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FACULTEIT LANDBOUWKUNDIGE EN TOEGEPASTE BIOLOGISCHE WETENSCHAPPEN
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DISSERTATIONES DE AGRICULTURA

Doctoraatsproefschrift nr. 550 aan de Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen van de K.U.Leuven

ANALYSING ROE DEER HABITAT SELECTION; METHODOLOGICAL PROBLEMS AND POSSIBLE SOLUTIONS

Proefschrift voorgedragen tot het
behalen van de graad van Doctor in de
Toegepaste Biologische Wetenschappen

door

Jim CASAER

Januari 2003

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Voorwoord

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Samenvatting

Het doel van dit werk is een bijdrage te leveren aan het proces van kennisverwerving betreffende de interacties tussen reewild populaties en hun omgeving. Om vragen omtrent de wisselwerking tussen dieren en hun omgeving te kunnen beantwoorden, wordt klassiek het habitatgebruik van de diersoort bestudeerd. Het domein van habitatselectie-studies wordt echter gekenmerkt door een veelvoud van methoden en technieken, elk met hun eigen beperkingen en veronderstellingen. Alhoewel er een uitgebreide literatuur bestaat rond deze problematiek en er nieuwe technieken ontwikkeld worden om tegemoet te komen aan de technische beperkingen van bestaande methoden, blijkt er een groot verschil te zijn tussen de theoretische mogelijkheden en de toepassing ervan in terreinstudies. Omwille van hun complexiteit worden veel van de nieuw ontwikkelde methoden ofwel niet, ofwel foutief gebruikt, zonder dat de voorwaarden die het gebruik ervan rechtvaardigen, gerespecteerd worden. Naast methodologische vragen kan men zich daarenboven vragen stellen bij sommige van de basisveronderstellingen waarop habitatselectie-studies gebaseerd zijn (hoofdstuk I).

Daarom besloten we de methoden, gehanteerd in de verschillende stappen van het bestuderen van habitatgebruik door reeën, te analyseren. De mogelijke invloed van bepaalde methoden en gehanteerde definities op de onderzoeksresultaten werd nagegaan (hoofdstuk II & VI). Verschillende basisveronderstellingen en gebruiksvoorwaarden werden geanalyseerd en waar nodig werden oplossingen gezocht door bestaande methoden aan te passen (hoofdstuk III), nieuwe technieken uit te testen (hoofdstuk IV) of zelf nieuwe methoden te ontwikkelen (hoofdstuk V). Hiervoor combineerden we theoretische inzichten met empirische testen.

Daarnaast bestudeerden we het gebruik van overgangszones tussen verschillende vegetatietypes door reekitsen (hoofdstuk VI). Deze directe toepassing van bepaalde theoretische oplossingen in een praktijkstudie maakte het mogelijk de bekomen resultaten te linken aan biologische vragen en de biologische zin van de bekomen resultaten na te gaan. Dit laatste is aan de hand van simulaties niet mogelijk. Hierdoor werd tevens vermeden nieuwe methoden te creëren die in de praktijk niet toepasbaar zijn.

In de volgende paragrafen worden die deelsaspecten van habitatselectie-studies, die in het kader van dit doctoraat onderzocht werden, kort beschreven.

***

De meeste habitatselectie-studies starten met het landschap op te delen in verschillende habitattypes en kennen vervolgens aan elk van deze habitattypes een waarde toe voor elk van de belangrijke habitatfactoren (voedsel, nestgelegenheid, dekking). Deze werkwijze gaat ervan uit dat habitatfactoren constant zijn in één habitattype en verschillen tussen de habitattypes. Door een bestaande methode om dekking te meten aan te passen voor het gebruik in reewild-studies, en de aangepaste methode vervolgens toe te passen (hoofdstuk III), onderzochten we de geldigheid van deze veronderstelling. Onze resultaten doen vragen rijzen over de geldigheid ervan. Daarom stellen we voor dat men in de toekomst eerst, gebruik makend van de aangepaste methode, de relatie tussen dekking en andere, eenvoudig te karteren, habitatkenmerken (vegetatietype, sluitingsgraad, topografie, beheer...) onderzoekt. Vervolgens zou deze informatie gebruikt kunnen worden om rechtstreeks de relatie tussen reewild en dekking te bestuderen, zonder de –twijfelachtige– omweg te maken via een habitattype.

Het uitvoeren van habitatselectie-studies is gebaseerd op het vergelijken van het aanbod en gebruik van habitatfactoren (meestal via de omweg van habitattypes). Een mogelijke methode hiervoor is het relatief aantal waarnemingen (fixes) van een dier (of groep dieren) binnen een bepaald habitattype te vergelijken met het relatief aanbod ervan (uitgedrukt als de relatieve oppervlakte van het habitattype binnen een bepaald gebied).

Dit veronderstelt echter dat de kans om een dier waar te nemen onafhankelijk is van het vegetatietype waarin het dier zich bevindt. Onze resultaten (hoofdstuk IV) geven duidelijk aan dat dit niet zo is wanneer gebruik gemaakt wordt van GPS(global positioning system)-halsbanden om de dieren te lokaliseren. Daarenboven werd de kans op een GPS-waarneming beïnvloed door de inclinatiehoek van de halsband. Indien er een relatie zou bestaan tussen de inclinatiehoek van de halsband en de activiteit van het bestudeerde dier (bv. eten) enerzijds en het vegetatietype waarin het dier zich bevindt anderzijds, is dit een tweede element dat in strijd is met de veronderstelling dat de kans op een waarneming onafhankelijk is van het

vegetatietype. We tonen aan dat het mogelijk is om, door middel van een pilootstudie, een model op te maken om verkeerde conclusies ten gevolge van het verschil in waarnemingskans (tussen de verschillende vegetatietypes) te vermijden (hoofdstuk IV).
Om de geografische nauwkeurigheid van de lokalisaties aan de hand van GPS-halsbanden te verbeteren stelden sommige buitenlandse onderzoekers voor gebruik te maken van een lineaire correctie methode (als alternatief voor differentiële correctie). Uit onze studie blijkt dat de nauwkeurigheid van de plaatsbepaling, na het toepassen van de lineaire correctie, onvoorspelbaar is. We stellen daarom dat het gebruik van de niet-gecorrigeerde plaatsbepalingen, waarvan de nauwkeurigheid wél gekend is, te verkiezen is (hoofdstuk IV) wanneer differentiële correctie niet mogelijk is.

Een andere maat (i.p.v. het aantal fixes) voor het gebruik van een bepaalde habitattype door een dier, is de relatieve oppervlakte van het habitattype binnen het door het dier benutte gebied (home range). Tal van methoden bestaan om uit de verzamelde 'fixes' het door het dier benutte gebied (home range) af te leiden. Naast het bovenvermelde probleem van de afhankelijkheid van de waarnemingskans van het vegetatietype, wordt het gebruik van tal van methoden beperkt door hun basisveronderstellingen (onafhankelijke fixes, veronderstellingen over de aard van de onderliggende 'ruimtelijke gebruiksfunctie'). Daarenboven worden de eindresultaten veelal zeer sterk beïnvloed door parameterwaarden die de onderzoeker vooraf dient in te geven.

We ontwikkelden daarom een nieuwe methode (hoofdstuk V), die niet vereist dat de fixes onafhankelijk zijn van elkaar, noch dat vooraf parameterwaarden ingegeven worden. De methode analyseert het ruimtelijk gebruik van het gevolgde dier enkel en alleen op basis van de verzamelde fixes en maakt geen veronderstellingen over de aard van een onderliggende gebruiksfunctie.

De klassieke habitatstudies analyseren habitatgebruik aan de hand van modellen gebaseerd op verschillende hiërarchische schalen (b.v. de keuze van een home range binnen een regio, de keuze van deelgebieden binnen de home range). Deze aanpak is gebaseerd op de veronderstelling dat dieren een gelijkaardig hiërarchisch systeem hanteren bij het selecteren van omgevingsfactoren. Onze resultaten (hoofdstuk VI) tonen echter de sterke invloed aan van de bepalingen, gehanteerd om de verschillende hiërarchische schalen te definiëren, op de eindconclusies van habitatselectie-studies. Dit hypothekeert in sterke mate de veronderstelde algemene geldigheid van conclusies uit dergelijke studies. Daarnaast wijzen onze resultaten ook op het belang van overgangszones in het habitatgebruik van reekitsen (hoofdstuk VI), en bevestigen zo het veronderstelde belang van trade-off's tussen verschillende omgevingsfactoren bij habitatselectie door dieren. Trade-off's zijn echter dikwijls het resultaat van omgevingsfactoren die op verschillende schalen (in tijd en ruimte) ageren. Ook dit resultaat stelt het gebruik van het klassieke 'hiërarchische schalen'-model in vraag.

Tenslotte illustreren de resultaten van deze studie (hoofdstuk II & VI) de sterke interactie tussen de gekozen schalen (afhankelijk van de onderzoeksvraag en de onderzoekshypotheses) en de potentieel geschikte onderzoeksmethoden die gehanteerd zouden kunnen worden.

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We beëindigen deze studie door, gebruik makend van de bevindingen van de verschillende hoofdstukken, een alternatieve aanpak te suggereren om een beter inzicht te kunnen verwerven in de interacties tussen reewildpopulaties en hun omgeving in het bijzonder, en dier-habitat interacties in het algemeen.

Summary

The overall aim of this research was to contribute to the process of gaining a better understanding of the interactions between roe deer and their environment. Wildlife biologists generally use habitat selection studies to answer questions regarding the role of environmental factors in population regulating processes. However this approach is characterised by a profusion of methods, each with their background assumptions and constraints. Though there is a vast literature on these problems and new techniques evolve to overcome the technical constraints, there is a large gap between the theory and the use of these new techniques in empirical studies. Due to their complexity many of the newly developed methods are not used, or wrongly used, without considering the conditions that should be met to allow their use. Finally, one could question several of the basic assumptions the habitat selection approach is based on (chapter I).

Therefore we analysed the methods used in the different steps of studying habitat selection. We compared the influence of the chosen research method or used definitions with the influence of other factors determining the research outcome (chapter II & VI). We reconsidered several classical assumptions of habitat selection studies and tried to overcome the main problems. For this purpose we combined, and confronted a theoretical approach with collected field data. Apart from testing new methods (chapter V) or modified methods (chapter III) and new techniques (chapter IV), we followed 8 roe deer fawns during the first months of their life and focussed on the use of ecotones (transition zones between different vegetation types) (chapter VI). The direct link of theoretical findings to biological questions allowed us to question the biological meaningfulness of our results and prevented the creation of new technical solutions that are hardly applicable in field studies.

The following paragraphs highlight those aspects of habitat selection studies, we focussed on for this Ph.D.

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Many habitat selection studies are based on dividing the landscape in different 'homogenous' habitat types and attributing values for each of the key environmental factors (food, cover .....) to the different habitat types. This method is based on the assumption that environmental factors are homogenous within 'habitat types' and differ between 'habitat types'. We modified a method, developed to estimate hiding cover for deer (*Odocoileus spp.),* to be applicable for roe deer (chapter III). Subsequently we used the adapted method to test the above mentioned assumption. Our results pose serious doubt on the validity of this assumption (chapter III). We therefore suggest to use, in the future, the modified method to establish the complex relationship between hiding cover and other (easily mappable) environmental characteristics such as vegetation type, canopy closure, land use.... Subsequently this information could then be used to study the direct relationship between cover and habitat use by roe deer, rather than the indirect approach using the 'habitat type'.

Studying habitat selection is based on comparing the availability and use of different environmental resources (often replaced by habitat types – see above). This is done by comparing the relative number of animal observations (fixes) in a certain habitat type and the relative availability of that habitat type (often expressed as relative area). This assumes that the probability of getting an animal fix is independent of the vegetation type. Our results (chapter IV) clearly show that this assumption is not valid when using GPS collars in temperate forest ecosystems. Moreover the observation rate of the GPS collars is influenced by the observation angle of the collar. Whenever there is a relation between the observation angle of the collar, the animal's activity and the habitat type (e.g. feeding activity), this violates the assumption of equal observation probability for all vegetation types. We showed the possible use of pilot studies, using stationary GPS collars in different vegetation types of the study area, to test the performance and accuracy of the collars. Subsequently we illustrated how the acquired information can be used in models to overcome the habitat-related differences in observation rate.

Several researchers proposed to use a linear correction method to improve the accuracy of raw GPS data, whenever post-processing differential correction is not possible. We showed that this method is not reliable because of the unpredictable outcome of the correction method, based on false assumptions concerning the functioning of GPS. We therefore suggest that it is more appropriate to use the non-corrected GPS locations, with a known error probability (chapter IV).

An alternative measure for the use of a certain habitat type by an animal, is the percentage of that habitat type within the area used by the animal (often referred to as home range). Many methods exist to derive the area used, from a collection of animal fixes. Apart from the above mentioned assumption of equal observation probability, most of the frequently used methods are limited in their applicability because of their basic assumptions (underlying utilisation distributions, independent observations ...). Moreover, many methods are strongly influenced by the auxiliary parameters chosen by the researcher. We therefore developed a new non-parametric method to derive space use directly from the animal fixes, without the need to define any ancillary parameters (chapter V). The method does not require independent animal observations and makes no assumptions on the underlying utilisation distribution.

The classical habitat selection studies are based on comparing availability and use of habitat types on different hierarchical scales, assuming animals use similar hierarchical scales to select environmental characteristics. Our results show however the strong influence of the definitions used to determine the different hierarchical scales on the final research outcome in habitat selection studies (chapter VI). This result questions the universality of the conclusions of such studies. Furthermore our results (chapter VI) illustrate the important use of edges by roe deer fawns, thereby highlighting the importance of trade-offs in habitat selection by roe deer. Trade-offs between different environmental factors are however the result of factors interacting at different spatial and temporal scales, thereby questioning the classical approach. Finally our result clearly show (chapter II & VI) the strong interaction between the chosen scale (depending on the research question and the research hypothesis) and appropriate research methods.

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We finish this study by suggesting a strategy to overcome the above-mentioned problems, combining the solutions given in the different chapters.

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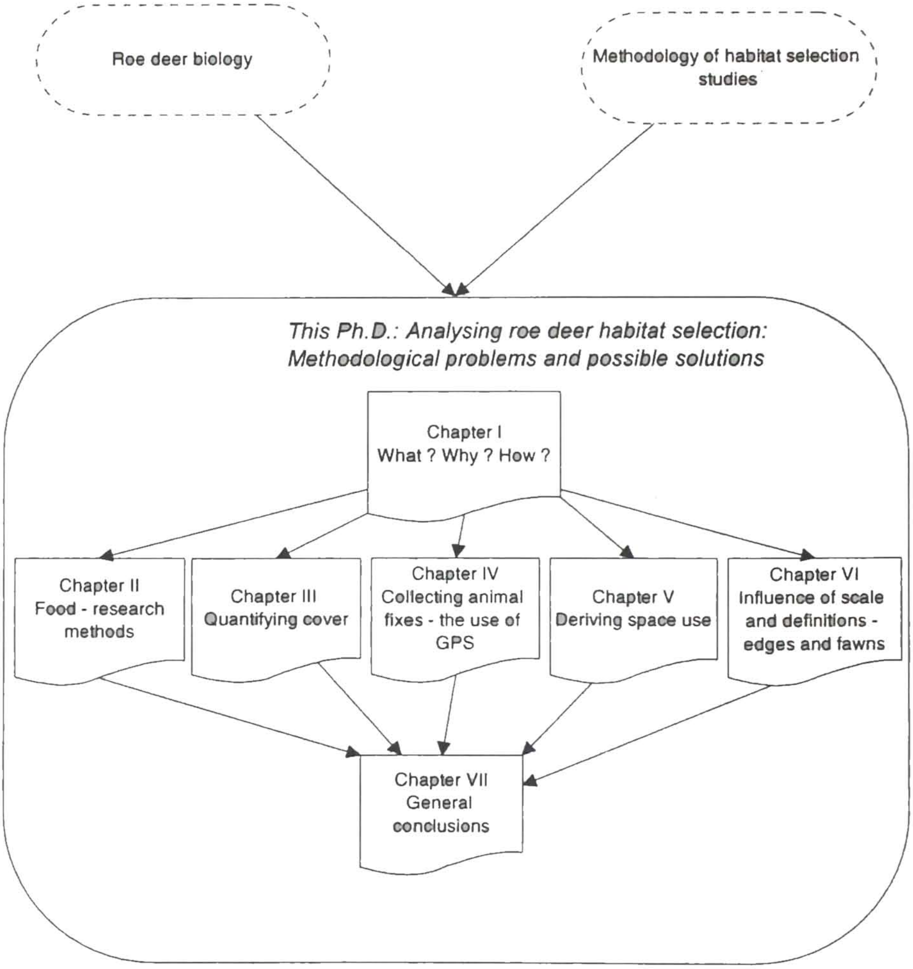

Figure 0.1: Structure of the Ph.D.

Because of the large amount of specific terms used in this work, a glossary was added at the end.

Chapter I. Setting the scene; roe deer, forests and the problems related to studying the interactions between them

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I.A Why study the interactions between ungulates and their habitat

> *'Denn nur Einsicht in die Wirkungen des gestalteten Waldes auf das Wild gibt umgekehrt die Möglichkeit, die Wirkungen des Wildes auf den Wald in ihren Ursachen richtig einzuordenen und von daher mögliche Konfliktlösungen zu suchen' Hans-Jürgen Otto (1979).*

All over Europe, traditional sylvicultural systems are shifting towards more ecological forest management. From a clearcut system, based on artificial regeneration on large areas, there is a trend towards more natural regeneration and smaller regeneration units. However, the presence of large herbivore species often poses difficulties when even aged, single species stands are to be converted to multi-species, and multi-aged, forest stands (e.g. Kuiters et al. 1996). Even more because many ungulate species have the habit of preferring the seedlings and sprouts of those plant and tree species that are rare (Reimoser 1986b).

This change in sylviculture also means a shift towards a more ecological forest management approach in general. Rather than regarding the forest as a timber production system, the forest is currently considered as a multipurpose ecosystem. The role of wildlife and more specific wild ungulates within this ecosystem became a subject to be included in forest management and research (Hunter 1990, Patton 1997).

Wild ungulate populations have been severely affected by human activity all over the world. Hunting, supplementary feeding, the extermination of predators and the loss of habitat occurred on a large scale all over Europe. During the last decades the populations of red deer (*Cervus elaphus)* and roe deer (*Capreolus capreolus)* have been growing at a considerable rate in Europe. Moreover, the geographical distribution of some species (e.g. roe deer) extended during this same period. Disentangling the causes for these recent changes in population characteristics is difficult. Changes in the habitat suitability, partly due to the abandonment of stock grazing in forests, changes in hunting legislation and the creation of nature reserves all over Europe, can be mentioned as possible factors (Kuiters et al. 1996). In Flanders a similar evolution took place over the last 40 years for roe deer (Figure. I.1).

Ungulates may have a high impact on the structure and the species diversity of forests and scattered forest fragments in rural areas. The negative consequences of this impact are well known. Apart from browsing plants, ungulates also influence the plant dynamics and tree growth due to physical disturbance. Red deer and moose (*Alces alces)* strip bark, and roe deer damage saplings by fraying with their antlers (Latham 1999). Less known are the possible positive effects of ungulate populations on their habitat, such as an increase in plant diversity and the selective browsing of unwanted competing species (Reimoser and Gossow 1996). However, ungulate populations require ecosystems that are 'close to nature' to fulfil their positive function in the forest ecosystem (Reimoser 1986a). Forest management often unconsciously ignores the possible effects of its management actions on the ungulates present, thereby provoking game damage.

Therefore, a better understanding of the interactions between ungulates and their habitat is a necessity to prevent unwanted effects, both in forestry and in wildlife management, rather than having to repair the damage, to wildlife populations or forest, afterwards.

I.B Why study roe deer

In Flanders roe deer is the largest free living herbivore. Though fallow deer (*Dama dama)* occurs sporadically, these always are individual animals, escaped from deer farms. With the exception of Voeren (Southeast of Flanders), wild boar (*Sus scrofa)* does not occur in free living populations, neither does red deer.

Though the annual roe deer cull has been rising during the last years, both the number of animals and their geographic range has been expanding constantly during the last 40 years (see figure I.1.). In the season 1999/2000 a total of 2452 animals has been shot and the actual roe deer population was estimated at approximately 17,000 animals.

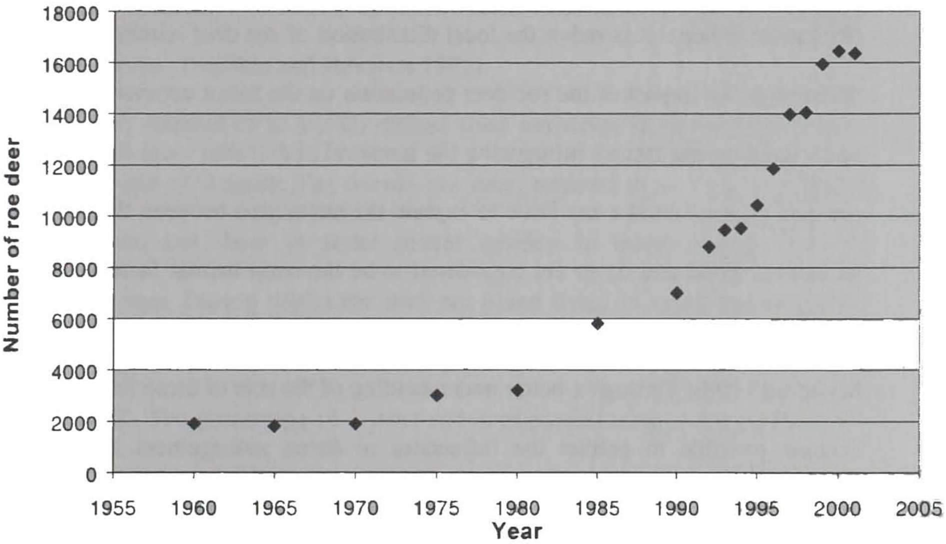

Figure I.1: Estimations of the roe deer population in Flanders during the last 40 years. Dots represent the population estimation by the Forest Service. (source: Afdeling Bos &Groen, de Crombrugghe and Wauters 1990).

In several places the animals show signs of local overpopulation (bad physical condition of the animals) and often there is a need to fence areas to achieve successful forest regeneration. The latter surely on those places where large, even aged forest stands are to be converted to a more diverse, mixed forest type. All these arguments together raise questions concerning the possibilities to manage roe deer populations and their impact on forests, by habitat manipulation alone or in combination with culling.

To predict the relative impact of roe deer on the forest ecosystem, a better understanding of factors controlling the population densities, the animal behaviour and its distribution are required (Latham 1999). Higher overall densities of roe deer do, however, not always result in a more severe impact on the forest vegetation (Reimoser 1986b). It is rather the local distribution of roe deer within the forest that determines the impact of the roe deer population on the forest ecosystem. Therefore, understanding the factors influencing the temporal and spatial local distribution of a roe deer population is a key issue to explain the interaction between the roe deer and its habitat. Food and cover are considered to be the main habitat factors influencing the habitat use by roe deer (e.g. Strandgaard 1972, Reimoser and Mauser 1986b, Mysterud 1998). Through a better understanding of the role of these factors, it should become possible to predict the influences of forest management actions on the distribution of the local roe deer population and consequently to manage more accurately roe deer populations and their impact on forests.

I.C Introducing the animal studied: roe deer

Though several good reviews on roe deer are available for the interested (Kurt 1991, Danilkin and Hewison 1996, Stubbe 1997, Linnell et al. 1998a), some aspects, important for a better understanding of the Ph.D., are recapitulated in the following paragraphs.

Roe deer are medium sized, forest dwelling herbivores. The average life weight varies between 20 and 30 kilogram and the average shoulder height varies between 65 and 70 centimetres (Stubbe 1997).

Roe deer are distributed all over Europe except Ireland (Andersen et al. 1998). The European roe deer *(Capreolus capreolus)* and the Siberian roe deer *(Capreolus pygargus)* are considered to be two different species. The latter is higher in shoulder height and heavier (Danilkin and Hewison 1996).

Male roe deer, referred to as bucks, defend their territories from the beginning of April till the end of August. The female roe deer, referred to as doe, live solitary during summer, but there is some spatial overlap in home ranges with the neighbouring does. During winter roe deer are found living in small family groups. The rut takes place between the 15th of July and the 15th of August (Danilkin and Hewison 1996). The percentage of 2 years old does participating in the reproductive process varies between 70 percent and 90 percent, depending on the equilibrium between the number of animals and the habitat (Gaillard et al. 1998). The presence of edges (between different habitat types), offering both food and cover at close distance, is considered to play a important role in determining the carrying capacity of the habitat (Von Raesfeld et al. 1980, Reimoser and Zandl 1993, Stubbe 1997).

Most of the young, referred to as fawns, are born between the 15th of May and the

15th of June, showing a birth-peek depending on the local climate (Linnell et al. 1998b). Roe deer is classified as a typical 'hider-species'. The neonatal survival strategy of the fawns is based on staying in well-hidden places most of the time, to prevent being noticed by predators (Linnell 1994). Only after several months, all traces of hiding behaviour fade and the fawns are continually associated with the doe, remaining at close distance most of the time (Linnell et al. 1998b). Several studies showed the importance of cover as a characteristic of the bedding sites for roe deer fawns (Gaillard and Delorme 1989, Linnell et al. in press). Non of these studies focussed, however, on the role of edges in the habitat selection of roe deer fawns, though the important role of edges is well known for adult roe deer (e.g. Reimoser 1986b, Tufto et al. 1996).

I.D Why study the methodological problems of habitat preference studies

> *"We are taught...that habitat is a critical component of any wildlife population. Yet the number of species for which measurable habitat characteristics can be related quantitatively (or even qualitatively in many cases) to the parameters governing a species' population dynamics, survival and recruitment, is minuscule" (White 2001).*

Habitat selection studies are considered to be 'the' instrument to gain a better, reliable knowledge of the species' needs and the factors determining its temporal and spatial distribution. Habitat management, whether to maximise the annual harvest, conserve endangered species, prevent damage to forest regeneration or promote biodiversity through an ecosystem-approach, should always be based on experience and research

(Chase et al. 2000). During the last decades wildlife research has, been criticised because it was unable to obtain the required reliable knowledge (Romesburg 1981, 1989, 1991, Gavin 1991, Murphy and Noon 1991, Nudds and Morrison 1991, Anderson 2001). Many wildlife management conflicts between different groups of stakeholders were impossible to solve because the basic biological knowledge to understand the problem is missing *'All stakeholders are right, given the assumptions each brings to the issue' (White 2001).*

The scale and the variability associated with the study of free-ranging animals is one of the reasons often hindering the formulation of definitive conclusions (Steury er al. 2002). However, the scientific methods applied in wildlife research, and the lack of methodological rigor, are also considered to slow down the progress in understanding nature and wildlife-ecosystem interactions.

Many studies are only describing associations between observed facts (Romesburg 1981). Though discovering associations between facts can help to take some management decisions, it does not provide any understanding of the process explaining the associations and does consequently not answer the 'Why – question'. (e.g. by Garshelis (2000) on the controversies concerning why the spotted owl prefers old-growth forest, despite the large number of habitat selection studies on this species). Wildlife research should focus on trying to understand the *mechanisms* driving population-dynamics and species-environment-interactions (Krebs 1995).

In wildlife research there is currently a general advocacy to reconsider the correct use, the predictive value, the limitations and the background assumptions of methods frequently used (e.g. habitat selection studies: Aebisher et al. 1993, Manly et al. 1993; hypothesis testing: Johnson 1999, Johnson 2002, Robinson and Wainer 2002, Steury et al. 2002; index values and convenience sampling: Anderson 2001; monitoring programs and adaptive management: White 2001).

As mentioned above, wildlife researchers commonly study habitat preference in order to assess a species' needs. Studying a species' habitat preferences is based on comparing the species' space use and the spatial distribution of vegetation characteristics and/or other environmental factors (such as disturbance). To gain reliable knowledge from habitat preference studies we therefore need to understand the limitations and basic assumptions of the methods used.

Indeed, during the last decades new methods were developed to derive space use (home ranges) based on animal fixes (places where animals were observed to have been, using visual observation, capturing methods or radio telemetry). Several papers were published on the differences between the various methods (Boulanger and White 1990, White and Garrot 1990, Lawson and Rodgers 1997). Simultaneously, statisticians developed new methods to compare the availability of environmental resources and their use by animal species (see Manly et al. 1993, Garshelis 2000). Finally, the progress in computer technology allowed the integration of geographic information systems (GIS) as a tool in wildlife habitat studies (McLaren and Braun 1993, Koeln et al. 1996, Corsi et al. 2000,).

Meanwhile those researchers collecting real field data still often apply old fashioned, theoretically rejected, methods (e.g. the use of Minimum Convex Polygons in home range studies (Boutin et al. 1991, Bideau et al. 1993, Koubek 1994, Mysterud et al. 1999) and the use of the quotient between observed and expected use as preference-index (e.g. Guillet et al. 1995)). This is mainly done because of the simplicity and the familiarity of such methods. Furthermore, many researchers use methods while violating the basic assumptions allowing the rightful use of the chosen methods (see Aebischer et al. 1993, Manly et al. 1993).

All these articles advocate and abundantly illustrate the importance of understanding the limitations of the applied methods and the necessity to quantify with rigor wildlife and environmental parameters, in order to gain reliable knowledge of the mechanisms driving wildlife-environment interactions.

To quote from Corsi et al. (2000) "*A common opinion among epistemologists is that we are facing a break between the development of advanced technologies [*and methods] *and our needs and abilities to use them.*"

I.E This study

We therefore decided to focus on the methodological aspects of studying habitat use by roe deer, rather than performing a new study on roe deer habitat use, rendering results that corroborate (or not) with previous studies, without understanding the impact and constraints of the methods used.

For each of the different steps in studying roe deer habitat use, we focus on the existing methods and technology, their limitations and applicability, their basic assumptions and possible impact on the results and research conclusions. If necessary, we modified existing methods, or developed new methods, and tested their performance.

Rather than using a purely theoretical approach we aim at combining, and confronting, as much as possible the theoretical, methodological aspects and the reality of data collected in the field and of biological questions on roe deer habitat selection. The use of field data allows, contrary to analysing different methods based on simulations, a direct link to the biological interpretation of the results found (Mclean et al. 1998).

We discern the following steps (and sub-steps) in the process of studying habitat selection (not necessarily to be taken chronologically);

- ✓ Quantifying the availability of the resources (quantifying environmental characteristics),
- ✓ Analysing space use of the animal studied
    - Collecting information on the whereabouts of the animals,
    - Deriving space use from the information on the whereabouts of the animals,
- ✓ Comparing the availability of the resources and their use by the animals.

I.E.1. Quantifying the availability of the resources (environmental characteristics) (chapter II & chapter III)

Food and cover are considered to be the main environmental factors influencing habitat suitability (Doncaster et al. 1996, Litvaitis et al. 1996). Previous studies on roe deer suggested the importance of both resources, the latter as protection against predators and adverse weather conditions (Henry 1981, Cederlund 1983, Cibien and Sempéré 1989, Aulak and Babinski-Werka 1990, Guillet et al. 1996, Tufto et al. 1996, Mysterud 1998). We focus on those two environmental characteristics as far as the quantification of the available resources is concerned.

Given the large amount of previous studies on roe deer diet composition, we review the existing literature to analyse the influence of the applied methods. As diet composition is considered to change throughout the year and to depend on the habitat, we compare the influence of the used research method, the habitat (study site) and the season, on the observed roe deer diet composition (chapter II).

Protection against predators and adverse weather conditions is provided both by ground vegetation cover and by canopy cover. Determining the availability of both aspects of cover requires methods to quantify canopy cover and ground vegetation cover, the latter also referred to as hiding cover. Canopy cover can be derived from the canopy closure in a forest stand. Consequently, one can use the information of forest inventory maps, to quantify the canopy cover provided by different forest and habitat types. Hiding cover, however, results from the presence or absence of ground vegetation, in combination with other characteristics of the habitat (Mysterud and Ostbye 1999).

The possibilities for an animal to hide in vegetation largely depend on the size of the animal. Standard procedures for quantifying hiding cover for different animal species are rare, and different researchers used different definitions and scales to quantify hiding cover (Henry 1981, Armstrong et al. 1983, Heugel et al. 1986, Lagory 1986, Mysterud and Ostbye 1995). In chapter III we refine the possible use of a cover pole to estimate hiding cover, since we assume that this method (developed by Griffith and Youtie (1988)) offers most possibilities for standardisation. We subsequently test its performance as a tool to estimate hiding cover for roe deer.

We further question the assumption that hiding cover characteristics change throughout the landscape and are constant within a ‘habitat type’. This assumption has to be true in order to draw conclusions on the role of hiding cover in the habitat selection process (by roe deer), from studies comparing the use and availability of different 'habitat types' (e.g. Aulak and Babinski-Werka 1990). This assumption also forms the base of many habitat suitability models (Reimoser and Suchant 1992, Van Deelen et al. 1997, Didier and Porter 1999).

I.E.2 Analysing the space use of roe deer - collecting the whereabouts of the animals (Chapter IV)

To determine the relative time the animal spends in different parts of its habitat, one needs to follow the movements of the animal and to derive subsequently the space use of the animal. Since we are interested in the influence of habitat factors on a local scale (roe deer being territorial animals using only several tens of hectares as home range (Danilkin and Hewison 1996)), space use has to be studied on a fine scale. This requires frequent and highly accurate animal locations (animal fixes). Manual field radio telemetry, using short intermediate time intervals, is labour intensive and time consuming, and consequently costly (Priede 1992). Furthermore, in some conditions, it is quite impossible and/or risky to record more or less continuously the localities of several animals synchronously. Finally, one of the greatest disadvantages of manual radio telemetry is the repeated disturbance of the animals, hereby possibly provoking changes in habitat use.

Therefore there is a clear need for the development of automated radio telemetry systems, allowing to localise the animals in a frequent and accurate way, without the need of a researcher to be in the field permanently, thereby disturbing the animals. The use of GPS collars as an instrument to collect accurate fixes with short time lags was introduced several years ago for larger mammals such as moose (*Alces alces)* *(e.g.* Moen et al. 1996, Edenius 1997, Moen et al. 1997, Rempel and Rodgers 1997), red deer (*Cervus elaphus)* (e.g. Janeau et al. 1998), white-tailed deer *(Odocoileus virginianus)* (e.g. Merrill et al. 1998, Bowman et al. 2000) or bear (e.g. Obbard et al. 1998). All previous studies on the use of GPS collars (except Janeau et al. 1998) took place in boreal forests ecosystems.

Since the current GPS collars, available for use on smaller mammals, do not allow post-processing differential correction, an alternative correction method, referred to as linear correction, was proposed by several researchers (e.g. Moore et al. 1997). Because of the mathematical algorithms involved we seriously question the use of this method.

Therefore we analyse, in chapter IV, the performance and accuracy of a GPS collar for medium sized mammals in temperate forests, and test the use of the linear correction method.

I.E.3 Analysing the space use of roe deer – deriving space use (Chapter V)

Once animal fixes are collected on regular time intervals, the space use has to be derived from this information in order to delineate the habitats used, as well as to identify the resources used.

Plenty of studies and reviews have been published during the last three decades on radio telemetry in general and on home range models or models used to analyse space use patterns (e.g. Worton 1987, Harris 1990, White and Garrot 1990, Boulanger and White 1990, Wray et al. 1992, Worton 1995). The fast development of computer technology over the last decades allows researchers to develop more complex and biologically more valid models. However, Lawson and Rodgers (1997) showed that even when applying the same "theoretical method", significantly different results may be found depending on the computer program and the so-called 'default parameters', used to calculate the space use patterns.

More than ever before the use of shorter time lags between the fixes necessitates the application of space use methods that retain their validity when the animal locations are highly auto-correlated. De Solla et al. (1999) pointed towards the biological importance of using all the collected fixes, rather than eliminating observations to achieve independent fixes. The latter being required by most parametric home range models. The further development of automated radio telemetry systems (see chapter IV) will return even larger sets of observations collected with very short intermediate time intervals. Consequently, the use of parametric home range models, requiring independent observations, becomes very unrealistic. Therefore there is a clear need to develop new non-parametric methods that allow deriving, accurately, space use from collected animal fixes.

In chapter V we evaluate the shortcomings and constraints of the existing methods and present a new method. We test the performance of this new approach and compare its results with those of one of the currently most used methods (Kernel distributions).

I.E.4 Comparing the availability of the resources and their use by roe deer (Chapter VI)

Several papers have been written on the statistical pitfalls that characterise each of the existing methods to compare the resources (habitats) used by, and those available to, the animals (Johnson 1980, Alldredge and Ratti 1986, Alldredge and Rattie 1992, Manly et al. 1993). At present most wildlife scientists agree that using compositional data analysis (Aebisher et al. 1993) is probably the best possible option (see Garshelis 2000, Kenward 2001). This method addresses most of the problems and constraints of the other methods. Compositional data analysis solves the problems resulting from the fact that the proportions of the used habitat types (and also of the available habitat types) are not independent. Furthermore, the individual animal, and not the observation, is used as the sample unit. The classic problem of pseudo-replication - because the same animal is localised once, or even several times, each 24-hour period - is thereby solved. However, the definition of the available habitat and the methods used to delineate the home range or used habitats, can strongly influence the results of the habitat selection analysis. In chapter VI we therefore analyse the sensitivity of compositional data analysis methods. We analysed the preference for edges (see I.C) of eight roe deer fawns during the first months of their lives. Comparing the results of using several possible methods and scales to define the available and used habitats in the compositional data analysis, we evaluate the influence of the used definitions on the research outcome. We apply an alternative GIS analysis to evaluate the biological meaningfulness of the results of the compositional data analysis. This chapter also allows us to apply the developed space use analysis method (chapter V) on real data rather than on simulations!

In chapter VII we summarise our findings. Apart from our methodological results we also describe the biological findings and conclusions of the work. We end the chapter by suggesting a modified strategy to study the interactions between roe deer populations and their environment.

Methodological questions of this Ph.D.

Chapter II

- ✓ What is the influence of the research method compared to the influence of the habitat and the season on the composition of the roe deer diet?

Chapter III

- ✓ How can we standardise the estimation of hiding cover for habitat selection studies?
- ✓ Can we ameliorate the method developed by Griffith and Youtie, in order to estimate better hiding cover for roe deer?
- ✓ To translate 'habitat types' into 'hiding cover', one needs to assume that cover is constant within a 'habitat type' and differs between the habitat types. Is this assumption valid?

Chapter IV

- ✓ Can we use GPS collars as an alternative for classic radio collars to study roe deer habitat use?
- ✓ What is the influence of the habitat type on the observation rate and on the accuracy?
- ✓ Can we overcome the bias in habitat preference resulting from possible habitat related differences in observation rate by modelling the influence of the habitat on the observation rate?

Chapter V

- ✓ What are the limitations and the shortcomings of the methods existing to derive space use from animal fixes?
- ✓ Can we develop a new method overcoming these problems?
- ✓ How well does a new method perform comparing to the best of the existing ones?

Chapter VI

- ✓ What is the influence of the definitions and methods used to compare habitat use and availability on the final research outcome?

II Impact of season, habitat and research techniques on roe deer (*Capreolus capreolus*) diet composition: a review

II.A Abstract

We summarise the information on the diet of roe deer (*Capreolus capreolus*) found in 33 European studies. After giving a short overview of the differences between the existing studies, we compare the information for each season. We submit the information, summarised in a matrix of 83 cases on 10 food groups, to a detrended correspondence analysis (DCA) and a two-way indicator species analysis (TWINSPAN). We calculate weighted averages grouping the information by season, habitat, research method and their cross products. The weighted averages are also used as input for a Multivariate Ratio Analysis.

Since the available food items dictate the possible diet composition we further investigate the influence of the habitat on the reported food selection. The influence of season on the diet composition is compared with the effect of the habitat, and other factors such as research method and geographical location of the study site. The review shows that there is relatively little seasonal variation in the diet composition which is more closely correlated to the habitat than to the season.

II.B Introduction

Roe deer (*Capreolus capreolus*) are widely distributed high impact herbivores which use a range of lowland and mountain habitats including large forest complexes and unwooded field areas (Danilkin and Hewison 1996). An understanding of feeding habits is essential when considering carrying capacities, improvement of deer habitat and reducing damage to forestry, agriculture or horticulture (Jackson 1974). Hence it is not surprising that all over Europe considerable attention has been devoted to their biology, in particular their feeding ecology.

To draw some general conclusions on the annual diet of roe deer, it is necessary to review the available literature. The review of Tixier and Duncan (1996) only considered the results of studies based on stomach content analysis. Faecal analyses were not included because the composition of the plant fragments in faecal samples differs considerably from stomach samples. Consequently, they could not investigate whether the research technique was a main source of variation in diets. It also means that a lot of valuable studies were not included. In this paper we review 33 different studies on the food selection by roe deer (see Table II.2). The aim is to summarise the most recurring trends in their annual diet. We also searched for factors explaining the variation in the food selection (habitat, season, research method and geographical location). For a better understanding of the cited studies, it is necessary to start with a short overview of the research techniques examining herbivore food selection.

II.C Research techniques

The diet composition of roe deer, or herbivores in general, can be examined in a variety of ways: direct observation of the animals, description of feeding traces, analysis of the rumen content, sampling of rumen- or oesophageal fistulae, faecal analysis or feeding experiments (Table II.1) (Jackson 1974, Goffin and de Crombrugghe 1976, Staines 1976, Maillard and Picard 1987 Roelvink 1988, Birkenstock and Maillard 1989). Some additional remarks are summarised in the following paragraphs.

Table II.1 Summary of some benefits and drawbacks of several research techniques to examine the food selection of herbivores (adapted from Roelvink 1988)

	Benefits	**Drawbacks**
Rumen or gullet fistulas	results are precise and accurate	requires expensive surgical operation not applicable to wild animals
Analysis of rumen contents	quantitative and qualitative results no expensive equipment required	animal has to be killed feeding place is not known rumen content changes all the time difficult to identify food particles
Faecal analysis	easy to collect and store material applicable to all animal species, at any time no disturbance	intensive work feeding place is not known the ratio of faecal fragments does not reflect the ratio of food intake difficult to identify food particles
Direct observation	simple and cheap gives also other information about the examined animal species	difficult to execute with shy animals or in unsurveyable sites identification problems if observation distance is large
Analysis of feeding traces	cheap little disturbance for the animal gives also information about the vegetation on the feeding place	difficult to classify traces on the level of animal species traces are not always perceptible or disappear fast in the growing season
Feeding experiment	accurate results each species can be tested apart from the others	food has to be collected animals have to be captured results do not represent feeding behaviour under free-ranging conditions

The most common method is surely the analysis of rumen contents (e.g. Gaare et al. 1977, Puglisi et al. 1978). Many samples can be supplied from animals killed for hunting or by traffic accidents. However this restricts the sample period mainly to the hunting season. This method can result in two types of data. The first type of data only yields the presence or absence of a certain plant species in the examined rumen (e.g. Jackson 1980, Fandos et al. 1987, Maillard and Picard 1987, Maillard et al.

1989) and consequently gives the percentage of the animals (= frequency) which ate a certain plant. It does not reveal any information concerning the amount of the eaten plants. The second type of data gives the amount of each plant species expressed as a percentage of the examined rumen content. The percentage can be the number of fragments compared to the total number of fragments as well as a volume percentage or a percentage of the dry weight. When both types of data are available one can distinguish between plants often eaten in very low quantities, plants that are sporadically eaten in large amounts and plants that are often eaten in large amounts (Cederlund et al. 1980).

However, the method requires a very good knowledge of the plant morphology and anatomy to recognise the different plants in the rumen content.

A second, often used method is the faecal analysis (e.g. Alipayo et al. 1992). The same population of herbivores can be continuously sampled without direct interference (Bhadresa 1986) and no animals have to be killed. The method rarely can take into account any information concerning the sex, the age or the physical condition of the animals, unless the faecal samples were collected from the spot on which the animal was observed defecating (Holisova et al. 1986a).

Basically, two methods are used for quantifying proportions of different epidermis fragments in faeces: counting the number of fragments and estimating or measuring the surface areas of fragments. Of course, it is also possible to record only the presence or absence of species in faecal samples (e.g. Hearney and Jennings 1983). Because of the differential interspecies digestibility of epidermis structures, difficulties in recognising certain fragments (Stewart 1967), the variability of fragment size and to the poor correlation between epidermal surface areas and dry weights of plants, large discrepancies are found when comparing the results from faeces analysis and those from the analysis of rumen contents. Holisova et al. (1986a) and Fitzgerald and Waddington (1979) suggest that an index of digestion must be used to correct the proportions of cuticle fragments if faecal analysis is to give an accurate estimate of the diet. Degrez and Libois (1991) conclude that faecal analysis and rumen analysis are complementary methods.

Direct observation of the animal, is a simple and cheap method to determine which plants are important in the diet composition, but it is difficult to execute with shy animals or in unsurveyable terrain. Results from Wallmo et al. (1973) suggest that the observer must be within 23 m of the deer to identify more than 80 % of the grazed species correctly. Multiplying the time spent feeding on a certain plant species with the average intake rate allows to translate direct observations into consumed dry weight of a certain plant species and consequently to analyse the diet composition. Tixier et al. (1997) determined the average intake rate by supplying tame animals during a fixed period branches and subsequently comparing the weight of the branches before and after consumption by the animals.

Analysis of feeding traces provides little disturbance for the animal, but it is difficult to make a distinction between related animal species (Birkenstock and Maillard 1989). Besides, this method is unreliable for herbs and it does not give any information about fungi and fruits (Maillard and Picard 1987). Feeding traces cannot be recognised for all plants and they disappear fast in the growing season (Roelvink 1988).

When excluding deer from certain areas by fencing and comparing afterwards the vegetation in and outside these enclosures, it is not only possible to deduce the influence of the animals on certain individual plant species, but also the influence of the animals on the vegetation composition in general and on the vegetative growth can be analysed (Jackson 1974, Hollins and Carroll 1997).

The main problem when using feeding experiments to analyse diet composition is to decide which plant species and how much of each species, will be on offer to the animals.

Diet composition studies can, for all methods, only be translated into feeding preferences when there is also information on the availability of the different plant species. If there is no information concerning the exact place of food intake one can use the average availability of the different plant species in the study area.

All methods are likely to yield some valuable information, but they also each have their theoretical and practical benefits and drawbacks.

II.D Annual diet of roe deer

II.D.1 Methods and assumptions

In order to compare the results of the food selection of roe deer in different studies, we reclassified food items into ten groups: graminoids, herbs, ferns, fungi, half wooden plants, dwarf shrubs, coniferous browse, deciduous browse, cultivated plants and others. Graminoids are all kind of wild grasses, sedges and rushes. Half wooden plants are *Rubus spp.*, *Rosa spp.*, *Hedera helix*, *Lonicera periclymenum*, *Ulex europaeus* and *Ribes spp.* Dwarf shrubs include all kinds of heather (*Calluna*, *Erica*) and bilberry (*Vaccinium myrtillus*). The category of coniferous browse contains needles, twigs and sprouts of conifers and that of deciduous browse twigs, sprouts, fruits (e.g. acorns, beech nuts, horse chestnuts, apples) and green leaves of broad-leaved trees and shrubs. Cultivated plants include rye, barley, wheat, potatoes, beets, maize, lucerne, cole-seed and clover. The category 'others' contains mosses and all the material that does not fit under one of the other categories (e.g. *Ilex aquifolium*) or that could not be identified. Gebczynska (1980) could not identify more than half of the rumen contents that she examined, because the particles were too small. That is why the category 'others' is so large in that study. These ten categories were chosen because they were quite consistent between the reviewed studies, although some studies still did not fit into it. Therefore the results of Matrai and Kabai (1989) and Homolka (1991) are not included in the data analysis. Since the categories are broader than the ones used in the original papers, not all differences between the studies will be clear. Fruits for example, are now included in the category of deciduous browse, but some authors distinguish fruits as a separate group (e.g. Fichant 1974, Jackson 1980, Maillard and Picard 1987, Maillard et al. 1989).

The results of different studies can only be compared if they are expressed in the same units. So, only the studies with quantitative results expressed in a percentage of the total amount of food intake are taken into account. This means that all results are expressed as a percentage of the dry weight of the rumen content, the volume of the rumen content, the total number of faecal fragments or the total faecal fragment area (see Table II.2)

Table II.2:Summary of the literature on the food selection of roe deer

Author (* = used in the statistical analysis)	**Research method**	**Habitat**	**Region**	**latitude**	**longitude**
* Birkenstock & Maillard (1989)	Rumen analysis (dry weight)	deciduous forest	the Vosges, northeast-France	48°12 N	7°20 E
* Boag et al. (1990)	Rumen analysis (volume)	agricultural area	east-Scotland	57° N	3° W
Borowski & Kossak (1975)	Analysis of feeding traces	mixed forest	Bialowieza, Poland	52°40 N	24° E
* Cederlund et al. (1980)	Rumen analysis (dry weight)	mixed forest	Grimsö, central Sweden	59°30 N	15°30 E
* Degrez & Libois (1991)	Faecal analysis (number of fragments)	mixed forest	the Ardennes, Belgium	50°15 N	5°27 E
* de Jong et al. 1 (1995)	Faecal analysis (area)	coniferous forest	Highfield, Northumberland, England	55°30 N	2° E
* de Jong et al. 2 (1995)	Faecal analysis (area)	coniferous forest	Pundershaw, Northumberland, England	55°30 N	2° E
* Fandos et al. 1 (1987)	Rumen analysis (dry weight)	deciduous forest	Cantabrian mountains, Spain	43° N	6 ° W
* Fandos et al. 2 (1987)	Rumen analysis (dry weight)	deciduous forest	Iberian system, Spain	42° N	2°40 W
* Fandos et al. 3 (1987)	Rumen analysis (dry weight)	mixed forest	Guadarram mountains, Spain	47° N	4° W
* Fandos et al. 4 (1987)	Rumen analysis (dry weight)	deciduous forest	southern mountains enclaves, Spain	39° N	4°30 W
* Fichant (1974)	Rumen analysis (volume)	mixed forest	the Ardennes, Belgium	49°40 N	5°40 E
* Gebczynska (1980)	Rumen analysis (dry weight)	mixed forest	Bialowieza, Poland	52°38 N	24° E
* Grigorov (1976)	Rumen analysis (dry weight)	mixed forest	Gabrovo , Bulgaria	42°52 N	25°19 E
Hazebroek & Groot Bruinderink (1995)	Rumen analysis (volume)	mixed forest	Veluwe, the Netherlands	52°10 N	5°50 E
Hearney & Jennings (1983)	Faecal analysis (frequency)	mixed forest	Norfolk/Suffolk, east-England	52°30 N	1° E
* Helle (1980)	Faecal analysis (number of fragments)	mixed forest	Muhos, central-Finland	64°45 N	26°11^{E}
* Henry (1978a)	Rumen analysis (volume)	coniferous forest	Durham, northeast-England	54°41 N	1°50 E
* Henry (1978b)	Faecal analysis (number of fragments)	coniferous forest	Durham, northeast-England	54°41 N	1°50 E
* Holisova et al. (1982)	Rumen analysis (volume)	agricultural area	southern Moravia, Czech Republic	48°57 N	16°29 E
* Holisova et al. (1984)	Rumen analysis (volume)	agricultural area	southern Moravia, Czech Republic	48°57 N	16°29 E

* Holisova et al. (1986b)	Faecal analysis (area)	agricultural area	southern Moravia, Czech Republic	48°57 N	16°29 E
Homolka (1991)	Faecal analysis (area)	mixed forest	southern Moravia, Czech Republic	49° N	16°30 E
* Hosey (1981)	Faecal analysis (number of fragments)	mixed forest	Dorset, south-England	51° N	2°40 W
* Jackson (1980)	Rumen analysis (dry weight)	mixed forest	Hampshire, south-England	51°06 N	1°19 W
* Kaluzinski (1982)	Rumen analysis (dry weight)	agricultural area	Czempin, west-Poland	58°08 N	16°45 E
* Maillard & Picard (1987)	Rumen analysis (dry weight)	deciduous forest	the Vosges, northeast-France	48°42 N	6°12 E
Maillard (1987)	Rumen analysis (dry weight)	deciduous forest	the Vosges, northeast-France	48°42 N	6°12 E
* Maillard et al. (1989)	Rumen analysis (dry weight)	deciduous forest	the Vosges, northeast-France	48°42 N	6°12 E
* Maizeret et al. (1986)	Faecal analysis (number of fragments)	mixed forest	Landes, southwest-France	44° N	0°20 W
* Maizeret et al. (1991)	Rumen analysis (dry weight)	deciduous forest	Chizé, west-France	46°10 N	0°20 W
* Maizeret & Tran Manh Sung (1984)	Rumen analysis (dry weight)	mixed forest	Landes, southwest-France	44° N	0°20 W
Matrai & Kabai (1989)	Rumen analysis (number of fragments)	mixed forest	Budapest, Hungary	47°28 N	19°26 E
Papageorgiou et al. (1981)	Feeding experiment	mixed forest	Serres, north-Greece	41° N	23° E
Poutsma (1977)	Direct observation	mixed forest	Eeldo, the Netherlands	53°10 N	6°40 E
* Siuda et al. (1969)	Rumen analysis (volume)	mixed forest	Olsztyn, Poland	53°43 N	21°36 E
* Tixier et al. (1997)	Direct observation transformed into consumed dry weight	deciduous forest	Chizé ,west-France	46°10 N	0°20 E

Another problem is that the different studies are not all expressed in the same time-unit. Therefore, we divided all data into four seasons. If a study had monthly data, then April, May and June are combined to form the spring season, July, August and September form summer, autumn is formed by October, November and December and winter consists of the months January, February and March (see Table II.3). This division agrees best with the studies that are already divided into seasons. That is why the data of Holisova et al. (1986b) are divided into two categories: the average of January, February and March forms the winter diet and the results of April are used as spring diet. Although Holisova et al. (1982) talk about the winter diet of roe deer, their results count for the autumn-period in this review, since the examined animals were shot between 20 September and 31 December. Holisova et al. (1984) divided their data into early and late summer; we took the average of both. Maizeret et al. (1991) investigated the summer and winter diet, but only the summer data are presented in their paper. Sometimes however, it was impossible to divide the data into those four seasons. Hazebroek and Groot Bruinderink (1995) for example, divided their results into spring/summer, summer/autumn, winter and late winter. Maillard (1987) made no distinction between autumn and winter diet and Homolka (1991) used six periods of two months.

Table II.3: Period and number of samples of each study used in the statistical analysis for each season

Season	nr	Author	period	Number of samples
Spring	1	Cederlund et al. (1980)	apr - jun, 73 – 79	20
	2	Degrez & Libois (1991)	apr - jun 88	29
	3	de Jong et al. 1 (1995)	may 93	3
	4	de Jong et al. 2 (1995)	may 93	1
	5	Fandos et al. 1 (1987)	28 apr - 20 jun, 72 – 80	7
	6	Fandos et al. 2 (1987)	17 apr - 18 jun, 76 – 80	4
	7	Fandos et al. 3 (1987)	25 apr - 29 may, 71 – 81	8
	8	Fandos et al. 4 (1987)	23 mar - 22 may, 79 – 80	3
	9	Gebczynska (1980)	11 apr - 1 jun	15
	10	Henry (1978a)	may, 73 – 74	35
	11	Holisova et al. (1986b)	apr 77, 79 - 82, 84	33
	12	Hosey (1981)	apr - jun 72	34
	13	Jackson (1980)	apr - jun, 71 – 72	31
	14	Kaluzinski (1982)	11 may - 21 jun	34
	15	Maizeret & Tran Manh Sung (1984)	15 mar - 30 jun	14
	16	Maizeret et al. (1986)	apr – jun	30
	17	Siuda et al. (1969)	22 mar - 21 jun	9
	18	Tixier et al. (1997)	apr – jun	7
Summer	19	Birkenstock & Maillard (1989)	1 jun - 30 aug 86	20
	20	Cederlund et al. (1980)	jul - sep, 73 – 77	20

	21	Degrez & Libois (1991)	aug - sep 88	19
	22	de Jong et al. 1 (1995)	jul - sep 92	9 – 30
	23	de Jong et al. 2 (1995)	sep 92	9 – 30
	24	Fandos et al. 1 (1987)	24 jun - 19 sep, 74 – 80	25
	25	Fandos et al. 2 (1987)	29 jun - 10 aug, 71- 80	9
	26	Fandos et al. 3 (1987)	11 sep - 15 sep 81	2
	27	Fandos et al. 4 (1987)	aug 80	5
	28	Gebczynska (1980)	2 jun - 10 aug	19
	29	Henry (1978a)	jul, 73 – 74	8
	30	Holisova et al. (1984)	19 may - 18 sep, 81 - 83	29
	31	Hosey (1981)	jul - sep 72	24
	32	Jackson (1980)	jul - sep, 71 – 72	8
	33	Kaluzinski (1982)	22 jun - 21 aug	11
	34	Maillard et al. (1989)	jun - aug, 85 – 87	13
	35	Maizeret & Tran Manh Sung (1984)	1 jul - 30 sep	17
	36	Maizeret et al. (1986)	jun – sep	30
	37	Maizeret et al. (1991)	jun - sep, 85 – 87	39
	38	Siuda et al. (1969)	22 jun - 21 sep	9
	39	Tixier et al. (1997)	jul – sep	7
Autumn	40	Birkenstock & Maillard (1989)	19 oct - 23 dec 85	17
	41	Cederlund et al. (1980)	oct - dec, 73 – 75	43
	42	Degrez & Libois (1991)	oct - dec 87	19
	43	de Jong et al. 1 (1995)	nov 92	9 – 30
	44	de Jong et al. 2 (1995)	nov 92	9 – 30
	45	Fandos et al. 1 (1987)	4 oct - 8 dec, 70 –79	21
	46	Fandos et al. 2 (1987)	3 oct - 21 nov, 74 – 79	6
	47	Fandos et al. 4 (1987)	27 nov - 28 nov, 78 - 79	2
	48	Fichant (1974)	5 oct - 27 nov 73	32
	49	Gebczynska (1980)	11 aug - 21 dec	33
	50	Henry (1978a)	nov 73	24
	51	Holisova et al. (1982)	20 sep - 31 dec 80	32
	52	Hosey (1981)	oct - dec 72	24
	53	Jackson (1980)	oct - dec, 70 – 72	22
	54	Kaluzinski (1982)	22 aug - 21 nov	16
	55	Maillard & Picard (1987)	12 oct - 20 nov 83	33
	56	Maizeret & Tran Manh Sung (1984)	1 oct - 30 nov	37
	57	Maizeret et al. (1986)	oct – dec	30
	58	Siuda et al. (1969)	22 sep - 21 dec	7
	59	Tixier et al. (1997)	oct – dec	7
Winter	60	Birkenstock & Maillard (1989)	24 dec 85 - 31 mar 86	34
	61	Boag et al. (1990)	feb 89	3
	62	Cederlund et al. (1980)	jan - mar, 73 – 77	12
	63	Degrez & Libois (1991)	jan - mar 88	25
	64	de Jong et al. 1 (1995)	jan - mar 93	9 – 30
	65	de Jong et al. 2 (1995)	jan - mar 93	9 – 30
	66	Fandos et al. 1 (1987)	25 dec - 8 mar, 70-80	14
	67	Fandos et al. 2 (1987)	30 dec - 14 feb, 73 – 78	3
	68	Fandos et al. 3 (1987)	17 feb - 18 mar 79	2
	69	Fandos et al. 4 (1987)	20 jan 80	1
	70	Gebczynska (1980)	21 dec - 10 apr	24
	71	Grigorov (1976)	nov - mar, 73 – 76	27
	72	Helle (1980)	jan - apr, 76 – 77	77

73	Henry (1978a)	jan - feb, 73 – 74	16
74	Henry (1978b)	jan - mar 74	105
75	Holisova et al. (1986b)	jan - mar, 77, 79 - 80, 82, 84	150
76	Hosey (1981)	jan - mar 72	37
77	Jackson (1980)	jan - mar, 71 – 73	44
78	Kaluzinski (1982)	22 nov - 31 jan	64
79	Maillard & Picard (1987)	21 nov 83 - 9 jan 84	34
80	Maizeret & Tran Manh Sung (1984)	1 dec - 15 mar	21
81	Maizeret et al. (1986)	jan – mar	30
82	Siuda et al. (1969)	22 dec - 21 mar	21
83	Tixier et al. (1997)	jan – mar	7

Since from the 33 studies only 29 expressed the data in percentages, from which 2 could not be rescaled into the time units used here and the results of 2 other studies could not be reclassified into the chosen food item categories, only 25 studies could be used for the statistical analysis. Because de Jong et al. (1995) had results from two sites in Kielder Forest, we named the results from Highfield de Jong et al. 1 (1995) and those from Pundershaw, de Jong et al. 2 (1995). We divided the four sites of Fandos et al. (1987) in the same way. So our final data matrix included 29 studies (marked with * in Table II.2).

As a first step, following the traditional approach (e.g. Siuda et al. 1969), we summarised the reviewed information for each season. The differences in diet composition during the year are influenced both by the changes in food item availability and by the changing food requirements of the animals during the year (lactation, mating, etc.) (van Wieren et al. 1997). In order to arrange the data of the selected studies for each season according to their similarity a two way indicator species analysis was applied, using 6 cut levels (0, 2, 5, 10, 20, 50) (TWINSPAN, Hill 1979a). The other parameters, being the minimum group size for division, the maximum number of indicators per division, the maximum number of species in the final tabulation and the maximum level of divisions, were set default.

To identify the main sources of variation in the food selection of roe deer (habitat, season, research method, geographical location), we submitted the data set to a detrended correspondence analysis (DCA), using DECORANA (Hill 1979b). For this purpose we generalised the locations of the different study areas, expressed as longitude and latitude, by rounding the degrees of latitude and longitude to the nearest 5° parallel or meridian. The 29 studies used in the data analysis include 20 rumen analyses, 8 faecal analyses and one direct observation transformed into consumed dry weight. Twenty-four studies were carried out in forests (4 in coniferous forest, 8 in deciduous forest and 12 in mixed forest) and 5 studies in agricultural areas (see Table II.2). Some studies include more than one season; there are 18 studies in spring, 21 in summer, 20 in autumn and 24 in winter (see Table II.3). Therefore the DCA includes 83 cases and 10 food groups. This matrix of 83 cases was also submitted to a TWINSPAN analysis to discover the main factors subdividing the observations. To confirm statistically the observed differences (DCA, TWINSPAN) we applied a Kruskal-Wallis test, using the co-ordinates on the I and II axis as input scores and the different factors (season, habitat, geographical location and method) as grouping factors.

To obtain a general overview of the diet composition a weighted average contribution of each of the 10 food items was calculated for each season, each habitat and each method and for the cross products of habitat and season, method and season and habitat and method. The weighted average was calculated by multiplying the % contribution of a food group in the total amount of food intake in a study by the number of samples in that study (see Table II.3) and divided by the total number of samples occurring in that specific subclass (e.g. diet composition in the winter in conifer habitats). For the data of de Jong et al. (1995) we used the minimum number of samples each time. To integrate the relationship between diet composition and other variables, the matrices containing the weighted averages were subjected to Multivariate Ratio Analysis (MRA) (Lewi 1989, Hermy and Lewi 1991). MRA produces bi-plots of both rows (season, habitat, method or a combination of two factors) and columns (food groups). It provides direct insight into the interaction and discriminating power of columns and rows of the data matrix.

II.D.2 Results

II.D.2.a Seasonal summaries

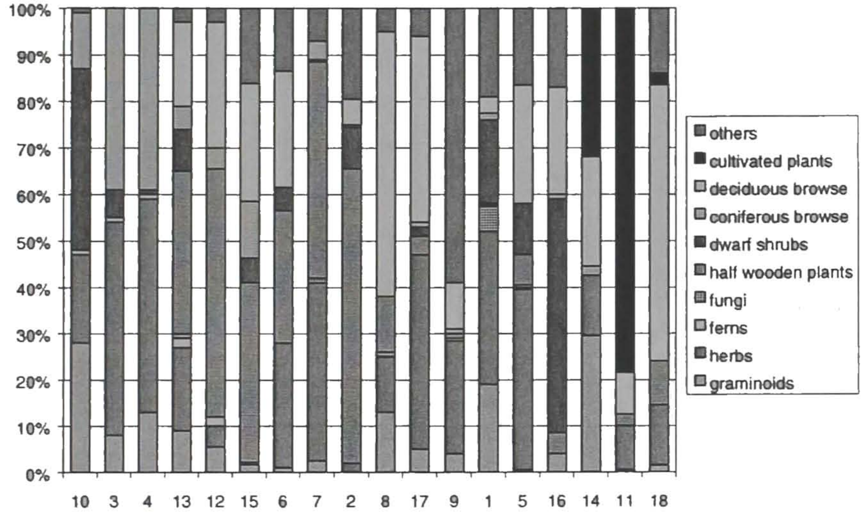

Figure II.1: Spring diet of roe deer per study (numbers of the studies, see Table II.3). The order and subdivision is determined by TWINSPAN.

In spring the observed diet variation is divided by TWINSPAN into four groups (Figure II.1): three studies (nrs 14, 11, 18) where cultivated plants partly compose the roe deer diet; three studies with a large amount of coniferous browse (10, 3, 4); two central clusters with relatively small differences in diet, except that the half woody plants are a much more important constituent of the diet in the left group (13, 12, 15, 6, 7, 2).

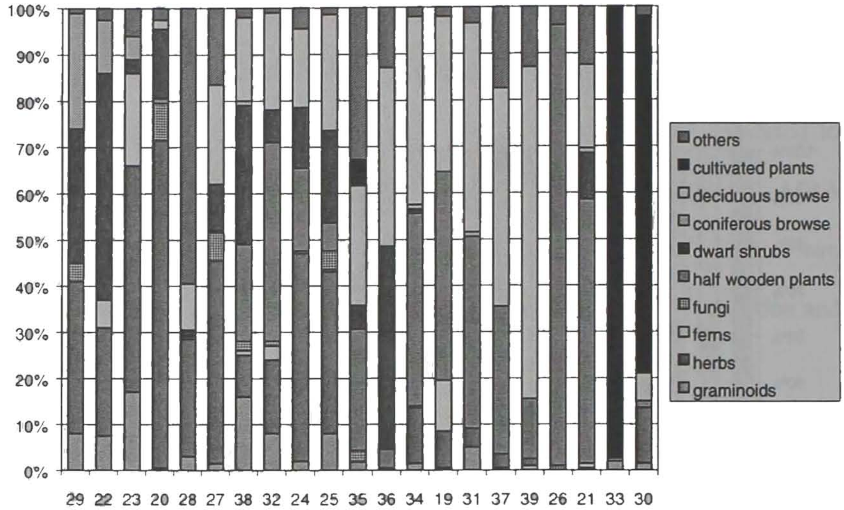

Figure II.2: Summer diet of roe deer per study (numbers of the studies, see Table II.3). The order and subdivision is determined by TWINSPAN.

For the summer diet TWINSPAN divided the sample into four major groups of studies (Figure II.2). In two studies the diet mainly consists of cultivated plants (33, 30). Secondly a group of studies differentiates through a high amount of coniferous browse in the diet (29,22,23). The large central group of studies may be divided on the basis of the combined presence (20, 28, 27, 38, 32, 24, 25, 35, 36) or absence of dwarf shrubs and fungi in the diet (except study 21).

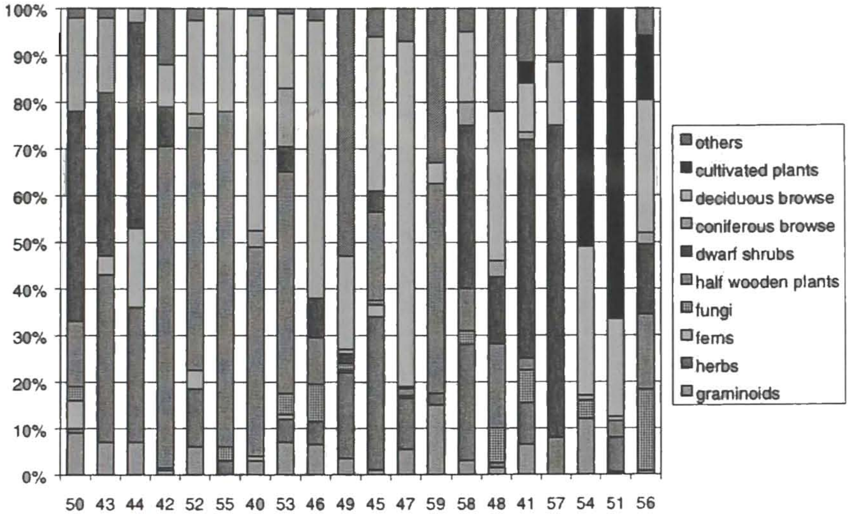

Figure II.3: Autumn diet of roe deer per study (numbers of the studies, see Table II.3). The order and subdivision is determined by TWINSPAN.

In autumn, studies are divided into five groups (Figure II.3). Three studies are differentiated through a considerable amount of cultivated plants in the diet (54, 51, 56). On the other side of the figure three studies are split off (50, 43, 44) on the basis of the considerable amount of coniferous browse and ferns, high amounts of dwarf shrubs and particularly the absence of deciduous browse and nearly absence of half woody plants. The central part is divided in three groups: one with a high amount of dwarf shrubs in the diet (58, 48, 41, 57) and two groups less clearly separated by differences in the food groups 'others', coniferous browse and half woody plants.

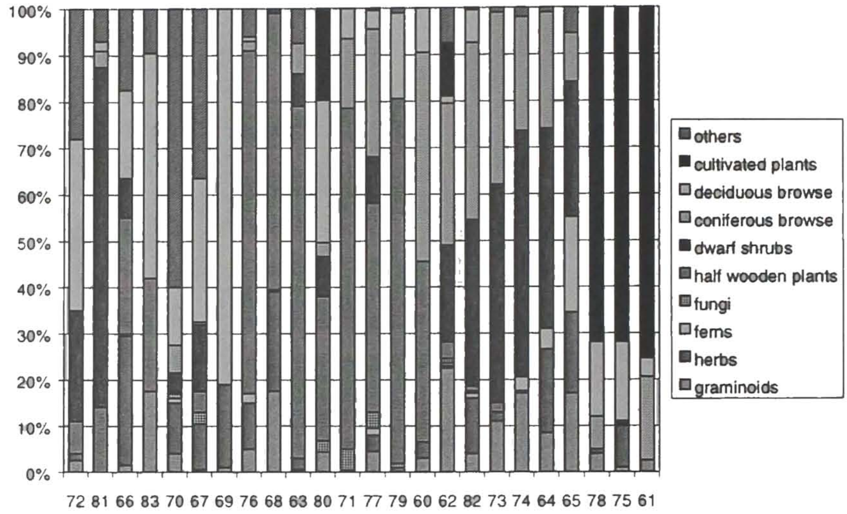

Figure II.4: Winter diet of roe deer per study (numbers of the studies, see Table II.3). The order and subdivision is determined by TWINSPAN.

In winter TWINSPAN divides the spectrum into four clearly defined groups (Figure II.4). In three studies the diet is composed almost entirely of cultivated plants (78, 75, 61). Next to it, six studies (62, 82, 73, 74, 64, 65) split off through a high contribution of coniferous browse and dwarf shrubs. The next cluster (76, 68, 63, 80, 71, 77, 79, 60) differentiates from the other through high amounts of half woody plants and the presence of fungi. In the remainder only deciduous browse and 'others' differentiate.

II.D.2.b DCA & TWINSPAN

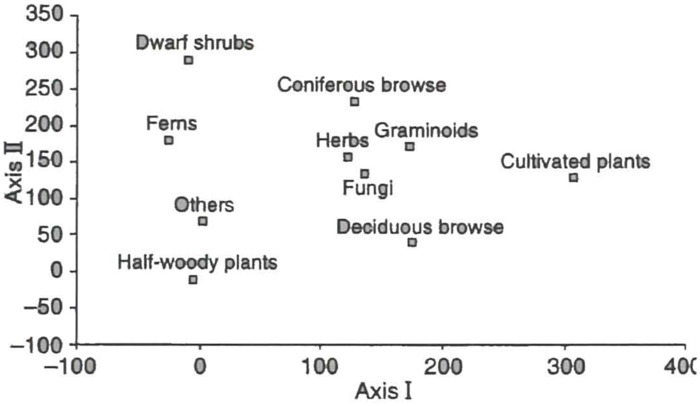

Figure II.5: DCA plot of all the observations (n=83) showing the positions of the food items.

The results of the DCA on all observations are visualised in Figures II.5 and II.6. The first and the second axis of the DCA jointly explain 51% of the total observed variation in the diet composition. Figure II.5 shows that cultivated plants have high scores on axis I. Axis II separates half wooden plants and deciduous browse from dwarf shrubs and coniferous browse. Figure II.6a shows clearly that axis I divides the studies into those that took place in agricultural areas and the other studies. The same division is found in the TWINSPAN table where all the studies that took place in agricultural areas are located in group *1 (Figure II.6f and Figure II.7). The Kruskall-Wallis test revealed a marginally significant difference (p = 0.066) in the mean ranks of the scores on axis I between the studies in agricultural areas and the other habitat types. Axis II separates deciduous from coniferous forests; mixed forests are located in between. This subdivision is also apparent in the TWINSPAN table where all the coniferous habitats are found in group *00, which also includes two observations in mixed habitats. All the observations in deciduous forest ecotypes are grouped in group *01. This group also includes the rest of the observations in mixed habitat types. The difference in mean ranks of the scores on axis II of the studies in coniferous forests and those in deciduous or mixed forest is highly significant ($p < 0.001$).

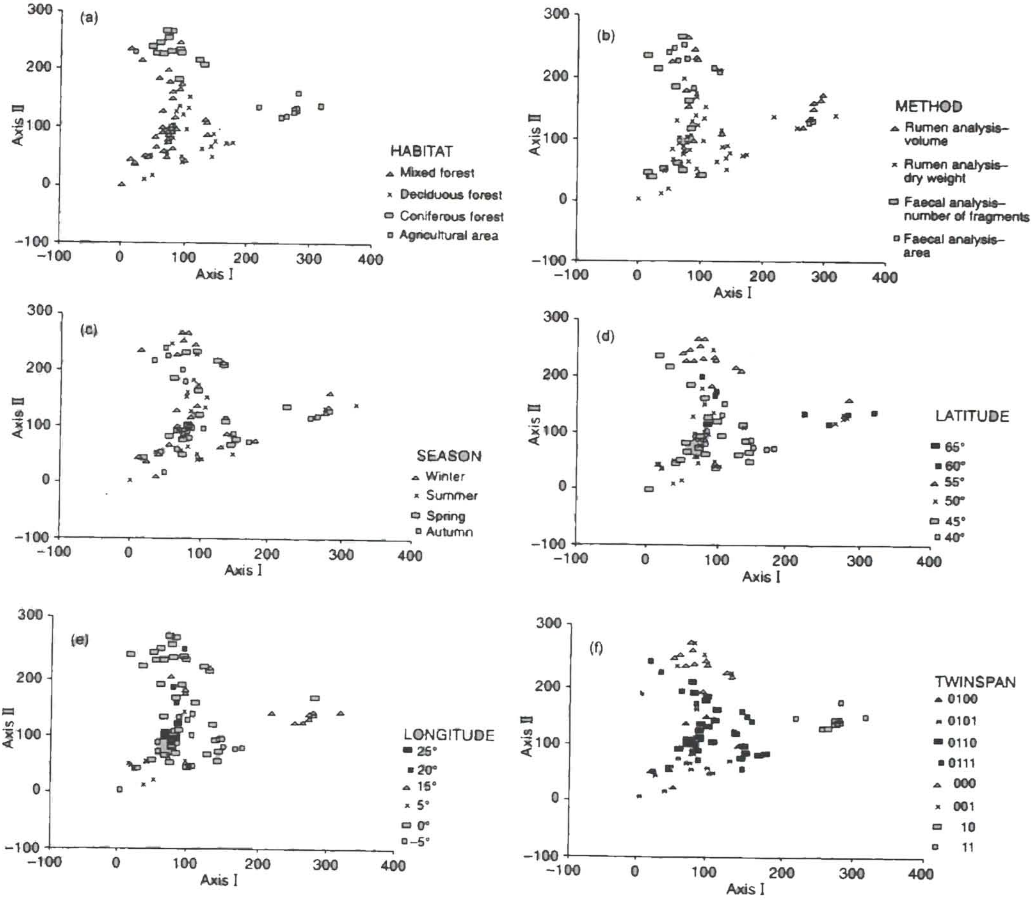

Figure II.6: DCA plot of the diet cases labelled by (a) habitat type, (b) research method, (c) season, (d) latitude, (e) longitude and (f) twinspan group

The used research technique is partly an explaining factor for the diet variation (Figure II. 6b). There is a significant difference ($p < 0.05$) between the mean ranks of scores on the first axis of the DCA of those studies using faecal analysis expressed as percentage of the total number of fragments and the scores of studies based on rumen content analysis methods. The second axis of the DCA separates the two types of rumen content analysis and the two types of faecal analysis. However the TWINSPAN table does not reveal any clear major divisions based on the research method. Through the nature of the TWINSPAN technique one can only find subdivisions based on the research method, on the lower levels.

Besides the habitat and the research technique, the variation is also explained by the geographical location. The different degrees of longitude and latitude are grouped together, although there is no clear transition from low to high values (Figure II.6d and II.6e). The differences in the mean ranks of the different groups do show some significant scores though no clear pattern can be found.

The season does not appears to be an explanatory factor for the variation in the diet composition (Figure II.6c), since the difference between the mean ranks of the scores on the first, respectively second axis, of the DCA is not significant ($p = 0.61$ and $p = 0.80$).