to be the same as the one at the beginning. The degree of smoothing is determined by generalized cross validation (Wood 2006). This approach results in a robust smoother that explains most of the variance while avoiding an over-fitting of the data. Therefore, in GAMs the shape of the function is not restricted by a parametric form, instead the function’s shape is determined by the data.

For each individual, we repeatedly measured the movement pattern, which entailed dependence between observations of the same individual, i.e. pseudo-replication. Mixed

models, by their use of random effects in addition to fixed effects, allowed us to avoid pseudo-replication. The integration of GAMs and mixed models has led to the development of Generalized Additive Mixed Models (GAMM; Wood 2006), which combines the flexible non-linear modelling of GAMs with the possibility of using random effects. Thus, we used GAMMs (R package “mgcv”; Wood 2006) to model movement patterns with individual as random effect and all other explanatory variables as fixed effects, using a cyclic cubic spline smoother for daytime only.

Because there is potentially temporal autocorrelation between successive relocations (fixes attempted every 30 min), we used a bootstrap procedure. By randomly sampling 1,000 points from each of our data sets (range $n = 2,281 - 34,594$) we avoided autocorrelation between relocations. We repeated this sampling 1,000 times, which allowed us to determine the confidence intervals of each estimated regression coefficient.

Model influence was assessed using the Akaike Information Criterion (AIC, Burnham & Anderson 2002, Johnson & Omland 2004) approach. Due to model selection uncertainty, we opted to use model averaging as a multi-model inference tool (Wintle et al. 2003). For each bootstrap, we calculated the weighted mean of the regression coefficients on the 128 models using the model's Akaike weight as weight (Burnham & Anderson 2002, Johnson & Omland 2004). As mentioned above, the 1,000 bootstraps provided us with the distribution of the weighted mean of the regression coefficients.

To simplify the interpretation of the daytime spline smoother, we determined peaks and valleys using the maximums and minimums of the spline of the null models, respectively. This allowed us to easily investigate periods of high and low mobility, and periods of linear and sinuous movement patterns.

RESULTS

Bears daily movement patterns

As expected, Scandinavian female brown bears showed a circadian movement pattern (and thus activity pattern) with 2 peaks around dawn and dusk and the main resting period during the day (Figure 1). The biological rhythm of bears followed the time of sunrise and sunset within seasons (Figure 2). Intensity and linearity of lone females' activity was greatest around 2.3, 2.2, 1.8 and 1.2 hours after sunrise for pre-mating, mating, post-mating and hyperphagia seasons, respectively. The second peak took place 1, 1.8, 2 and 0.7 hours before sunset for the

same seasons, respectively. The same pattern was found for females followed by cubs, although there was a timing difference compared to lone females. During the pre-mating season, females with cubs tended to be most active during only one period, 7 to 10 hours after sunrise. During the mating season, they started to establish a bi-modal movement pattern, although they still were more active in the middle of the day (4:15 after sunrise and 3:30 before sunset), about 2 hours later than lone females for the first activity peak and 1.5 hours earlier for the second peak. Both categories of females tended to show comparable patterns during post-mating season.

Daily variation in speed and linearity of movement

The speed and sinuosity of movement varied greatly among biological seasons and reproductive categories. The averaged daily speed of lone females was 1 km/h during the pre-mating season, 1.9 km/h during the mating and post-mating seasons, and 1.5 km/h during the hyperphagia season. Females with cubs moved more slowly, but increased their movement through the year: 0.1, 0.5, 1.2 and 1.5 km/h for the same seasons, respectively.

Lone females progressively increased their movement speed and linearity throughout the year until the post-mating season (Figure 3 & 4; speed increased about 175% between the pre-mating and mating seasons, and 80% between the mating and post-mating seasons). During the hyperphagia season, however, they decreased their movement rate slightly (speed decreased 35% compared to the post-mating season). Females with cubs increased their movement throughout the year and this trend was even more pronounced than for lone females: increase of 250% from the pre-mating to the mating season, 300% from the mating to the post-mating season, and 75% from the post-mating to the hyperphagia season (Figure 3). However, their averaged speed was much lower than that of lone females, except during the hyperphagia season, where the contrary was found. Lone females moved 5.5, 4.5 and 2 times more than female with cubs during the pre-mating, mating, and hyperphagia seasons, respectively. Females with cubs moved 1.1 times more than lone females during hyperphagia season.

Bear movement seemed to differ with age of individuals (Figure 5i). Older lone females moved less than younger lone females during the post-mating season and much less during the hyperphagia season. When accompanied with cubs, older females moved less than younger females during the pre-mating, mating and post-mating seasons, but showed no difference during the hyperphagia season.

Environmental factors influencing movement patterns

To facilitate interpretation of the effect size for all the factors, we report the range of values for each studied variable in Table 1.

Effect of vegetation types

To assess the effect of vegetation on movement speed according to our predictions (faster movements in risky habitats), we compared closed, resource-rich vegetation types (coniferous, mixed and young forests) to open, resource-poor habitats (bogs). Bogs were therefore used as the reference in the GAMM models and all other vegetation types were compared to this reference. During the pre-mating season, there was a strong difference in movement speed between bogs and the three other vegetation types for lone females (Figures 5). They moved more slowly in the latter vegetation types (on average 3 km/h slower than in bogs). The difference was least during the mating season, but the same pattern was evident (on average 1 km/h slower than in bogs). There was no effect of vegetation type on movement speed during the post-mating season. During the hyperphagia season, they moved more slowly in coniferous and young forests (on average 1 km/h slower than in bogs), but we found no difference for mixed forests.

Females with cubs, on the contrary, moved as fast in bogs as in coniferous and mixed forests during the pre-mating season. They only tended to move faster in young forest than in bogs (1.8 km/h faster than in bogs). During the mating season, they moved faster in forested areas than in bogs, contrary to lone females (0.1 to 2.8 km/h faster than in bogs). During the post-mating season, vegetation types had little influence on movement speed by females with cubs. The effect of vegetation type seemed to be higher during hyperphagia, when females with cubs moved more slowly in all forested habitats than in open habitats (1.5 to 2.9 km/h slower than in bogs).

Effect of human presence

For both reproductive categories, human presence had the same effect during the pre-mating season; females moved faster in areas with more human presence (Figure 5; about 0.4 km/h faster). The same trend was found during hyperphagia, although the effect was less (0.1 and 0.25 km/h faster for lone females and females with cubs, respectively). During the mating season, females with cubs were even more sensitive to effect of human presence (moved 0.7 km/h faster in these areas). On the contrary, lone females seemed to show the opposite

behaviour; they moved more slowly in areas with human presence (0.1 km/h slower in areas with human presence). For both reproductive categories, human presence did not seem to have any effect on movement behaviour during the post-mating season.

For both reproductive categories, movement speed was different on slopes only during the post-mating and hyperphagia seasons (Figure 5h). When bears moved in steeper areas, they tended to move more slowly (an increase of 5° entails an increase of 0.4 to 0.75 km/h for lone females and females with cubs, respectively).

Effect of weather and daylight duration

Temperature had a significant and positive influence on movement speed for both categories of females in all seasons (Figure 5b). Females moved faster when daily temperatures were higher. This relationship was even more pronounced for lone females during the pre-mating season and females with cubs during the post-mating season (increasing 5°C entailed an increase of about 0.65 km/h).

Precipitation had a significant effect on movement speed, but a small effect size (Figure 5; the effect reached its maximum for lone females during the mating season, with an increase of 0.1 km/h for each increase of 5 mm of rainfall)

Daylight duration had a significant influence on movement speed, especially during the pre-mating season (Figure 5a; a daylight increase of 30 min corresponded with an increase of 1 km/h), but the effect was less in the following seasons (increases of 0.1 km/h and less). However, it should be noted that there might be a confounding effect of time, with daylight duration increasing with time of the day, especially during the pre-mating season. Indeed, the females might increase their movements over the year, independently of daylight duration.

DISCUSSION

We investigated daily movement patterns of female brown bears using an integrated approach, investigating key factors that could be involved in search behaviour. Searching tactics involves a series of intimately related decisions on when, where, and how to move (or search), according to the animal's requirements and constraints (Bell 1991). In particular, the use of daily movement patterns allowed us to investigate the “when” and “how” questions.

Bears' daily movement patterns: the result of internal and external factors

Consistent with the literature on European brown bears (Kaczensky 2006, Gervasi et al. 2006, Moe et al. 2007) and with our predictions, we found that Scandinavian female brown bears tend to be crepuscular (and to some extent nocturnal), with 2 peaks of maximum activity around dawn and dusk and a main resting period during the day (Figure 4). As the timing of sunrise and sunset varies greatly according to season in central Scandinavia, females adapted their activity pattern to this variation (Figure 2). This is consistent with the findings of Aschoff (1966), who stated that activity peaks should be further apart when daylight increases.

At first sight, the crepuscular pattern exhibited by the female bears did not seem to be optimal according to optimal foraging theory. Although the sensory modes for foraging are not well known in brown bears, we expected that females in our study area should exhibit the same diurnal activity as observed in North American brown bear populations (Gende et al. 2001, Klinka & Reimchen 2002), because their diet component (forbs, berries, ants) should be more detectable during daylight (Klinka & Reimchen 2002). Indeed, in North America, several brown bear populations have been reported to be active during the day (Klinka & Reimchen 2002). However, bears tend to shift to nocturnal activity in areas with high human density (Klinka & Reimchen 2002) to avoid disturbance. Kaczensky et al. (2006) also reported nocturnal activity in response to human disturbance by brown bears in Croatia and Slovenia. Although the human density in our study area is low, the road network is well developed and forests are managed intensively by foresters. Moreover, our results demonstrate that human activity, often confined to daytime hours, can be disruptive for bears, especially during the pre-mating season (bears moved faster in areas with human presence, probably to avoid risks of encountering humans; Figure 5g). In our study area, females might therefore exhibit a crepuscular activity, partly to avoid humans.

To our knowledge, the effect of weather on activity pattern has never been assessed to explain nocturnal or crepuscular activity patterns of bears, although several studies have investigated the effects of weather on ungulate activity patterns (Beier & McCullough 1990, Dussault et al. 2004, Aublet et al. 2009). Our results highlighted the influence of temperature on bear behaviours. During the mating, and particularly during the post-mating season, lone females moved more when temperatures were high (contrary to our hypothesis), but changed their activity pattern toward more nocturnal activity (Figure 4). This behavioural response to high temperatures can be seen as a least-cost thermoregulation tactic to limit the costs

associated with autonomic temperature regulation (Maloney et al. 2005). In our study area, bears seek shade and wet soil when resting during the day (Brunberg, pers. comm.). North American brown bears, which have been reported to be diurnal (Gende et al. 2001, Klinka & Reimchen 2002), are been studied in cooler areas (e.g. Bristol Bay in Alaska, Yellowstone National Park, La Mauricie National Park in Canada) which might explain their diurnal activity patterns. In our study area, temperatures can reach 22°C during summer (see Table 1). Crepuscular activity exhibited by the females might thus be an optimal foraging strategy, balancing the most efficient foraging technique (using daylight to detect food components) and costs associated with diurnal activity, i.e. thermoregulation and avoidance of disruptive human activities. However, we were not able to assess the relative contributions of these factors to explaining crepuscular activity.

As expected, females accompanied by cubs showed the same activity pattern as lone females, except during the pre-mating season, where they tend to be active mainly during the day. Kaczensky et al. (2006) suggested that cubs are more active during daylight, leading to a shift in diurnal activity by their mother. We found that females with cubs tend to establish a bimodal activity pattern during the mating season, but with a temporal shift in peak of maximum activity compared to lone females. Indeed, they remained active during daylight hours (about 1.5 hour later than lone females for the morning peak and 1.5 hour before lone females for the evening peak). This behaviour could be a strategy to avoid contact with conspecifics, especially infanticidal males (Ebensperger 1998, Dahle & Swenson 2003a), which has been reported to be an important cause of cub mortality on our study area (Swenson et al. 1997). We do not have data on males to confirm this hypothesis. However, we assume that males should exhibit the same activity pattern as lone females, especially during the mating season, in order to increase the probability of encountering prospective mates. Indeed, it has been documented that males and lone females roam to mate during this period (Dahle & Swenson 2003a). After the mating season, females with cubs tend to establish almost the same pattern as lone females, when males no longer pose a threat to their young. During the mating season, females with cubs should thus be more sensitive to interactions with their conspecifics than to disruptive effects of human activities.

Movement characteristics: the result of internal and external constraints*Global effect of seasons and reproductive status*

Animal requirements, as well as food quality and abundance, vary greatly among seasons. According to our hypothesis, our results highlighted a strong variability in bears' movements, according to season. Indeed, irrespective of the reproductive category, females moved slower (and therefore less) after den emergence where the energetic requirements of females are high. Females that gave birth in the den have much higher energetic requirements, because they stay an additional month in the den, on average, than lone females (Friebe et al. 2001) and lactation entails additional energetic costs (Loudon 1985). As expected, they exhibited very convoluted and slow movements (Figure 3 & 4) during the pre-mating season due to the low movement capacity of cubs. Slow movements reduce associated energetic costs and convoluted movements reduce predation risk (by males) on their cubs, as it reduces the probability of encountering males (Duvall & Schuett 1997). As we expected lone females to exhibit efficient foraging movements during the pre-mating season, females with cubs clearly showed less efficient foraging movements, because they stayed within a limited area, where resources could be depleted rapidly. Having cubs therefore entails less efficient foraging and therefore a trade-off between searching for food and risk avoidance.

Consistent with our hypothesis, lone females increased the intensity and linearity of their movements the following seasons (Figures 3 & 4) as they become less limited by movement costs. Moreover, during mating and hyperphagia season, they have additional requirements (search for mates and intensive search for food, respectively) and it has been shown that searching along straight-line paths is more efficient to increase the probability of finding resources (mate or food; Duvall & Schuett 1997). Indeed, they can orient their movements towards targets that they can detect using their sense of smell or sound (Duvall & Schuett 1997). It should be noted however that during the hyperphagia season, lone females move less than in the previous season (post-mating season), but the movements are as linear. Reducing their movements might be a strategy to avoid humans, as this period corresponds to the bear hunting season and when also humans pick berries. Indeed, it has been reported that bears tend to be wary of humans in hunted populations (see Swenson 1999). During the post-mating season however, females are more nocturnal (Figures 3), so the probability of encountering humans is lower. As a consequence, females may be less wary in their movements, moving principally during nocturnal periods. In addition, the berries begin to ripen. As these food

items are patchily distributed throughout the study area, a better foraging strategy would be to increase the speed and linearity of movements.

Females with cubs started to increase the intensity of their movements during mating season, but they still showed slow and sinuous movements. There may be a trade off between security for cubs (avoiding infanticidal males) and search for food resources, because Dahle & Swenson (2003a) stated that reduced movements of females during this period are not explained by the youngs' low movement capacity. Female with cubs adopted a movement pattern similar to those of lone females only during post-mating season. Cubs therefore no longer seemed to be a constraint for efficient foraging movements. Moreover, females with cubs moved more than lone females during this period (Figures 3 & 4), probably to search for food resources more efficiently to compensate for their lower body conditions compared to lone females.

Older females moved less during the post-mating season than younger females (Figure 5), perhaps because they have a better knowledge of their home range, and therefore do not need to explore their environment as much as younger females. Moreover, they also might have more experience, particularly of human disturbance, so they might reduce their movements to avoid encountering disruptive humans or anthropogenic structures.

Effect of environmental factors

Female brown bear movements conformed with our hypothesize on search efficiency, because they had globally slower movements in forested areas (coniferous forest, mixed forests and young forests) than in open habitats (bogs), which are resource-poor habitats that are more exposed to risks (Figure 5). Our results also showed that females with cubs reacted differently to vegetation types than lone females. Actually, they moved only on a very limited area under coniferous forest cover and almost never used bogs during the pre-mating season (which explained why there was no influence of vegetation at all during this period) and not much during other seasons (Martin unpublished). Therefore, these results should be interpreted cautiously (Figure 5).

Females in both categories avoided human presence, especially during the pre-mating season, probably because of their low body condition. Indeed, the maximal values for human influence were lower (Table 1) and females moved faster in areas with humans (Figure 5). During the mating season, females with cubs were even more affected, probably because they started moving more and therefore increased the probability of being closer to anthropogenic

structures. As cubs still were vulnerable, females may have avoided areas with human activity (Table 1) and encountering humans by moving faster in areas with human activity (Figure 5).

During the post-mating and hyperphagia seasons, there was no effect of human influence on female movements (Figure 5), for the same reasons mentioned previously (shift toward nocturnal behaviour). However, females (whatever the reproductive category) tended to move more slowly on slopes. During this season, they selected slopes during daylight hours (Martin, unpublished), probably for security reasons (easier visual and olfactive detection).

All females moved more when the temperature was high, contrary to our hypothesis stating that they should move less with increasing temperature during hot seasons. As stated earlier, they actually changed their activity pattern toward nocturnal activity, but were more active during the day with high temperatures. This is consistent with previous studies on ungulates that reported an increase in activity during hotter days, but a behavioural shift to reduce thermoregulation costs (Merrill 1991, Dussault et al. 2004, Aublet et al. 2009).

Conclusions

Our integrated study of bear movements highlighted a strong variability in movements and activity patterns by female brown bears in response to internal and external factors. Our findings also revealed the constraints on search for resources entailed by having cubs of the year. Indeed, females with cubs not only have to face the low movement capacity of cubs, but also to make trade-offs between searching for food efficiently and reducing the encounter rate with conspecifics and humans.

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Table 1: Range of value for the different external and internal factors that could influence female brown bears' movement in central Sweden.

	Lone females				Females with cubs			
	Pre-mating	Mating	Post-mating	Hyper-phagia	Pre-mating	Mating	Post-mating	Hyper-phagia
Daylight (min)	796 1026	1032 1211	1063 1210	496 1057	796 1026	1032 1211	1063 1210	496 1057
Temperature (°C)	-0.55 12.60	0.5 21.3	10.2 22.0	-6.75 20.30	-0.55 12.60	0.5 21.3	10.2 22.0	-6.75 20.30
Precipitation (mm)	0 14.5	0 23.05	0 20.3	0.0 31.8	0 14.5	0 23.05	0 20.3	0 31.8
Disturbance	0 0.89	0 0.96	0 0.96	0 0.94	0 0.29	0 0.64	0 0.63	0 0.63
Slope (°)	0 22.8	0 19.93	0 18.59	0 18.9	0 10.11	0 13.38	0 14.43	0 16.88
Age (Year)	3 14				4 15			

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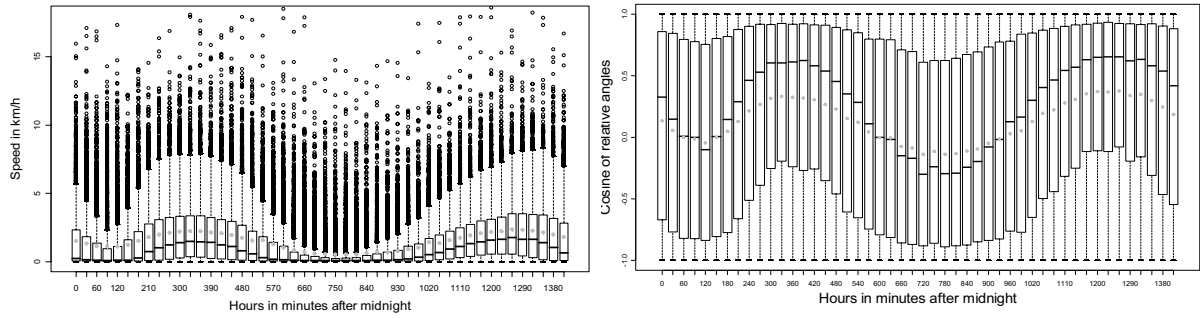


Figure 1: Boxplot representation of hourly speed (on the left) and cosine of relative angles (on the right) by female brown bears in central Sweden. Gray dots correspond to average values.

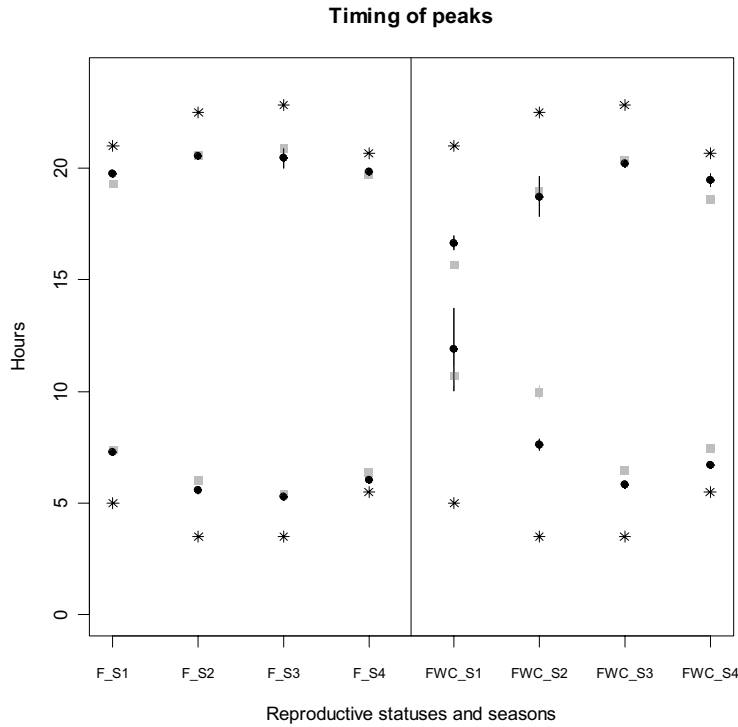


Figure 2: Timing of movement peaks by female brown bears in central Sweden according to their reproductive status and season. Black circles represent the average speed ($\pm 2*SE$) and gray squares the average linearity ($\pm 2*SE$) of parameter estimates on all bootstraps, calculated with null models. “F” corresponds to lone females and “FWC” to females with cubs of the year; S1 to S4 corresponds to the pre-mating, mating, post-mating and hyperphagia seasons, respectively. Stars correspond to the average times of sunrise and sunset.

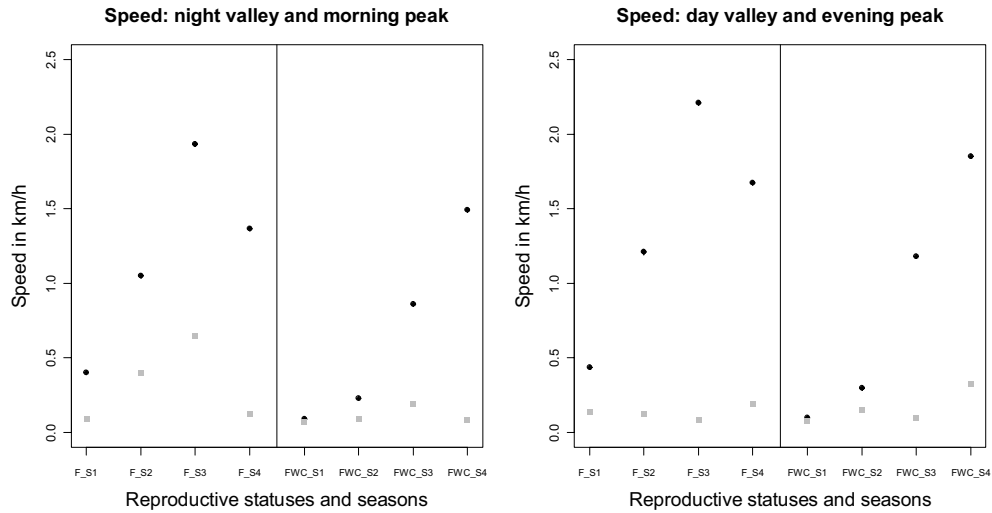


Figure 3: Speed of movement, in km/h, by female brown bears in central Sweden during periods of maximal (black circles) and minimal (gray squares) movement. Mean ($\pm 2*SE$) of parameter estimates on the null models for all bootstraps for the morning peak (on the left) and evening peak (on the right) of maximum speed.

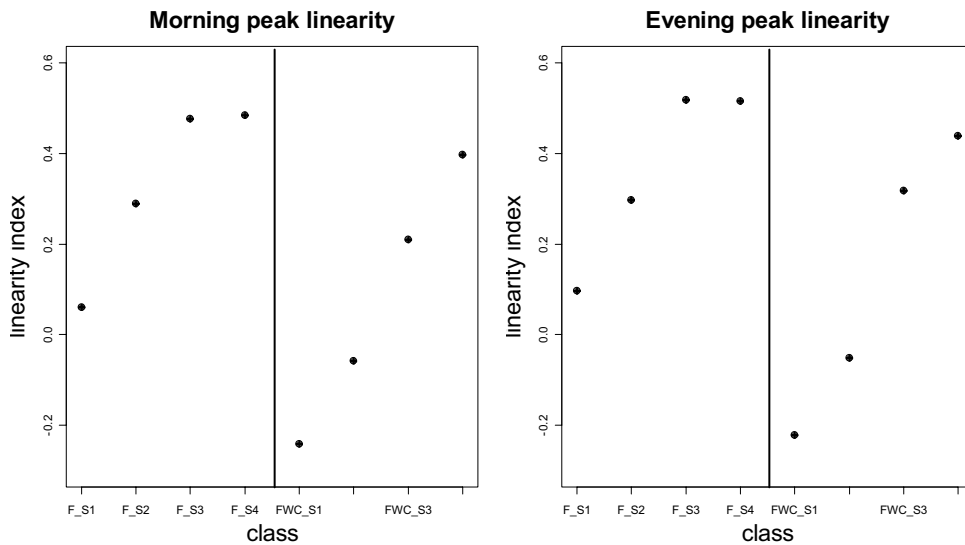


Figure 4: Degree of linearity of movement peaks by female brown bears in central Sweden. Mean ($\pm 2*SE$) of parameter estimates on the null models for all bootstraps for the morning peak (on the left) and evening peak (on the right) of maximum linearity.

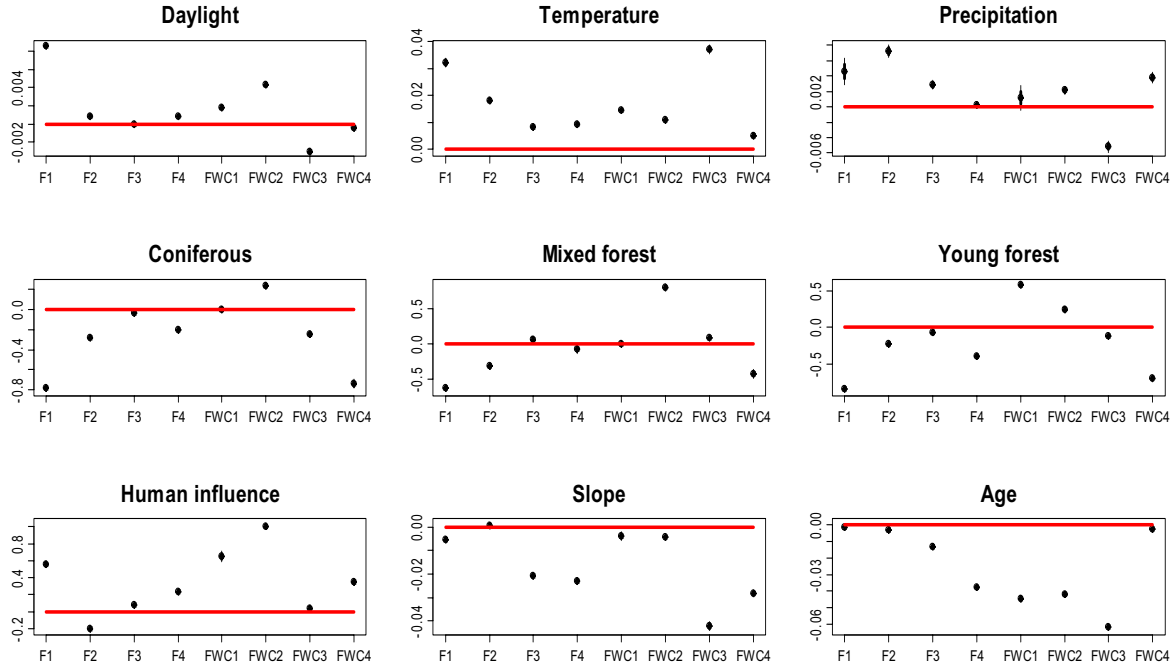


Figure 5: Estimated coefficient ($\pm 2*SE$) for the effect of the different factors on speed for each reproductive statuses and seasons. The horizontal line corresponds to the 0. Therefore, if the $2*SE$ do not cross the line, the coefficients are significant at $\alpha = 5\%$. Coefficients above the red line mean positive relationship, and coefficients below the red line mean negative relationship. F1 to F4 corresponds to the lone female category during pre-mating, mating, post-mating and hyperphagia seasons, respectively. FWC1 to FWC2 corresponds to the female with cubs category during the same seasons.

Paper V

UNDERSTANDING AND PREDICTING HABITAT SELECTION PATTERNS OF BROWN BEARS AT GLOBAL AND LOCAL SCALES

Jodie MARTIN^{1,2*}, Pierre-Yves QUENETTE³, Javier NAVES⁴, Dominique ALLAIN¹ & Jon E. SWENSON²

¹ Université de Lyon, F-69000, Lyon ; Université Lyon 1 ; CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France.

² Department of Ecology and Natural Resource Management, Norwegian University of Life Science, P.O. Box 5003, NO-1432 Ås, Norway

³ Office National de la Chasse et de la Faune Sauvage, 85 bis avenue de Wagram, BP 236, F-75822 Paris Cedex 17, France

⁴ Department of Applied Biology, Estación Biológica de Doñana CSIC, Avenida María Luisa s/n, Sevilla 41013, Spain (JN, AF-G, CR, MD)

ABSTRACT

Conservation and management of remnant brown bear (*Ursus arctos*) populations in western Europe require the quantification of suitable areas at large scales, but also connectivity of these habitats. In this study, we built separate quantitative habitat model two key demographic feature (survival and reproduction) using large-scale variables. The combination of models demonstrated agreement in habitat selection of Cantabrian bears and Pyrenean bears and allowed us to map habitat quality for bears in entire countries of France and Spain. Bears were located mainly in rugged terrain, in forested areas that produce hard-mast and with high forest connectivity, with few roads and agricultural areas. A second quantitative model at finer scale in the Pyrenees highlighted allowed us to more precisely identify suitable areas for bears in Pyrenees. The association of the global and local models should be a useful tool for conservation planning in the Pyrenees, in particular to identify habitats that should receive high priority for conservation or those where potential reintroductions should be located.

Keywords: *Habitat model; Brown bear; Ursus arctos; Pyrenees Mountains; Cantabrian Mountains; Source-sink*

* Correspondence : martin@biomserv.univ-lyon1.fr, Tel : + 33 04 72 43 35 84, Fax: +33 04 72 43 13 88

INTRODUCTION

The space occupancy by organisms should reflect choices of particular habitat characteristics that maximize their fitness (Fretwell & Lucas, 1970, Synopsis). As such, it is often assumed that the observed distribution of a species, population or individuals is a good proxy of habitat quality. Predictive models aiming at identifying and predicting habitat suitability for a given species have become an important tool in conservation planning or wildlife management (Schadt et al., 2002). Often, large scale analyses are required for this purpose (Noss et al., 1996; Schadt et al., 2002), though fine scale studies should not be neglected as complementary analyses of species or individual requirements (Paper II). In particular, an interesting question is to identify the general processes that govern habitat use for different populations of a given species. From an evolutionary perspective, regardless of whether the species is a habitat generalist or specialist, the general processes should be congruent across populations although local processes should differ due to adaptations to local environments. Large-scale global models transferable over broad range of habitats are therefore consistent tools for species conservation or management (Klar et al., 2008), especially for rare and elusive animals for which data are not available or not of good quality.

The management and conservation of large carnivore is difficult task, because of their large spatial requirements (Noss et al., 1996; Schadt et al., 2002) and their socio-political stakes (Breitenmoser, 1998; Treves & Karanth, 2003, Synopsis). In particular, the primary habitats of carnivores have been reduced and fragmented by human activities and infrastructures, which has led to an increase in the proximity of humans and carnivores and therefore conflicts. Conservation and management of such species therefore require the quantification of suitable areas at large scales, but also connectivity of these habitats to restore or maintain sufficiently good habitats and to anticipate the potential expansion of the populations.

For populations that live in heterogeneous environment, it is common that individuals occupy different habitats, therefore varying in quality (Dias, 1996). In meta-population theory, this observation gave rise to the concept of source-sink system, where demographic parameters differ according to habitat characteristics (Pulliam, 1988). In source habitats, the reproductive rate is higher than the mortality rate, whereas in sink habitats the reproductive rate can not compensate for the mortality rate (Pulliam, 1988). When individuals misperceive

the quality of sink habitats, it can lead to maladaptive behaviors, i.e. individual will select for “apparently” good habitats but where the reproduction is low or the mortality rate is high (Delibes, Gaona & Ferreras, 2001). This kind of habitat has been called “attractive sink” (Delibes et al., 2001). For large carnivores, attractive sinks are often the result of a failure to detect human-caused risks in habitats with otherwise good quality for reproduction (Naves et al., 2003). Identification of source-sink habitats is crucial for conservation as source habitats are key habitats for population persistence (Dias, 1996).

After almost becoming extinct in the past century in Europe, the brown bear now is found only in small and isolated populations in western Europe (Breitenmoser, 1998; Linnell, Swenson & Andersen, 2001). The most endangered populations in Europe are those in the Pyrenees (France-Spain) and Cantabrian Mountains (Spain). Both of these relict populations are divided in two sub-populations with little individual exchange. In particular, the western core of the Pyrenean population is composed almost only of males (no more female since 2004) and therefore will be driven to extinction if no more female exchanges are possible. For this critically endangered population, a thorough understanding of habitat quality is required to identify suitable areas to be maintained and areas for potential new reintroduction.

Here, we conducted two habitat selection analyses. First, we aimed to identify “global” habitat selection patterns for the Cantabrian Mountains (Cantabrian) population and the Pyrenean population. We used large-scale environmental variables and grain to increase the generality of our predictive model. This model therefore will allow identification of the potential congruence of habitat selection patterns for the two populations. We used the approach developed by Naves et al. (2003) which is based on the source-sink theory. Assuming that bear mortality is mainly caused by human activity and reproduction is related to natural factors (such as forest cover and vegetation productivity), their approach consists of constructing two different models related to these two demographic parameters. The final association between the survival model (with anthropogenic variables as explanatory variables; “human model”) and the reproduction model (with natural variables as explanatory variables; “natural model”) allows a finer classification of habitat quality than classical models that include all explanatory variables (see Figure 1). In particular, it allows the separation of sources habitats (safe habitats good for reproduction), attractive sink habitats (good for reproduction but high mortality risk), refuge habitats (safe habitat with low quality for reproduction), sink habitats (risky and poor habitat for reproduction), and avoided matrix (non-habitat areas). Based on this, we expect that high quality habitat would be forests that

produce abundant hard mast for bear food and with low human influence. Forest connectivity also should influence bear presence positively.

Second, we performed a “local” habitat selection analysis for the Pyrenean population, using finer environmental variables to identify more local adaptations by the bears. This analysis will help obtaining a more precise knowledge of the ecological niche of Pyrenean brown bears and potentially identify suitable habitats in the Pyrenean Mountains at a finer spatial resolution. The combination of global and local models will provide an important tool for conservation planning for brown bears in the Pyrenees.

The aims of this study are therefore: (1) determining if habitat selection patterns are congruent between the Cantabrian and Pyrenean brown bear populations; (2) quantifying the amount of suitable habitats for both populations, but focusing particularly on the Pyrenean population; and (3) identifying the connectivity between the core areas of the populations, but also with potential non-occupied habitats of high quality.

MATERIAL AND METHODS

1 Bear data sets

1.1 Cantabrian Mountains

The two study areas (Cantabrian and Pyrenees) were divided in 5×5 km cells (or pixels). In Cantabrian, bear presence has been recorded between 1982 and 1991 during systematic investigations (see Naves et al., 2003) resulting in 321 cells of with bear presence (classified as 1). A cell is classified with bear presence when one or more indices of presence were found within it. We then randomly sample 321 cells without bear presence (classified as 0) in the neighbourhood of the bear distribution to make sure that bears could have visited these cells. Then, 80% of these data were used to build the logistic-regression models (training dataset) and the remaining 20% were used for a cross-validation of the model in the study area (validation dataset).

1.2 Pyrenees Mountains

Global scale study

In Pyrenees, we used bear presence (e.g. scats, visual observation) collected from 1996 to 2007. Data were collected both systematically (during systematic monitoring by the “brown bear network”; see Synopsis) and non-systematically (observations made and reported by e.g.

hikers). We used all the data on bear presence for the global-scale study. The mixture of different types of data collection is not a concern here, because we deal with bear presence and not abundance. A total of 179 cells were classified with bear presence (1).

Local-scale study

For this study, we used a finer grain, dividing the study area into 200×200 m cells. To study the Pyrenean brown bear ecological niche and to draw a local Habitat Suitability Map (HSM), we only used non-systematically collected data, to avoid a mixture of designs. Here, this mixture could bias the results and the resulting map could reflect the sampling protocol, rather than a real HSM. We choose non-systematically collected data to ensure that indices were randomly sampled in the study area, because systematic monitoring was carried out where bears were known to be present.

To analyse the ecological niche of bears, the available area was defined using a polygon encompassing all the indices of bear presence. We therefore avoided including areas that were not accessible to bears. For the HSM however, the goal was to map the relative quality of the entire Pyrenees. As we used a method that did not require a comparison of used data with available data (see § 3 of this manuscript), we therefore extended the study area to encompass all the Mountains chain and its valleys. We also used telemetric data from the only female that recently almost belonged to the western population (2006) for a graphical representation on the different habitat quality maps.

2 Habitat variables

2.1 Global-scale analyses

To identify the general pattern of habitat selection by bears, we used large-scale variables that we expected would be important for bears at this scale (Table 1). These variables are summarized and described in Table 5.1. For both countries, slope layer used to calculate the index of terrain ruggedness was derived from a 90-m digital elevation model freely available at <http://srtm.csi.cgiar.org/> and vegetation variables were derived from Corine Land Cover (CLC00) obtained from the European Environment Agency's website (EEA) at <http://dataservice.eea.europa.eu/dataservice/>. The French human population density was obtained from the "Institut National de la Statistique et des Etudes Economiques" at www.insee.fr and the Spanish human population density from the "Instituto Nacional de Estadística" at <http://www.ine.es/>.

2.2 Local-scale study

For this study we used finer habitat variables (Table 2). The digital elevation model and vegetation types were obtained from the same source as for the global-scale analysis. We performed a Principal Component Analysis (PCA) on the environmental variables in the study area to identify a potential local structure of the landscape. As the variables had different units, we used a normalized PCA. Moreover, we were interested in the structure of the landscape and not just effect size. We therefore choose to use a centered PCA.

Table 1: Description and units of environmental variables used in the global-scale logistic regression models for brown bears in the Cantabrian Mountains (Spain) and Pyrenean Mountains (France). Values for each variable are reported to one pixel.

Variables	Label	Type	Description	Range	Mean ± SD presence	Mean ± SD absence
Terrain ruggedness	Rugged	Natural	(mean + standard deviation) of slope in degrees	1.2 48.6	25.33 ±6.59	17.40 ±9.79
Shrub cover	Shrub	Natural	% of shrub	0.00 0.88	0.34 ±0.20	0.28 ±0.20
Open areas	Open	Natural	% of natural open areas	0.00 0.78	0.05 ±0.7	0.06 ±0.1
Forest cover	Forest	Natural	% of forest	0 1	0.41 ±0.21	0.30 ±0.19
Mast tree cover	Mast	Natural	% of deciduous and mixed forest cover	0.00 0.98	0.35 ±0.21	0.24 ±0.18
Forest connectivity r=1	F_connect_1	Natural	% of forest in the pixels adjacent to the focal pixel (5 km)	0.01 0.79	0.40 ±0.15	0.32 ±0.15
Forest connectivity r=2	F_connect_2	Natural	% of forest in the pixels surrounding the focal pixel up to 10 km	0.03 0.62	0.40 ±0.12	0.32 ±0.12
Forest connectivity r=3	F_connect_3	Natural	% of forest in the pixels surrounding the focal pixel up to 15 km	0.04 0.55	0.39 ±0.11	0.32 ±0.11
Human population density	Pop_dens	Human	Number of inhabitants	1 1076	12.67 ±14.21	34.48 ±94.92
Agricultural areas	Agri	Human	% of agricultural area	0 1	0.04 ±0.11	0.17 ±0.27
Road	Road	Human	length of roads (in km)	0.00 27.78	1.30 ±2.67	2.34 ±4.16

Table 2: Description and units of environmental variables used for the local-scale analysis of ecological niche of Pyrenean brown bear and the Habitat Suitability Map.

Variables	Label	Description
Elevation	elev	In meters
Slope	slope	In degrees
Distance to urban areas	d_urban	Include towns and anthropogenic structures such as building, artificial areas... In meters
Distance to agricultural areas	d_agri	Include arable lands, permanent crops, pastures... In meters
Distance to roads	d_road	Public roads with high traffic. In meters
Distance to deciduous forests	d_decid	Deciduous forests are mainly made of European beech (<i>Fagus sp.</i>), European chestnut (<i>Castanea sp.</i>), oaks (<i>Quercus sp.</i>) and birch (<i>Betula sp.</i>). In meters.
Distance to coniferous forests	d_conif	Coniferous forests are mainly made of fir. In meters.
Distance to mixed forests	d_mixed	Mixed forests (deciduous and coniferous) In meters.
Distance to shrubs	d_shrub	Vegetation with low and closed cover, dominated by bushes, shrubs and herbaceous plants. In meters.
Distance to regenerating forests	d_regfo	Forest regeneration (after degradation) or colonisation. In meters.
Distance to lake	d_lake	In meters.
Distance to natural open areas	d_open	Natural grassland. In meters.

3 Analyses

3.1 Global-scale analysis

Logistic-regression models

Following the approach of Naves et al. (2003), we built 3 different logistic-regression models with bear presence and absence: a general model (f_g), including all the explanatory variables; a natural model (f_n), including only variables that might affect reproductive rate; and a human model (f_h), including anthropogenic variables that might affect bear survival (Table 1). We used the data from Cantabrian to fit the models.

We performed backward stepwise analyses for each of the 3 classes of models and we used the Akaike Information Criterion (AIC) to select for best models. Among potential models (smaller AIC) with small ΔAIC , we choose the best models based on simplicity (low number of variables). We then evaluated each of the models with the validation dataset. The models were also evaluated outside the calibration range using the bear presence in the Pyrenees. We estimated the proportion of localizations for which the models gave a high probability of presence (> 0.6 and > 0.5).

We then classified habitat quality into five categories within to the two-dimensional space based on the best natural and survival models (Figure 1), according to the approach of NAVES ET AL. (2003).

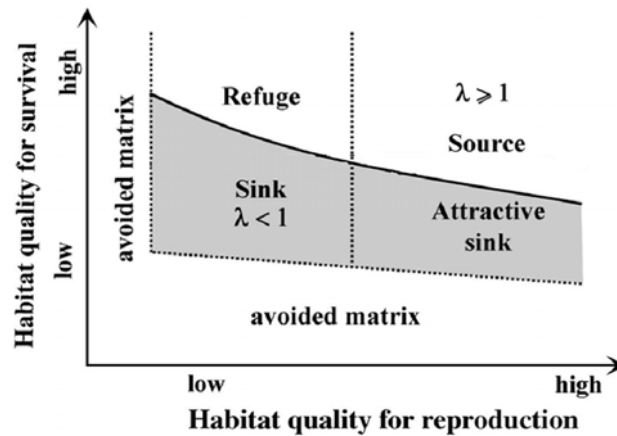


Figure 1: Two-dimensional space of habitat quality according to the conceptual framework from Naves et al. (2003). Habitat quality for reproduction is determined by the natural model; habitat quality for survival is determined by the human model. Adapted from Naves et al. (2003).

3.2 Local scale analysis

Ecological niche analysis

We used the statistical framework developed by Calenge & Basille (2008) to study the ecological niche of the Pyrenean brown bear population. The “General Niche-Environment System Factor Analysis” (GNESFA) is a hindcasting approach that relates species (or population / individuals) to its environment. Two dataset are compared in this analysis: (i) the weighted values of the variables of the available environmental units (EU, e.g. pixels) (e.g. the proportion of a particular patch among all patches of habitat in the study area) and (ii) the weighted values of the variables in the EU used by the species (e.g. the proportion of the detection of the species in a habitat patch) (Figure 2). The set of values of environmental variables available to the species is referred to as the “available distribution” and the set of values of environmental variables used by the species as the “utilisation distribution”. The GNESFA aims to find the ecological directions in which the two datasets are the most different, which is referred to as niche patterns.

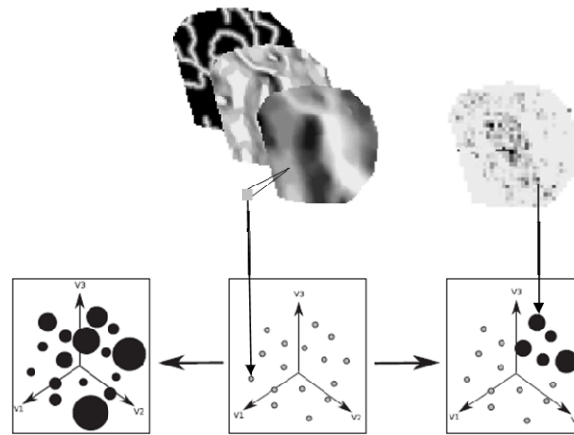


Figure 2: Data used in the conceptual framework of the General Niche-Environment System Factor Analysis (GNESFA). The values of the environmental variables (V1 to V3) in each environment unit (EU) (gray square) are recorded (bottom center) from GIS layers or field collection (top left) and weighted according to their occurrence in the study area (bottom left). The weights therefore describe the availability of the EU to the species. Abundance of the species occurrence (top right) is reported on available EU and used as weights to describe the intensity of use of each EU by the species (bottom right). Adapted from Calenge & Basille (2008).

According to the question of interest, the GNESFA implies a choice of a reference and a focus dataset (available distribution or utilization distribution). As we were interested in the identification of the pattern displayed by the niche in the ecological space, we chose the utilization distribution as focus and the available distribution as reference. Hence, we performed a Factor Analysis of the Niche Taking the Environment as Reference (FANTER,

Calenge & Basille, 2008). In this analysis, the available distribution is distorted to take a standard spherical shape (Figure 3). The focus distribution is then investigated in this standardized space and any deviation from the spherical shape will indicate a pattern (Calenge & Basille, 2008). In this analysis, both the first and the last components have a biological meaning. The first axes are those for which the marginality of the species niche is maximized whereas the last axes are those that maximize the specialization of the species (see Synopsis).

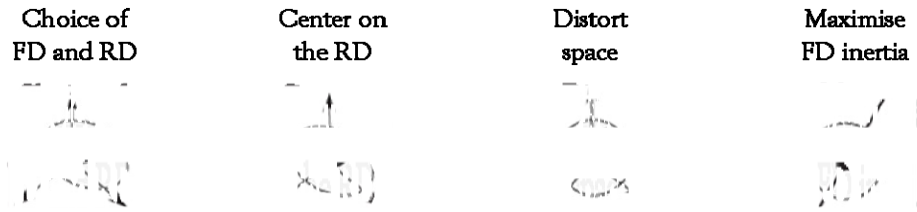


Figure 3: Manipulation of the two datasets in the General Niche-Environment System Factor Analysis (GNESFA) framework. The light gray ellipses represent available distributions and the dark gray ellipses represent utilisation distributions in the ecological space. In the case of the Factor Analysis of the Niche Taking the Environment as Reference (FANTER), the researcher defines the available distribution as reference distribution (RD) and the utilization distribution as the focus distribution (FD). The ecological space is centered on the RD and distorted to make the RD spherical. The analysis then maximizes the FD inertia by defining the ecological directions where the two distributions are the most different. The first axes of this analysis are therefore those that maximize the marginality of the species and the last axes are those that maximize the specialization of the species. Adapted from Calenge & Basille (2008).

Habitat suitability map

We then computed a HSM using Mahalanobis distances statistics (Clark, Dunn & Smith, 1993). One of the interesting properties of this method is that it overcomes the problem of availability definition. Indeed, this method is only based on the environmental characteristics of the EU where a species is present, as the niche of the species is defined using the probability density function of its presence in the ecological space. It therefore gives an index of habitat suitability of the environmental variables of the study area by calculating the departure from the species' niche optimum (centroid of the distribution of the species occurrence). Therefore, an EU with a low value means low distance to species' niche optimum and is therefore a suitable EU (Clark et al., 1993). The distances are calculated as follows:

$$\text{Distance}^2 = (\mathbf{x} - \hat{\mathbf{u}})' \Sigma^{-1} (\mathbf{x} - \hat{\mathbf{u}}),$$

where $\mathbf{x}$ is the vector of habitat characteristics, $\hat{\mathbf{u}}$ the mean vector of habitat characteristics estimated from the utilization distribution, and Σ the estimated covariance matrix from the utilization distribution. The squared Mahalanobis distances therefore represent the dissimilarities between $\mathbf{x}$ (environmental characteristics of the study area) and $\hat{\mathbf{u}}$ (the species optimal habitat). These distances are then spatialized to obtain a map of suitable habitats.

RESULTS

1. Global-scale analysis

1.1 Model outcomes

The three logistic-regression models were retained after the model selection procedure (Table 3). The general model contained six variables: % shrub cover (shrub), terrain ruggedness (rugged), % forest containing hard-mast species (masting), forest connectivity at the scale of 15 km (F_connect_3), roads (length), and human population density (pop_dens). This model had the smallest AIC and was the simplest model among candidate models with lowest AIC. The next parsimonious model ($\Delta\text{AIC} = 0.55$) did not include forest connectivity at the scale of 15 km but included forest connectivity at scales of 5 and 10 km; the next one ($\Delta\text{AIC} = 0.93$) included forest connectivity at the scale of 5 km in addition to the first model.

Table 3: Logistic-regression models of the habitats of brown bears at the global scale, based on data from the Cantabrian Mountains (Spain), resulting from the model selection.

Models	Variables	β	S.E.	p-value
General model	constant	- 3.53	0.52	< 0.001
	Shrub	1.87	0.66	0.004
	Rugged	0.07	0.01	< 0.001
	Road	- 0.08	0.03	0.018
	Masting	2.16	0.69	0.002
	F_connect_3	3.00	1.26	0.018
	Pop_dens	- 0.02	0.005	0.001
Natural model	constant	- 4.10	0.52	< 0.001
	Shrub	2.17	0.65	< 0.001
	Rugged	0.07	0.01	< 0.001
	Masting	2.06	0.67	0.002
	F_connect_3	3.26	1.22	0.008
Human model	constant	0.79	0.13	< 0.001
	Road	- 0.07	0.03	0.023
	Pop_dens	- 0.02	0.005	< 0.001
	Agri	- 4.46	0.73	< 0.001

The most parsimonious and simple natural model contained the same natural variable as the general model (i.e. shrub cover, masting cover, terrain ruggedness and forest connectivity at 15 km). The next parsimonious model ($\Delta AIC = 1$) did not include the forest connectivity at 15 km but forest connectivity at 10 km.

The human model we retained contained roads and human population density, as did the general model, but also included the % of agricultural areas (agri) and was far the best model considering AIC (ΔAIC with the next model = 3.3).

1.2 Model evaluation

The general model was reliable in predicting bear presence. This was true in both areas; with the validation dataset in Cantabrian (the model gave a probability higher than 0.6 and 0.5 for 72% and 82% of the bear presence, respectively) and with the data from Pyrenean bear population (the model gave a probability higher than 0.6 and 0.5 for 65% and 80% of the bear presence, respectively).

The same trend was found for the natural model for both datasets: 80% and 66% of the bear presence in the Cantabrian Mountains had a probability higher than 0.5 and 0.6, respectively. In the Pyrenees, 59% and 74% of the bear presence had a probability higher than 0.5 and 0.6, respectively.

The human model was even better than the general model in predicting bear occurrence in Cantabrian with 92% of the bear presence having a probability higher than 0.5 and 72% a probability higher than 0.6. The same trend as the general model was found when evaluating the model in Pyrenees: 81% and 63% of the bear presence had a probability higher than 0.5 and 0.6 respectively.

1.3 Habitat classification

Following Naves et al. (2003), we used the linear regression between the general model and the average of the natural and human models to determine the thresholds for the habitat quality classification (Figure 4). The explained variance of the linear regression was high: $R^2 = 0.91$. We classified habitat as source-like when $f_n > 0.5$ and $f_h > 0.5$; attractive sink-like when $f_n > 0.5$ and $f_h < 0.5$; refuge when $f_n < 0.5$ and $f_h > 0.5$; sink-like when $f_n < 0.5$ and $f_h < 0.5$. Habitat was classified as avoided matrix when $f_n < 0.175$ or $f_h < 0.165$.

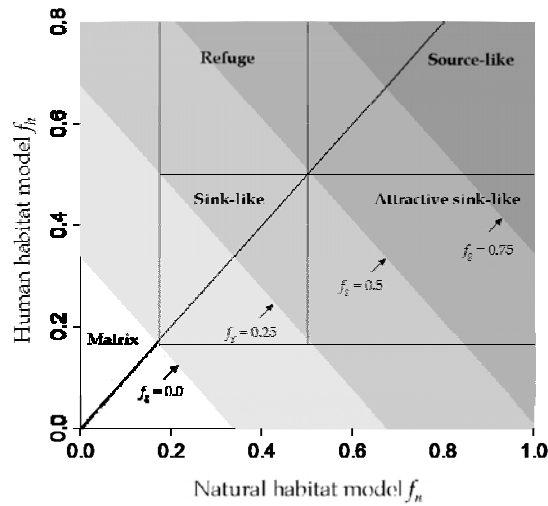


Figure 4: Habitat quality classification using the two-dimensional space of the natural habitat model and the human habitat model. The thresholds are estimated using the equation of the regression between the general model and the average of the human and natural model: $(fn+fh)/2 = 0.17 + 0.67fg$.

We spatialized these classifications to obtain a map of habitat quality in the Pyrenees (Figure 5), in the Cantabrian (Figure 6), and in the entire countries of France and Spain (Figure 7). Most (68%) of the Pyrenean bear presence was found in source-like habitats; 16% in refuge habitats; 7% in attractive sink-like habitats; 6% in sink-like habitats and 3% in the avoided-matrix habitat.

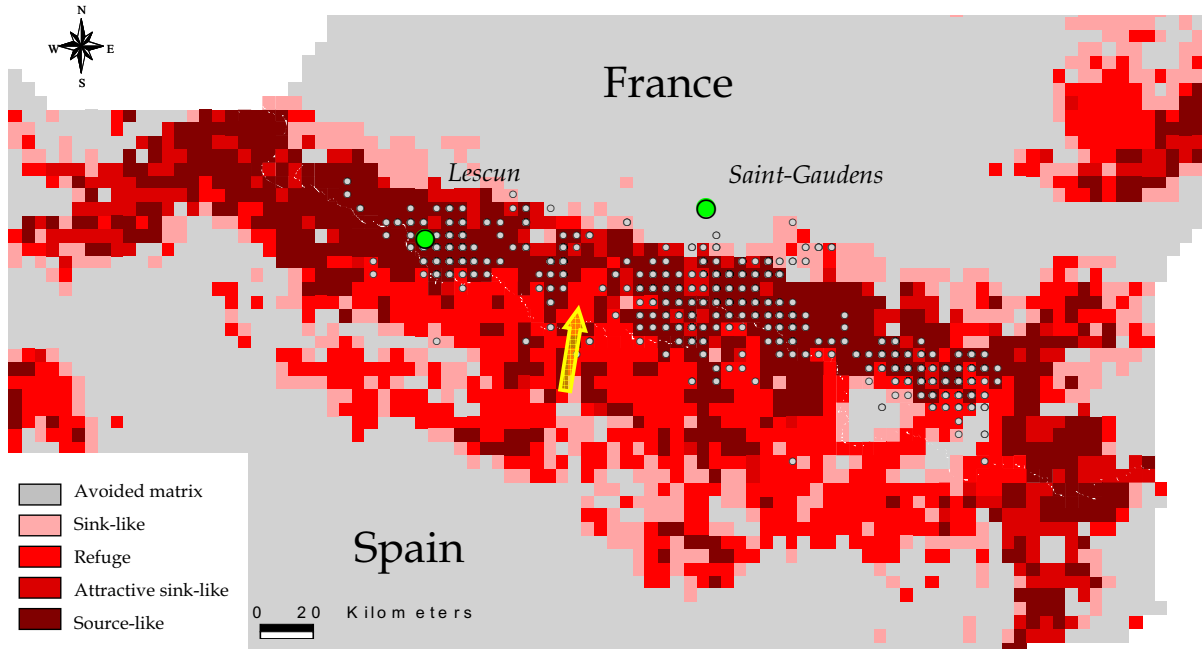


Figure 5: Map of habitat quality for the brown bear in the Pyrenees using the conceptual approach of Naves et al. (2003). Gray dots identify cells with bear presence. The yellow arrow shows the area between the two subpopulations.

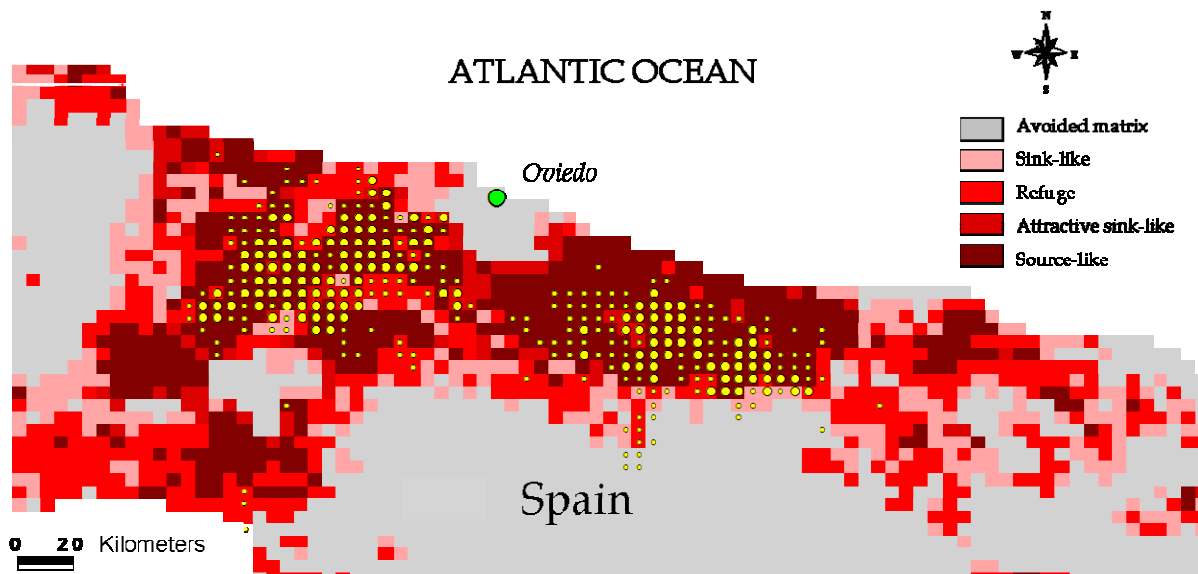


Figure 6: Map of habitat quality for the brown bear in the Cantabrian Mountains using the conceptual approach of Naves et al. (2003). Small yellow dots identify cells with sporadic bear presence (<3 observations); large yellow dots show regular bear presence (≥ 3 observations).

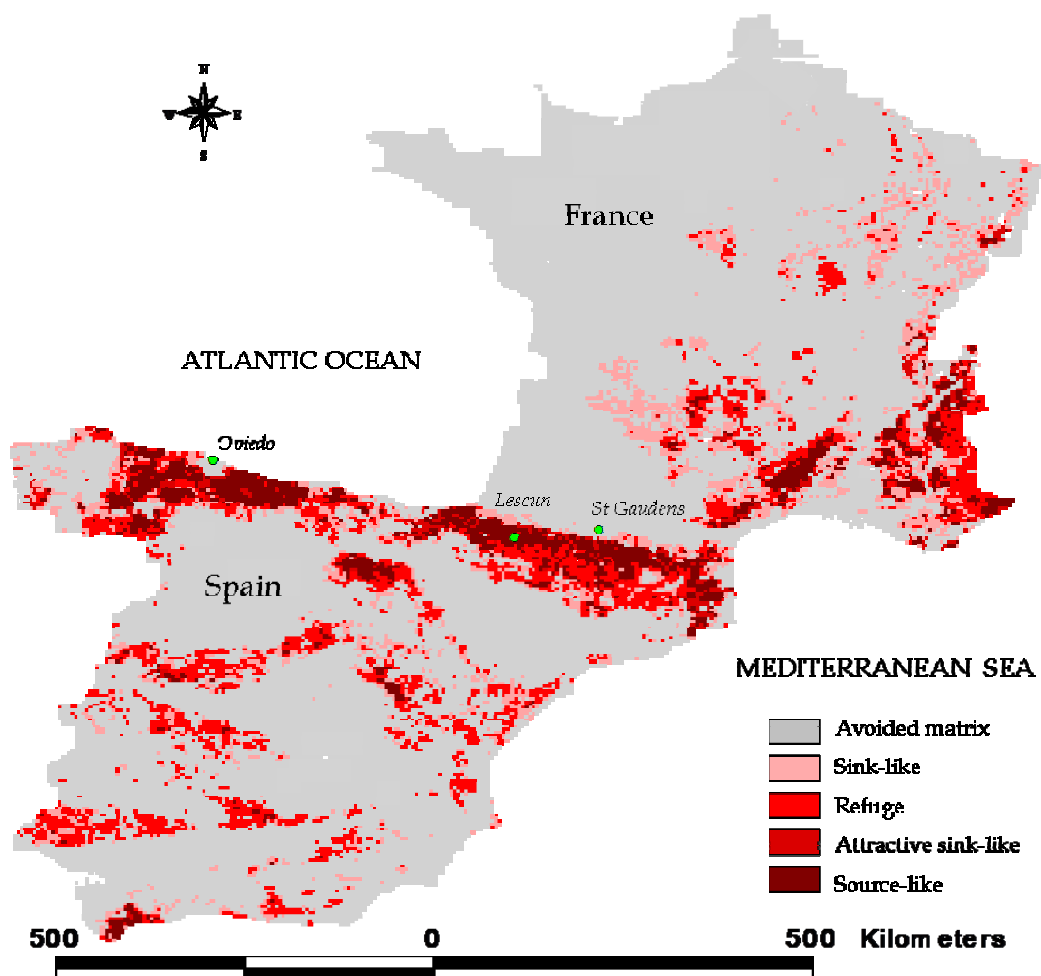


Figure 7: Map of habitat quality for the brown bear in France and Spain.

2. Local scale

2.1 Landscape structure

Two axes of the PCA explained 45% of the variability of the landscape structure (30% and 15% for the first and the second axes, respectively, Figure 8). The PCA separated human areas from more natural areas on an elevational gradient. Urban areas, roads and agricultural areas were located at low elevations and flat terrain, whereas natural open areas were located at high elevation on steep slopes. Deciduous forests tended to be located close to human areas whereas coniferous, mixed and regenerating forests were not particularly associated with particular elevations or types of area (human areas or natural areas).

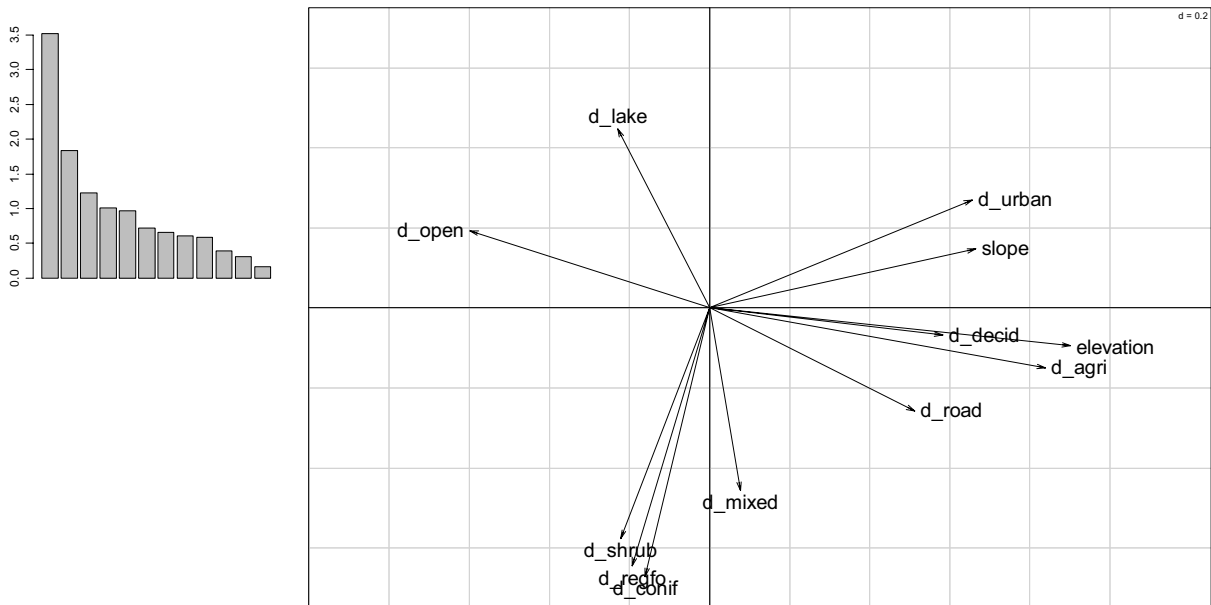


Figure 8: Projection of the environmental variables of the Pyrenean study area (France-Spain) in the factorial plan of the PCA. Left: representation of the eigenvalues of the analysis.

2.2 Ecological niche analysis

Using the broken-stick method (Jackson, 1993), we chose to keep the first and the last axes of the FANTER (Figure 9). The first axis was mainly correlated with mixed forests, coniferous forests, roads, agricultural areas and regenerating forests (see scores of the variables on the first axis in Table 3). The pattern of the utilization distribution compared to the available distribution is obvious on the scatterplot of the niche (Figure 9) and allowed us to identify the preferred habitats of the Pyrenean brown bears. The ecological niche of the bear indeed presents a strong marginality (Figure 9 & 10), bears being located preferentially in steep areas

with forests, far from agriculture and regenerating forests, compared to what was available in the study area. Paradoxically, roads were associated positively with bears distribution, but to a lesser extent.

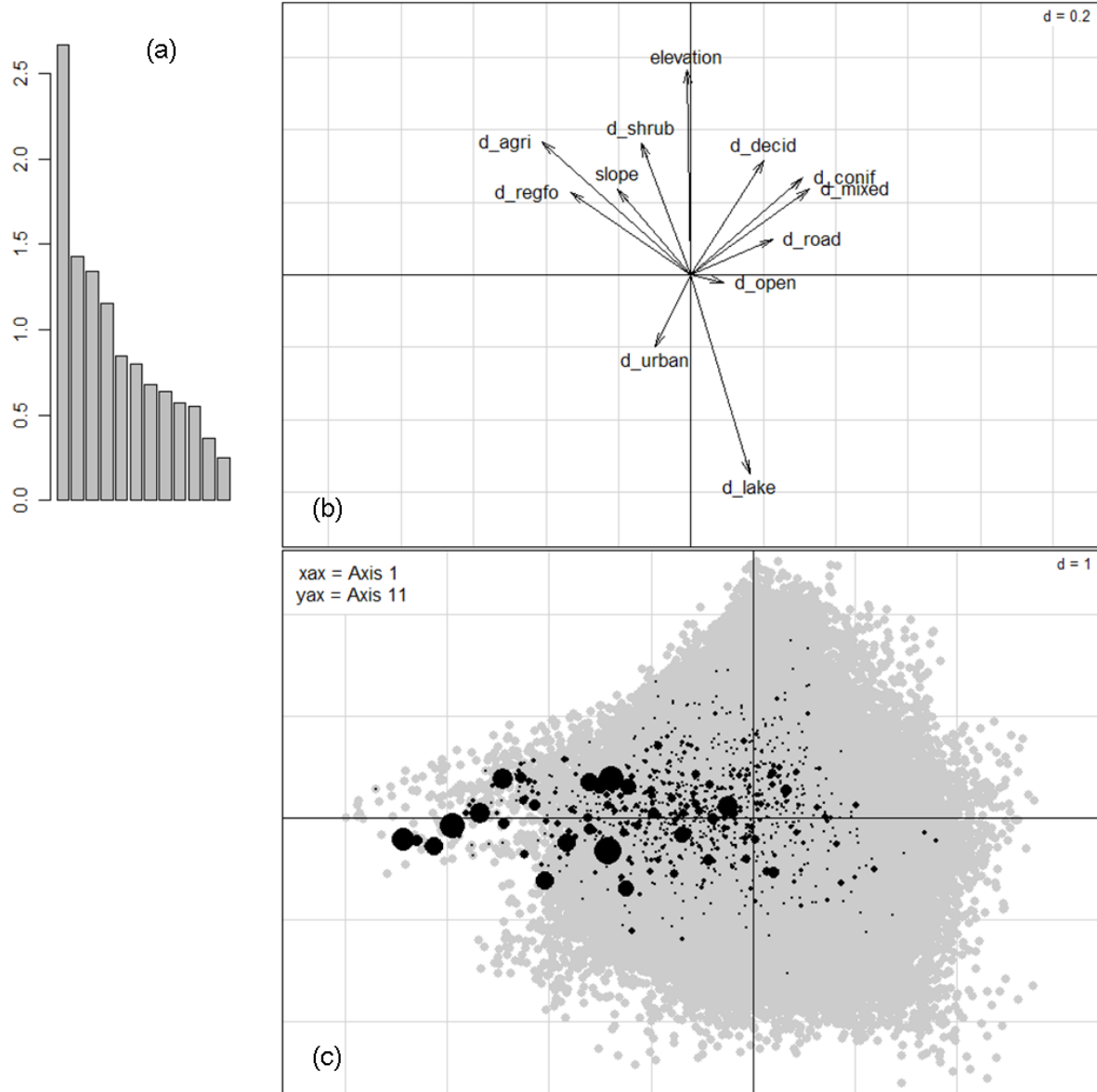


Figure 9: Results of the Factor Analysis of the Niche Taking the Environment as Reference (FANTER). (a) Representation of the eigenvalues of the analysis. (b) Correlation of the environmental variables with the first axis (which maximizes the niche marginality) and the last axis (which maximizes the specialization) of the FANTER. For each variable, the length of the arrow represents the strength of the correlation with axis. The longer the arrow, the stronger the correlation. The direction of the arrows on the first axis defines the marginality or the specialization by bears. For example, arrows that are highly correlated with the first axis and in the direction of the niche mean that high values of the variable are preferred by bears. Arrows that are highly correlated with the last axis and in the direction of the niche means a strong specialization for high values of the variable. (c) Projection of available distribution (gray dots) and the utilization distribution (weighted black dots).

Table 3: Correlation of the habitat variables from the Pyrenean study area (France) on the first and last axes of the Factor Analysis of the Niche Taking the Environment as Reference (FANTER).

Habitat variables	First axis	Last axis
elev	- 0.009	0.567
slope	- 0.204	0.237
d_agri	- 0.411	0.366
d_conif	0.309	0.267
d_decid	0.202	0.316
d_lake	0.162	- 0.549
d_mixed	0.328	0.236
d_open	0.091	- 0.022
d_regfo	- 0.333	0.228
d_road	0.228	0.098
d_shrub	- 0.136	0.364
d_urban	- 0.098	- 0.197

Bears appeared to specialize on the medium range of elevations (Figure 9 & 10; correlation with the last axis = 0.567; no particular direction on the first axis) and areas close to lakes. To a lesser extent, bears specialized on areas far from agriculture and without shrubs, but close to deciduous forests.

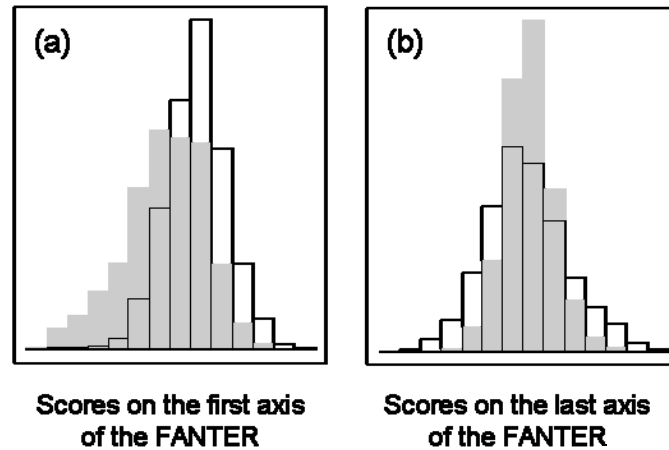


Figure 10: Scores of available distribution on the Pyrenean study area (France-Spain) (white bars) and utilisation distribution by brown bears (gray bars) on the first (a) and last (b) axes of the Factor Analysis of the Niche Taking the Environment as Reference (FANTER). The scores on the first axis highlight the marginality of the niche compared to what is available. The scores on the last axis show the specialization of the bears (variance of the utilization distribution is lower than available distribution).

2.3 Habitat suitability model and map

Our local model was also reliable in predicting indices of presence of bears. In this model, 97%, 91% and 46% of the data used to fit the model (from 1996 to 2006) were at $d^2 \leq 10$, $10 < d^2 \leq 20$ and $20 < d^2 \leq 30$, respectively. We used data from 2007 and 2008 to evaluate the model, and 96%, 78% and 36% of these data were at $d^2 \leq 10$, $10 < d^2 \leq 20$ and $20 < d^2 \leq 30$, respectively. The spatialization of the square Mahalanobis distances are shown on Figure 11.

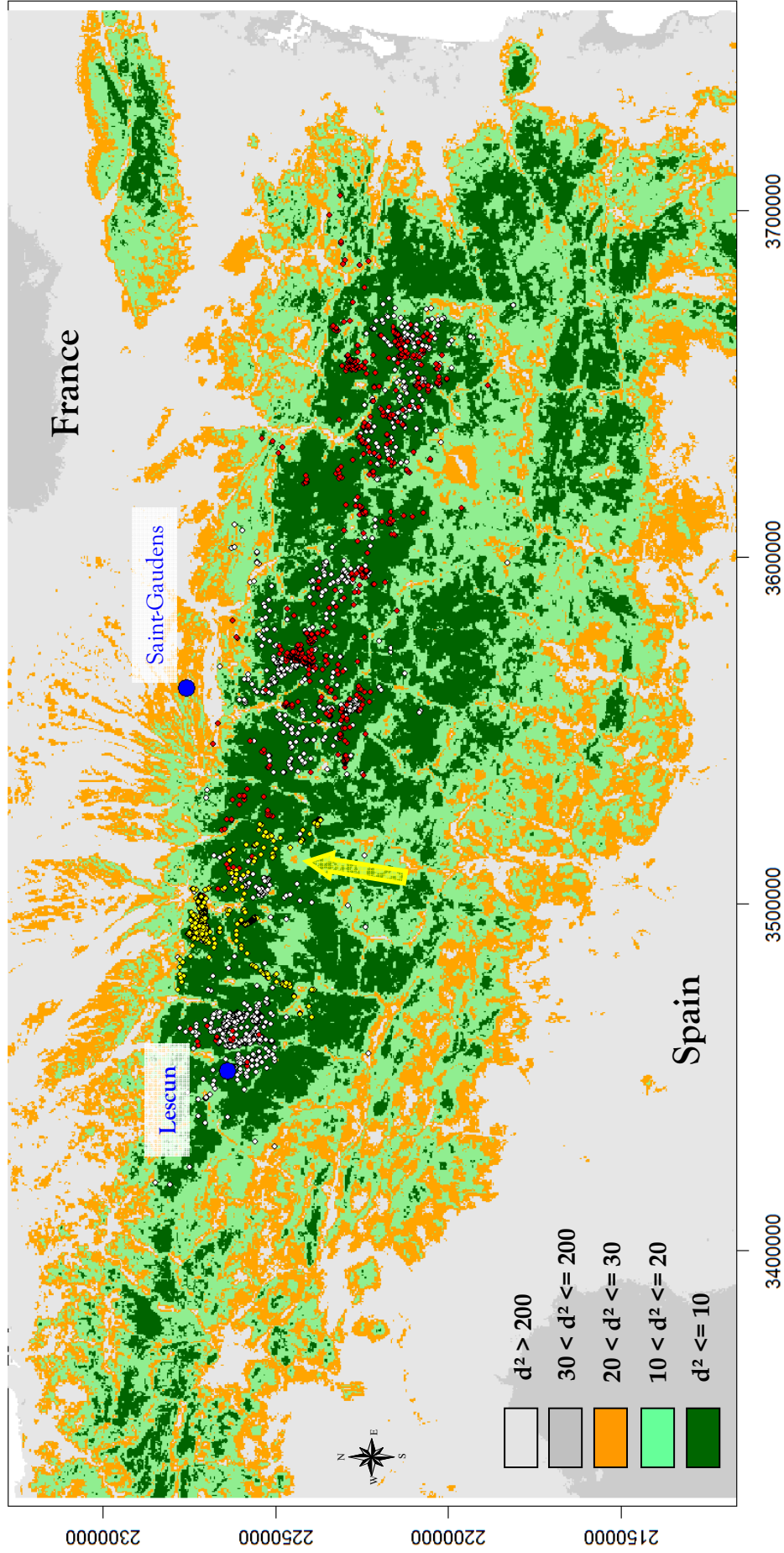


Figure 11: Habitat suitability map of the Pyrenean brown bears in the Pyrenees. Green areas correspond to areas close to the bear niche optimum ($d^2 \leq 20$). Gray dots show indices of presence used to fit the model. Red dots show indices of presence used to evaluate the model (indices of presence collected in 2007 and 2008). Yellow dots show the telemetric relocations of the only female belonging to the western core area. The yellow arrow shows the area between the two subpopulations.

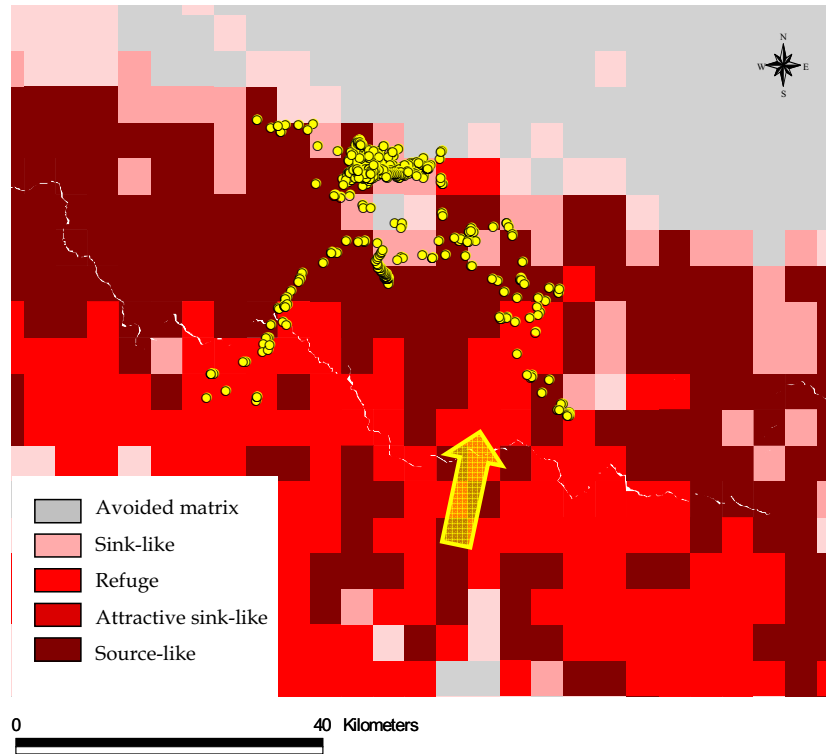


Figure 12: Telemetric relocations (2006) of the only female belonging to the western core of the Pyrenean brown bear population on the habitat quality map resulting from our global model. The yellow arrow shows the area between the two subpopulations.

DISCUSSION

We studied habitat selection patterns of brown bears at a global scale (for two European populations, on a large extent) and at a finer scale in Pyrenees (finer grain and more accurate environmental variables). The global-scale analysis allowed us to (1) detect a common pattern of habitat selection among the Cantabrian population and the Pyrenean population, (2) therefore to quantify the amount of suitable areas in both study areas and also on larger extent, and (3) to detect potential connectivity or barriers between the subpopulations in each areas and between the two populations.

The logistic-regression model we built using bear data in Cantabrian fitted well in Pyrenees where 80% of the bear presence had a probability higher than 0.5. As expected, brown bears preferred areas with a high cover of tree species that produce hard mast. Bears were also located preferentially in rugged areas, which is consistent with the literature (at different spatial scales, Apps et al., 2004; Nellemann et al., 2007, Paper II), and seek for areas with sufficient forest connectivity at large scale (15 km). Surprisingly, bears also were located in areas with greater shrub cover. The general model indicated that bear presence was

negatively correlated with areas with high road density and high human population density, as expected. The human model, however, also highlighted the negative influence of agricultural areas. Although agricultural areas are not particularly correlated with human population density ($\text{cor} = -0.02$), they are located mainly at low elevations and on flat terrain, therefore not associated with rugged terrain ($\text{cor} = -0.59$) and might be perceived as risky areas by bears.

The agreement of habitat selection patterns in Cantabrian and in Pyrenean allowed us to model habitat quality for bears using the source-sink theory (Naves et al., 2003; Pulliam, 1988) for both population ranges. Within Cantabrian, the two sub-populations (Western and Eastern) are disconnected by low-quality habitats (Figure 6). In the north, around Oviedo, areas have been classified as matrix habitat by the model, probably due to the high human density, which prevents any exchange between the subpopulations. The large areas of source habitats where the bears are present, are separated by areas of attractive sink, which is good for reproduction negative for bear survival. Actually, although the forest cover is relatively high within this area, high road density decreases the quality of the habitat. Further south, a more “secure” connection might be found in refuge habitats which are good for survival but not for reproduction. However, the low habitat quality for reproduction might prevent exchanges of females, as they should be more selective than males. It should also be noted that a large area of source-like habitat is not occupied by bears, at least not regularly. Actually, this area was historically occupied by bears, as shown by Naves et al. (2003). In their study however, half of this area was classified as attractive-sink like.

In Pyrenees, our model also highlighted the low quality habitat separating the subpopulations (Figure 7). However, these are mainly refuge areas, i.e. sub-optimal habitat for bears. Indeed, long-lived species such as bears are less sensitive to reproductive parameters than survival (Wiegand et al., 1998). However, as stated previously, these habitats might be perceived negatively by females, which we assume seek out good habitats for reproduction, and might also prevent them from colonising the western subpopulation in Pyrenees. The spatial behavior of the female belonging to the western area showed that she is located half in source habitat and half in attractive sinks (Figure 12). Note, however, that these telemetric data were collected the year after it was released in the Pyrenees. Its spatial behavior might therefore correspond to exploration of new habitats and it might thus be less selective about habitat. In the north however, a remnant connection between source habitats from the western part and the central part of the Pyrenees could represent a potential corridor between the subpopulations, especially for females.

The map of habitat quality for the entire countries of France and Spain do not portend a possible natural colonization of good-quality habitats by the bears. Indeed, the eastern part of the Pyrenees and the potential patch of good habitat in the “Massif Central” are separated by at least 20 km of matrix habitats, and the adjacent low-quality habitats are severely disconnected. The distances between the large areas of source habitats (which could contain viable populations) range from 150 to 200 km.

In the Pyrenees, we found a strong agreement between the patterns observed at the local scale and the global scale. Bears preferentially used forested areas and particularly those that produce hard mast, compared to available areas. Although deciduous forests tend to be close to human infrastructures (Figure 8), we found that bears were marginal on short distances to this type of forests but not particularly on short distances to urban areas. We interpreted this to show an avoidance of these structures by bears (Figure 9). Moreover bears are marginal on areas far from agricultural areas (Figure 9). They are specialized on a medium range of elevations, probably because human density and human infrastructures are found at low elevations and vegetation productivity becomes low at high elevations (Figure 8). Relief is not limiting in itself, as brown bears, also are found at low elevations (Scandinavian population, Dahle et al., 1998) and very high elevations (Pakistani population, Bellemain et al., 2007). In Pyrenees, the observed pattern related to elevation might therefore be a trade-off between vegetation productivity and low disturbance. Paradoxically, bears tended to be located near roads, contrary to previous results. At a global scale, bears might prefer areas with low road density, but they seem not to particularly avoid roads at a local scale. It should be noted however that bear mortality due to car accidents is not negligible in the Pyrenees as well as in other brown bear populations (Italy, 8 collisions with vehicles in nine years, C. Groff, pers. com.).

This model did not distinguish between the different types of habitat quality (source-sink theory) and the quantity of good habitats ($d^2 \leq 20$) encompassed larger areas than source habitats predicted by our global model. Also, the separation between subpopulations seemed to be more reasonable with the global model, and we could identify the lower habitat quality of these habitats (Figure 11). A combination of these two models might therefore be more powerful in determining areas of high interest for conservation purposes.

LIMITATION OF OUR MODELS

Several concerns should be addressed concerning interpretation of the models. First, the bear presence dataset comes from expanding populations. Therefore, areas where bears are absent might be unsuitable habitats or suitable habitats not yet occupied by bears, which leads to underestimation of the power of explanatory variables (Boyce & McDonald, 1999). As a consequence, high-quality habitats classified by our models are minimum suitable areas for bears whereas low-quality habitats might actually be suitable. Second, our models are based on the collection of presence data. The map of the distribution of habitat quality might therefore mirror the sampling protocol or habitat accessibility to humans. Indeed, indices of presence might be more abundant in areas easily accessible by humans. The sampling protocol might affect the reliability of a statistical model, as monitoring frequency may differ between areas. A better protocol would be collection of data on random transects over the entire Pyrenean Mountains instead of subjective transects. However, this kind of protocol is difficult to apply in the field, especially in rugged terrain (steep slopes at high elevations). However, we used indices of presence collected non-systematically to fit our local model, which reduced this potential bias. We are therefore quite confident in the prediction of high-quality habitat by our model, although it might be too conservative and might have overlooked areas that could be suitable.

CONSERVATION IMPLICATIONS AND PERSPECTIVES

Overall, our models have proven to be useful in mapping the distribution of suitable habitats for brown bears in Cantabrian Mountains and Pyrenees. As we used environmental variables at a large enough to be easily applied in different areas, our global model fitted in Cantabrian showed a good transferability outside its calibration range, i.e. in Pyrenees. Therefore, it seems to be a reliable tool to predict brown bear habitats over broad spatial extents. For example, we can expect the same habitat use pattern at the European scale. Even if habitats differ across Europe, habitat use patterns using these variables should be consistent. However, fitting this model in all of Europe would require validation in other brown bear populations, such as the Scandinavian population. We could not validate our model on Scandinavian bear presence data, as some variables were not available at the time we performed this analyses.

This model allowed us to estimate the quantity of available suitable habitat and the fragmentation of these habitats. We therefore can see that in the Pyrenees, a large area of

suitable habitats is not (at least not anymore) occupied by bears (Figure 7; in the western part of the Pyrenees Mountains), which is connected with the western core of brown bear population. However, the local model revealed more isolated patches of suitable habitats in this area. Nevertheless, as mentioned earlier, unsuitable areas might have been overlooked by our model. The association of the global and local models should however be a useful tool for conservation planning, in particular to identify habitats that should receive high priority for conservation or those where potential reintroductions should be located.

Our global model also highlighted the relatively poor habitat quality between subpopulations in both areas. However, in Pyrenees this is essentially refuge habitat, which might favor an exchange of males. In the north, some source habitats and attractive sink habitats are still connected, which might encourage female exchanges. As conservation planning should indeed focus on the connectivity of these two subpopulations, actions might be more efficient within this area, allowing females from the central subpopulation to access the western subpopulation (almost only composed of males).

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SCANDINAVIAN BROWN BEAR RESEARCH PROJECT
DEPT. OF ECOLOGY AND NATURAL RESOURCE MANAGEMENT
NORWEGIAN UNIVERSITY OF LIFE SCIENCES
P.O.Box 5003
NO-1432 Ås, NORWAY
PHONE: +47 64 96 57 30
www.bearproject.info



NORWEGIAN UNIVERSITY OF LIFE SCIENCES
NO-1432 Ås, NORWAY
PHONE +47 64 96 50 00
www.umb.no, e-mail: postmottak@umb.no