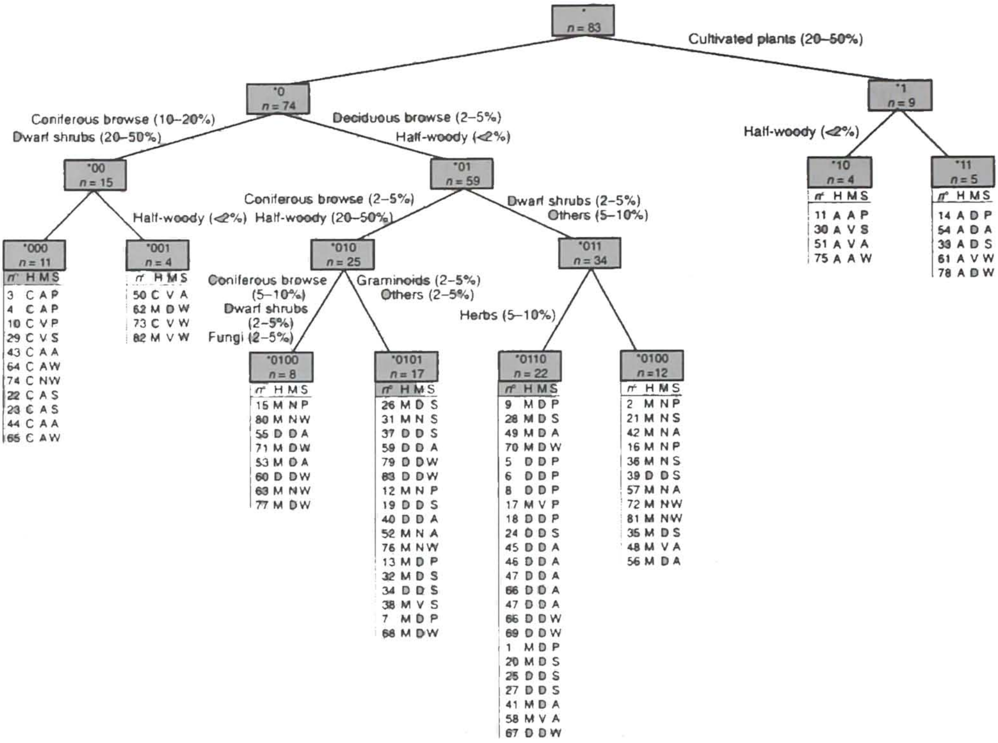

Figure II.7: Twinspan classification of roe deer diet cases (n=83). N, number of cases; H, habitat(A, agricultural; C, coniferous; D, deciduous; M, mixed forest); M, research method (A, faecal analysis – area; D, rumen analysis – dry weight; N, faecal analysis – number of fragments; V, rumen analysis – volume);S, season (A, autumn; P, spring; S, summer; W, winter)

II.D.2.c Weighted averages

Following the traditional approach which emphasises the seasonal variation in the diet and the results of the TWINSPAN- and DCA-approach which strongly suggest the overall importance of habitat differences, we calculated the weighted averages of those two factors. Table II.4 and II.5 allow us to make a general comparison between the four seasons and the four habitats.

Table II.4: Weighted averages of the food selection of roe deer per season (%)

	Graminoids	Herbs	Ferns	Fungi	Half woody plants	Dwarf shrubs	Coniferous browse	Deciduous browse	Cultivated plants	Others
Spring	10.12	14.50	0.57	0.51	19.56	12.59	3.95	16.48	11.66	10.06
Summer	2.97	16.80	1.60	1.04	20.26	10.51	1.27	24.23	10.24	11.07
Autumn	3.74	7.86	1.29	3.94	22.58	17.93	3.40	20.39	8.62	10.24
Winter	5.22	4.80	0.96	0.54	19.57	17.01	11.60	12.64	20.94	6.71
Yearly weighted average	5.32	9.34	1.08	1.41	20.38	15.29	6.54	17.17	14.58	8.88

From the yearly weighted averages it is clear that half wooden plants, deciduous browse, dwarf shrubs and cultivated plants are the most important food items for roe deer. Together they form more than two thirds of the diet. Half wooden plants, such as bramble and ivy, are eaten in approximately the same proportion during each season. Graminoids are more eaten during spring than during the other seasons. Herbs are much more important in spring and summer than in autumn and winter. This is compensated by dwarf shrubs which are eaten more during autumn and winter. During the summer period the consumption of broad-leaved trees and shrubs reaches its maximum. When the broad-leaved trees and shrubs have dropped their leaves, roe deer switch to coniferous browse, where it is available. Fungi are practically only available during the autumn, which is also reflected in the diet.

Table II.5: Weighted averages of the food selection of roe deer per habitat (%)

Habitat	Graminoids	Herbs	Ferns	Fungi	Half woody plants	Dwarf shrubs	Coniferous browse	Deciduous browse	Cultivated plants	Others
Agricultural area	4.59	7.41	0.00	0.17	0.84	0.00	1.86	16.25	68.51	0.37
Coniferous forest	15.59	11.29	4.66	0.42	1.50	44.07	20.57	0.00	0.00	1.90
Deciduous forest	2.26	12.79	1.00	0.91	37.72	3.06	5.04	30.26	0.05	6.91
Mixed forest	3.91	8.38	0.59	2.36	27.46	18.05	5.17	17.62	1.48	14.98

Cultivated plants are of course most important in agricultural areas. It is not surprising either that the highest proportion of deciduous browse and coniferous browse was found in deciduous and coniferous forests respectively. Dwarf shrubs are mostly eaten in coniferous forests, while half wooden plants were practically only found in mixed and deciduous forests. Finally, herbs are more eaten in coniferous and deciduous forests, although their proportion is considerable in the other habitats as well.

II.D.2.d MRA

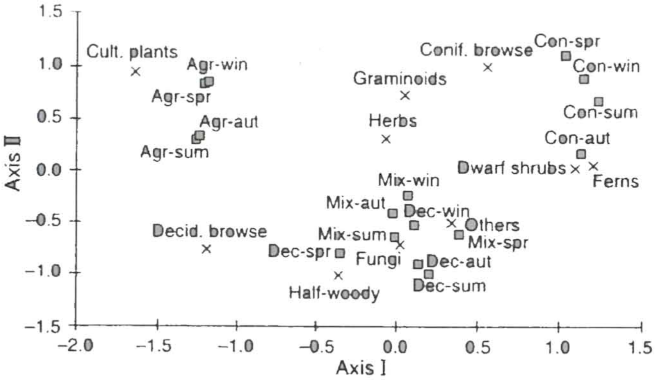

Figure II.8: Multivariate ratio analysis of the weighted averages for habitat (Dec, deciduous forest; Mix, mixed forest; Con, coniferous forest; Agr, agricultural area) and season (Aut, autumn; Spr, spring; Sum, summer; Win, winter). The boxes represent the scores of the diet composition in each season – habitat combination, relative to the scores of the food groups (crosses).

For the same reason as the weighted averages, we combined only the season and the habitat in a MRA. The bi-plot clearly shows the grouping effect of the habitat type, rather than the season, and indicates the relations between the different groups of food items and the two factors. 'Cultivated plants' is closely aggregated with agricultural areas, coniferous browse with coniferous forest and deciduous browse with deciduous and mixed forest ecotypes. The graminoids and herbs seem to occur together with cultivated plants and coniferous forest rather than with mixed or deciduous forest types.

II.E Discussion

Drawing conclusions from the DCA and the TWINSPAN table as well as the interpretation of the Kruskall-Wallis tests and the subsequent multiple comparisons was complicated by the fact that most of the factors were highly correlated. The Cramers measure of association for categorical data and the associated significance tests revealed highly significant associations between the geographical location and the habitat (V = 0.95 for easting and 1 for northing), the latitude and the longitude (V = 1) and even, though to a far lesser extent, between the method and the habitat type (V = 0.54).

The results of our research on the impact of the different factors influencing the roe deer diet composition reported in literature, made us question the decision of Tixier and Duncan (1996) not to include the results from faecal analysis since "the species composition of the fragments in faecal samples differs considerably from stomach samples". They are surely right that the different research techniques return different results when applied on the same animal, or even on the same population, since each technique has a bias towards certain food item groups (see 'research techniques'). However, our results indicate that whenever comparing the diet composition of roe deer populations spread a large range of habitats and geographic locations, the habitat (the available food items) has a stronger influence on the observed roe deer diet compostion than the used research method. These findings argue in favour of using all available studies, rather than limiting the number of studies to those that used the same research method. The following discussion therefore takes all the reviewed studies into account.

Our conclusion that the variation in the food intake of roe deer is mainly explained by the habitat in which they live (see Figure II.6a and II.7), is also confirmed by other authors (e.g. Jackson 1980, Holisova et al. 1986b, Tixier and Duncan 1996). This tendency is here even more clear than in the review of Tixier and Duncan (1996). The habitat is responsible for the food availability but major differences in the food availability are still possible in the same type of habitat. For example, when comparing the composition of the roe deer's diet in two Polish forests, namely the Pisz Forest (Siuda et al. 1969) and the Bialowieza Primeval Forest (Gebczynska 1980), significant differences are apparent between them, although both forests are classified as mixed forests and both studies used the same method of analysing rumen contents. The fundamental difference consists in the fact that in the first case it was concluded that the basic food of the roe deer consists of leaves and twigs of trees, shrubs and dwarf shrubs, and that herb layer plants came second in order. In the second case it was found that roe deer feeds chiefly on herb layer plants, and although the percentage of trees and shrubs consumed increases in autumn and winter, herb layer plants continue to form the basic food in these seasons as well. The reason for these differences is the different food availability.

The quantity and quality of the available food can undergo some major changes during the seasons (see Table II.4), but the observed differences in roe deer diet appear to be more influenced by the research method and the location than by the season. So, if one would like to compare the diet composition of different seasons, one should use the same research method and the same location, including the same habitat.

The results of this review also justify the statement that the food supply of roe deer living in a forest habitat is composed of trees, shrubs, dwarf-shrubs and herbs (see Table II.5). As a rule, the representation of tree and shrub sprouts in the diet is higher than 30 % in the course of the year, often amounting to more than 60 % of the diet (Homolka 1991). A lower representation of woody plants in the roe deer diet is found in field habitats (Kaluzinski 1982, Holisova et al. 1982, 1984, 1986b), which is easily understood considering the scarcely wooded agrocoenoses.

The use of clear cutting in forest exploitation and nitrogen-deposition have enabled *Rubus fruticosus* and *Rubus idaeus* to spread considerably in forests. This fact has increased the food supply for deer not only in the growing season, but also in winter (Homolka, 1991). The considerable importance of *Rubus spp.* as a food source is indicated by their representation in the roe deer's diet in various parts of Europe: in France (Maillard and Picard 1987, Birkenstock and Maillard 1989, Ballon et al. 1991), in England (Hosey 1981, Hearney and Jennings 1983), in Belgium (Fichant 1974, Degrez and Libois 1991), in the Netherlands (Poutsma 1977), in Czech Republic (Homolka 1991), in Bulgaria (Grigorov 1976), in Poland (Siuda et al. 1969), etc.

Coniferous browse constitutes a considerable part of the roe deer diet in winter (Figure II. 4), especially in periods with snow (Siuda et al. 1969, Henry 1978a and 1978b, Cederlund et al. 1980, Birkenstock and Maillard 1989). In the growing season this component is shunned, except when there is no deciduous browse available (Henry 1978a, de Jong et al. 1995). The high proportion of coniferous browse in the winter diet of roe deer may be connected with the fact that it is the only food of high quality that is still available in large amounts. It has a high content of proteins, water and sugars (Matrai and Kabai 1989). In the northern part of its range roe deer eat arboral lichens as well as dwarf shrubs and twigs of trees and shrubs (Helle 1980).

Foods such as fruit and fungi are available only strictly seasonally, which is reflected in the analyses of the diet (Fichant 1974, Jackson 1980, Maizeret and Tran Manh Sung 1984). Forest fruits and seeds are fairly heavily utilised, but there is a large variation of fruits in the diet, due to the irregularity of fruit production (e.g. acorns).

Cultivated plants are the most important in open fields (see Table II.5), though there is no direct unfavourable effect on plant production (Kaluzinski 1982, Holisova et al. 1984). However, when possible, field roe will supplement their diet by browsing in pockets of woodland such as windbreak belts and small copses (Holisova et al. 1982 and 1984, Putman 1986).

Considering the high percentage of woody plants in the roe deer diet, it is obvious that the deer may be of considerable importance in forest management by damaging shoots of broad-leaved and coniferous woody plants (Gill 1992, Picard et al. 1994). Roe deer may suppress, distort or kill economically important species in a variety of manners. Some, such as fraying and trashing, are associated with the buck's territorial behaviour whereas browsing results directly from the animal's feeding activities (Hoolboom 1976).

II.F Comments:

The chapter clearly shows the importance of the habitat in determining the diet composition of roe deer. Roe deer are found all over Europe. With the exception of the high alpine zones above the treeline and the most open grasslands, their geographical distribution goes from the north of Sweden and Norway (spread out during the last century) to the Mediterranean region, and from the United Kingdom in the west, to the Ural Mountains, Greece and Turkey in the east (Linnell et al. 1998a). Since roe deer are apparently able to adapt their diet to the plant species composition of highly different plant communities (sub-alpine and boreal vegetation, marshes and man-made agricultural areas, and dry Mediterranean zones) food supply clearly is not the only, or determining, factor in habitat use by roe deer. However, on a finer scale of habitat selection, early successional habitats are generally preferred over climax habitats (Linnell et al. 1998a). This preference for early successional habitats can, partly, be explained by the food preferences. Indeed, a large proportion of the diet consists of herbs, half woody plants, deciduous and coniferous browse (below 1.1m high) and dwarf shrubs (see Table II.4), all vegetation types that require light and are typical for early successional habitats.

This chapter was published as: "Cornelis, J., Casaer, J. and Hermy M. (1999). Impact of season, habitat and research techniques on diet composition of roe deer (Capreolus capreolus): a review. Journal of Zoology, London. 248: 195-207" The first author participated as a thesis student in the research project, more specific focussing on the effects on the natural regeneration of introduced roe deer in Bos t'Ename and roe deer diet composition.

III Quantifying visual obstruction for roe deer habitat selection studies

III.A Abstract

The need to quantify habitat factors (environmental characteristics) in habitat utilisation studies leads us to look for an observer independent, repeatable method for measuring the presence of visual cover in different habitat types. Visual cover was defined as the degree to which an animal, in this case a roe deer, is concealed by the surrounding vegetation. We further refined the technique of using a cover pole to estimate hiding cover (as developed by Griffith and Youtie (1988)) since we assume that this technique offers most possibilities for standardisation. Griffith and Youtie estimated the hiding cover in each 0.5 meter interval by counting the number of 0.1 m bands that were concealed by the vegetation (0 – 5). Using directly the information of each 0.1 m interval, thereby omitting the intermediate step, we ameliorated the method. We further compared the influence *(i)* of using small (0.1 m) rather than large (0.5 m) measuring intervals, *(ii)* of weighting the results of each measuring interval with the proportion of the animal potentially visible in this interval and *(iii)* of weighting the results according to the number of cardinal directions (North, East, South, West) in which cover was observed. As a measure for the accurateness of each of these methods, we used the correlation between the calculated cover value and the concealment of a cardboard roe deer silhouette. We repeated these tests for three different distances, being 10, 15 and 25 meters, and repeated the test with a silhouette of a standing and one of a bedding roe deer.

The results showed that *(i)* using smaller measuring intervals and *(ii)* weighting for the proportion of the animal potentially visible in that height interval, significantly improved the correlation and thus the accuracy of the hiding cover estimation. However, *(iii)* there was no significant improvement when weighting for the number of cardinal directions in which cover occurred.

The method allows the use of the cover pole measurements to estimate the hiding cover for different animal species, whenever the body dimensions of the animal species are known.

For our study site 10 meter was the optimal observation distance to estimate the hiding cover.

In many habitat studies and in Habitat Evaluation Procedures (HEP) that use Geographic Information Systems (e.g. Didier and Porter 1999) it is assumed that hiding cover changes throughout the landscape but is constant within a habitat type. Our study demonstrates the large variation in hiding cover within one type of forest stand, thereby questioning the above-mentioned assumption.

III.B Introduction

To study the importance of a habitat factor for an animal species, one needs to be able to define and quantify the factor accurately. Food and cover are the main habitat factors for most deer species - e.g. Strandgaard 1972, Henry 1981, Aulak and Babinska-Werka 1990, Reimoser and Mauser 1993, Mysterud and Ostbye 1995, Danilkin and Hewison 1996, Mysterud 1996, Mysterud and Ostbye 1999 for roe deer; Euler and Thurnston 1980, Armstrong et al. 1983 for white-tailed deer (***Odocoileus virginianus)*** and Schwab and Pitt 1991, and Demarchi and Bunnel 1995 for moose

(*Alces alces*). The most important role of vegetation cover for deer is protection against predators and humans (Peek et al. 1982, Cook et al. 1998) and against adverse weather conditions (Reimoser and Mauser 1993, Bookhout 1996).

Vegetation cover can be subdivided into a horizontal and a vertical component. The horizontal component is unambiguously defined as the projection of above ground parts of a plant species. This is often referred to as just 'cover' and can be described by a set of standard scales among which the Braun-Blanquet scale (Westhoff and Van der Maarel 1978) is probably the most common one. Canopy cover is often measured using leaf area indexes (Demarchi 1995). Defining the vertical component of vegetation cover, mostly referred to as hiding cover (Peek et al. 1982, Griffith and Youtie 1988), is far more difficult. Several authors have described hiding cover, each using their own definitions and scales, making comparisons between the studies almost impossible (Henry 1981, Armstrong et al. 1983, Heugel et al. 1986, Lagory 1986, Mysterud and Ostbye 1995).

A first attempt to standardise the measurement of hiding cover, was made by Wight in 1939 (see Bookhout 1996). His method, however, did not give any information on the vertical distribution of the visual obstruction (Nudds 1977, Bookhout 1996). Nudds (1977) used a '*vegetation silhouette board*', as was used by MacArthur and MacArthur in 1961. This is a 2.5 m high board, divided vertically into 5 square sections. Description of the concealment of each of the 0.5 m intervals allows comparison between the obstruction patterns of different habitat types or between different seasons for the same habitat type. Because of the impractical size of the vegetation silhouette board, Griffith and Youtie (1988) proposed the use of a cover pole (a 2 meter high, 2 section collapsible pole see Figure III.1). They compared the results obtained with the two instruments and tested if the estimation of the hiding cover, using each instrument, is observer independent. They concluded that both instruments are observer independent and that the results did not differ significantly. Finally they tested the similarity between the concealment of the cover pole and of a cardboard silhouette of a deer (*Odocoileus spp.)*. They found a significant correlation for the silhouette of a standing deer but not for the silhouette of a bedding deer.

Griffith and Youtie estimated the visual obstruction for each 0.5 meter interval (of a 2 meter pole) by counting the number (1-5) of 0.1 m intervals that were >25% concealed by the vegetation. For the subsequent analyses these values were converted to percentages and the observed value of each 0.5 m interval was multiplied by the proportion of the silhouette potentially visible in each interval. For each height interval the 'potentially visible proportion' of the animal equals the proportion of the silhouette occurring in that height interval (see Figure III.1 and Table III.1)

Our working hypothesis is that omitting the intermediate step of recalculating the observed visual concealment of the 0.1 m bands into visual obstruction values for the 0.5 m intervals, will ameliorate the results. For roe deer, being a medium sized animal, this will probably allow a better estimation of the hiding cover.

We measure hiding cover using the cover pole and compare the subsequently computed cover values with the concealment of a roe deer silhouette. We test the influence of three factors, supposedly influencing our ability to estimate hiding cover accurately.

First, we test if using smaller measuring intervals (0.1 m compared to 0.5 m) increases the correlation between the concealment of the cover pole, and of the roe deer silhouette, for both a standing and a bedding roe deer.

Secondly we compare this influence with the effect of weighting the results for each measuring interval (0.5 m or 0.1 m) with the proportion of the animal potentially visible in that interval. We calculated the proportions both for the silhouette of a standing and of a bedding roe deer (see Figure III.1)

Because we consider the number of cardinal observation directions, in which hiding cover was observed, as an important characteristic of the cover present, we weight the hiding cover values for the number of cardinal directions in which cover was present.

In order to allow comparison between different study areas, we try to define a standard distance for measuring visual obstruction for roe deer studies. Even more because the use of a standard distance enables one person to take the cover measurements without help. Thereby reducing the man-hours spent on data collection (see Nudds 1977, Vincent and Bideau 1982 and personal experiences).

Finally we apply the refined method by using it to compare the hiding cover in the different forest stand classes in the study area. Hereby we question the often applied method of translating forest inventory maps (giving the different forest classes) into hiding cover maps, based on the assumption that differences in forest classes corresponds with differences in hiding cover for animals (Lagory 1986, Aulak and Babinski-Werka 1990, Tufto et al. 1996)

III.C Study area

Most of the study plots were situated in the Meerdaal forest complex, a state owned forest, east of Brussels, Belgium. The total area is approximately, 1320 ha and it consists of oak (*Quercus petraea* and *Quercus robur)* and beech (*Fagus sylvatica)* stands, respectively 25%, 3% and 31% of the total area; a fourth main species is Scots pine (*Pinus sylvestris)* (Rijmenans 1983). Other plots were situated in Langerode, a small (20ha) university owned forest. This forest consists mainly of poplar stands (*Populus serotina)*, with a rich understorey of alder (*Alnus glutinosa)* and ash (*Fraxinus exelsior)* (Casaer 1993).

III.D Methods

We defined hiding cover as the 'degree to which the vegetation obstructs the visibility of an animal (or any other object)'. A 2 meter high cover pole (diameter 2.5 cm) was used, divided into 0.1 meter sections painted alternately red and black, and white and black to improve the contrast. Each 0.5 m interval was marked with a reflective tape.

A cardboard silhouette was constructed, derived form published measurements of European roe deer (Danilkin and Hewison 1996). We used 0.7 meters as the height for the withers and calculated the other dimensions using the proportions as drawn by Stubbe (1997). The silhouette was subdivided into 0.01 m^2 squares that were also painted alternately red and white. The 'legs' of the silhouette could be folded to simulate a 'bedded' roe deer (Figure III.1).

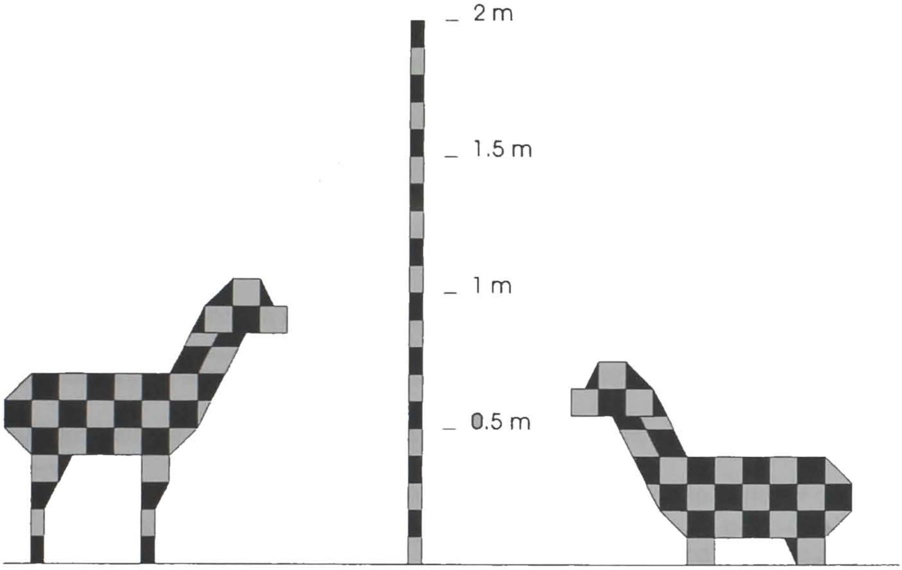

Figure III.1: Standing and bedding roe deer silhouette and the cover pole as used in this study. Each square of the roe deer silhouette is 0.01 m^2.

For 51 plots cover measurements were made, 46 of these plots were situated in Meerdaal and 5 in Langerode. The plots were chosen to achieve a maximal range in the level of concealment of the silhouette.

The cardboard silhouette was placed in the centre of the plot and turned perpendicular to the cardinal direction from which the concealment was estimated. For each of the four cardinal directions (North, East, South, West) we estimated the concealment of the cover pole and the concealment of the silhouette of both the standing and the bedding roe deer. These estimations were done from respectively 10, 15 and 25 meters from the centre of the plot. To measure the distance between the silhouette (or the cover pole) and the observer we used a DME 201 (Haglof). This measuring instrument consists of two parts; an ultrasonic transmitter and a receiver. This instrument is accurate to within one decimetre. A SILVA compass was used to determine accurately the cardinal directions for the measurements.

We estimated the concealment for each 0.1 meter height interval of the cover pole and each 0.01 m^2 square of the silhouette. Three levels of concealment were differentiated; total visibility, intermediate concealment and total concealment of the section. These levels were indicated with the values 0, 0.5 and 1 respectively.

All measurements were taken from a standard height of 1 meter above ground level. The measurements took place at the end of the vegetation period (September, October 1997) when the understorey was still fully developed. Since both estimations (cover pole and silhouette) were made at the same time, the influence of weather conditions on the visibility of both instruments was assumed to be the same. Therefore weather conditions were not recorded.

III.D.1 Processing the observed concealment values

In order to obtain single 'cover estimates' to express the cover pole concealment for each plot, 7 different methods were used to process the cover pole readings. All values were expressed as the percentage of the maximum value (occurring if the vegetation covers the whole length of the cover pole). The first two hiding cover estimates were simply based on averaging the observed cover pole readings, estimated for each interval of 0.5 m (1*[1]) or 0.1 m (2*) of the cover pole over the 4 cardinal directions.

By multiplying the obstruction values for each height interval of the cover pole by the proportion of the roe deer silhouette potentially visible in this height interval (see Table III.1) we calculated new hiding cover values. We used respectively the values

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[1] * the number of the method is used as a reference in Figure III.2 and Table III.3

measured in each 0.5 m measuring interval (3*) and those measured in each 0.1 m intervals (4*). The 'proportion potentially visible' used for these calculation was chosen according to the silhouette for which the hiding cover had to be estimated.

Table III.1: Proportion of the roe deer silhouette potentially visible in each height interval.

Height interval (cm)	Standing roe deer			Bedding roe deer		
	Absolute (dm^2)	Proportion (0.1 m)	Proportion (0.5 m)	Absolute (dm^2)	Proportion (0.1 m)	Proportion (0.5 m)
200	0.000	0.000	0.000	0.000	0.000	0.000
190	0.000	0.000		0.000	0.000	
180	0.000	0.000		0.000	0.000	
170	0.000	0.000		0.000	0.000	
160	0.000	0.000		0.000	0.000	
150	0.000	0.000	0.026	0.000	0.000	0.000
140	0.000	0.000		0.000	0.000	
130	0.000	0.000		0.000	0.000	
120	0.000	0.000		0.000	0.000	
110	0.875	0.026		0.000	0.000	
100	2.500	0.073	0.631	0.000	0.000	0.195
90	2.625	0.077		0.000	0.000	
80	2.000	0.058		0.875	0.028	
70	7.250	0.212		2.500	0.081	
60	7.250	0.212		2.625	0.085	
50	6.000	0.175	0.343	2.000	0.065	0.805
40	2.250	0.066		7.250	0.236	
30	1.500	0.044		7.250	0.236	
20	1.000	0.029		6.000	0.195	
10	1.000	0.029		2.250	0.073	

Further, we computed weighted averages to correct for the number of cardinal directions in which obstruction was present. As the obstruction was measured from four cardinal directions, and the resulting values should vary between 0 and 1, the following equation was used.

$$Wa = \left[\left(\sum_{i=1}^{4} obs_i\right)/4 + 0.5\right] * Q/6$$

Wa = weighted average

obs_i = obstruction value for one of the four cardinal directions

Q = number of cardinal directions for which $obs_i > 0$

We computed three hiding cover estimates based on this equation.

The first (6*) is the weighted average using for each direction the sum of the obstruction values over the whole cover pole as the obs_i value.

To compute the second (7*) we first weighted the obstructions values for each 0.1 m interval according to the above mentioned equation and subsequently summed these values to calculate the total obstruction.

Finally we multiplied the weighted averages for each 0.1 m interval (as used in 7*), with the potentially visible proportion of the roe deer in this interval (see Table III.1). This results in an average that is weighted for the number of cardinal directions in which obstruction occurs as well as for the proportion of the roe deer situated in a certain height interval (5*).

To express the concealment of the silhouette as a 'single value', three different methods were applied. First, we simply computed the average over the four cardinal directions for the standing as well as for the bedding roe deer. Secondly, we computed a weighted average by using the total obstruction value of each cardinal direction and weighting the average according to the number of directions for which the obstruction was greater than 0. Finally, a third value was computed by summing the weighted averages of each 0.01 m^2 square. The absolute hiding cover values were subsequently expressed as the percentage of the cover value that would occur if the vegetation covers the whole roe deer silhouette. This resulted for each plot and for each distance in three concealment values for the bedding roe deer silhouette and three concealment values for the standing roe deer, totalling in 9 values for the bedding and 9 values for the standing roe deer.

Since the Kolmogorov-Smirnov normality test revealed that not all the resulting estimates were normally distributed, we used the Spearmans rho to analyse the correlation between the obtained 'cover estimates' (based on the cover pole readings) and the values expressing the concealment of the roe deer silhouette (Siegel and Castellan 1988). For each of the three distances we computed the Spearmans rho correlation coefficients between the concealment values of roe deer silhouette and the different values used to estimate the hiding cover.

We applied the Wilcoxon Signed Ranks test ($\alpha = 0.05$) to compare the correlation coefficients for the silhouette of a standing roe deer with those for the silhouette of a bedding roe deer. We performed this test for all 7 different estimation methods together, resulting in 63 comparison pairs, and for each of the 7 estimation methods separately, resulting in 7 times 9 paired comparisons. We applied the Friedman Two-Way analysis method to test if there were significant differences between the various methods used to estimate the hiding cover. Subsequently, we evaluated the influence of the different methods on the accuracy of the hiding cover estimates, using multiple comparison tests between the mean ranks of the different methods (Siegel and Castellan 1988).

III.D.2 Optimal distance

We defined the optimal distance to measure the hiding cover as the distance that results in the maximal variation in the observed levels of concealment of the roe deer silhouette. This equals the distance for which the distribution of the observed concealment values is most similar to a uniform distribution. We therefore compared the distribution of the concealment values of the standing and the bedding roe deer silhouette, and a uniform distribution. We applied a Chi^2 test to calculate the probability that the concealment values could be drawn from a uniform distribution.

III.D.3 Applying the developed method

We measured the hiding cover from a distance of 10 meters on 88 plots in 7 different forest classes at the end of the vegetation period (September) and repeated the sampling after leaf fall (February). The number of trees and the diameter at breast height were measured for a sample plot with a radius of 10 meter.

The canopy closure was estimated using three classes; < 33%, between 33% and 66% canopy closure and > 66%. The tree species composition was described using the percentages of the canopy of each of the four following tree species groups. The first two groups subdivide the coniferous trees into those that filter out most light in a forest stand, such as Silver fir (*Abies alba*), Douglas fir *(Pseudotsuga menziesii)* and Norway spruce (*Picea abies*) (group 1), and those that still allow light to enter in the forest stand, allowing a stronger development of the understorey, such as larch (*Larix spp.*) and pine (*Pinus spp.)* (group 2). The deciduous trees were also subdivided into the shade bearing trees such as beech (*Fagus sylvatica*) and maple (*Acer pseudoplatanus*) (group3) and shade intolerant trees such as oak (*Quercus spp.*), ash *(Fraxinus excelsior)*, alder (*Alnus sp.*), birch (*Betula spp.*) and poplar (*Populus spp.*) (group 4). Finally we estimated the percentage of the sample plot covered with ground vegetation. Though the distribution of the plots over the different forest classes was the same for the winter as for the summer period, the geographic location of the plots within the forest stands were not exactly the same. This resulted in slightly different characteristics for the canopy layer (Table III.2).

Table III.2:Characteristics of the sample plots for the different groups of forest classes

		young deciduous	middle aged deciduous	old deciduous	uneven aged deciduous	young coniferous	middel aged coniferous	old coniferous
	% canopy closure	54	62	66	56	60	57	61
W	% group1	0	2	0	0	59	36	28
I	% group2	0	10	0	18	36	50	59
N	% group3	7	13	92	27	0	9	12
T	% group4	93	75	8	56	5	5	2
E	Number of trees / ha	1557	488	138	570	3029	617	489
R	Basal area (m2/ha)	12	27	59	21	17	33	35
	% ground cover	41	22	10	37	49	33	42
	% canopy closure	54	62	66	56	60	60	60
S	% group1	0	2	0	0	59	42	36
U	% group2	0	9	0	8	36	48	47
M	% group3	7	13	92	36	0	5	15
M	% group4	93	75	8	57	5	5	2
E	Number of trees / ha	1525	446	127	535	2563	632	500
R	Basal area (m2/ha)	12	26	54	18	18	32	36
	% ground cover	56	38	25	50	55	45	51
	Number of plots	10	16	3	10	8	21	20
	Reference number in Figure III.4	**11**	**12**	**13**	**14**	**21**	**22**	**23**

*** Group 1-4: different groups used to describe the tree species composition in the canopy (see also text). Group 1 and 2 are coniferous trees, 3 and 4 deciduous trees / Groups 1 and 3 block the penetration of light into the forest to a higher extent compared to respectively group 2 and 4.*

III.E Results

III.E.1 Testing the modified method

Figure III.2 shows the resulting Spearman rho correlation coefficients which were all significant ($\alpha < 0.05$ level). The Wilcoxon Signed Ranks test revealed that the overall correlation between the hiding cover estimates and the concealment of the silhouette was higher ($p < 0.001$) for the standing roe deer than for the bedding roe deer.

However, when comparing the results for each of the estimating methods separately, the tests revealed that this difference in accuracy disappeared when weighting for the proportion of the roe deer potentially visible in each height interval (see Figure III.2, methods 4 & 5).

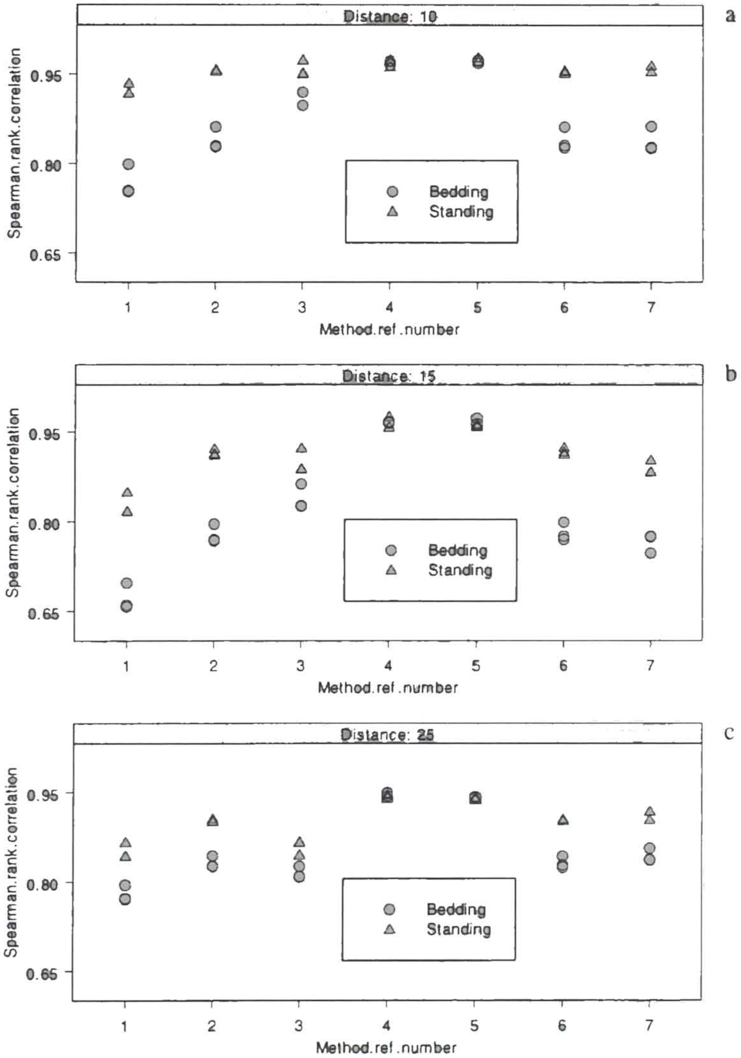


Figure III.2: Spearman rank correlation coefficients between the hiding cover estimates and the concealment of the roe deer silhouette Figure III.2.a,b,c represent the rank correlations for the three different distances, being respectively 10, 15 and 25 meters. For the explanation of the different methods used see Table III.3.

Table III.3: Used methods and their differentiating characteristics.

Reference number in Figure III.2 and in the text.	Weighted for the potentially visible proportion	Weighted for the directions in which cover occurs	Measuring interval
1	No	No	0.5 m
2	No	No	0.1 m
3	Yes	No	0.5 m
4	Yes	No	0.1 m
5	Yes	Yes, using each measuring interval	0.1 m
6	No	Yes, using total obstruction for each direction	0.1 m
7	No	Yes, using each measuring interval	0.1 m

The highest mean rank of correlation coefficients was found for the combination of using both smaller measuring intervals and weighting for the potentially visible proportion of the roe deer silhouette.

The Friedman test indicated that there were significant differences in the correlation coefficients using the different methods ($p < 0.001$). When comparing the mean rank values for the different methods the results revealed a significant amelioration in the accuracy of the hiding cover estimation when using smaller intervals (comparing method 4 with method 3 and method 2 with method 1). Weighting for the potentially visible proportion always returned significantly better results, independent of the measuring intervals used (comparing method 4 with method 2, method 3 with method 1 and method 5 with method 7). However, weighting for the number of cardinal directions in which cover occurred, did not improve the accuracy of the hiding cover estimation (comparing method 5 with method 4, and method 7 with method 2).

The most uniform distribution for the obstruction of the standing roe deer will be found at a distance between 10 and 15 meter. For the bedding roe deer a distance below 10 meter would probably return the most uniform distribution since even at 10 meters many of the measurements returned high obstruction values (see Figure III.3a and III.3b). For the standing roe deer silhouette both the estimates from a distance of 10 meters and those from 15 meters could, statistically, be drawn from a uniform distribution (Chi^2 test, $p = 0.84$ for 10 meters and $p = 0.95$ for a distance of 15 meters). However, for the bedding roe deer the distribution at 15 meters differs significantly ($p < 0.05$) from a uniform distribution. Only the distribution of the concealment of the bedding roe deer measured from a distance of 10 meters could be uniform ($p = 0.23$).

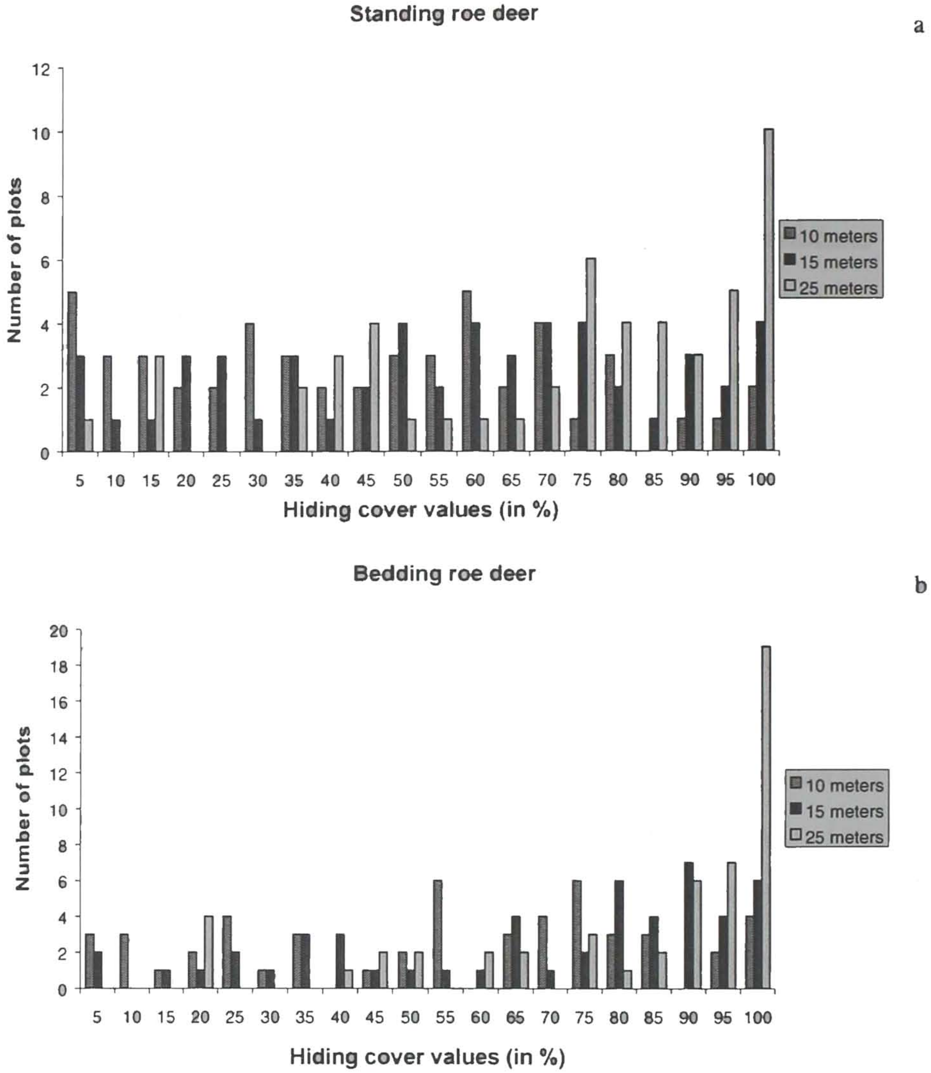


Figure III.3: Distribution of the hiding cover values of the roe deer silhouette of a standing (a) and a bedding (b) roe deer, measured from respectively 10 m, 15 m and 25 m distance.

III.E.2 Applying the developed method

Though the estimated hiding cover did not differ significantly between the forest classes, the results (Figure III.4a and III.4b) show a tendency for hiding cover in the deciduous forest stands to be lower in the older, even aged forest stands, which have a closer canopy. The coniferous stands however show a different trend. Old and young coniferous stands offer more cover than middle aged coniferous stands.

For both the bedding and standing roe deer the development of ground vegetation in the summer resulted generally in a better hiding cover. The differences in hiding cover were however less clear for mature deciduous forest stands, and young-even aged coniferous forest stands.

However, our results clearly indicated the large variation in hiding cover that occurs within a single forest class and the large overlap in hiding cover estimates between the different forest classes.

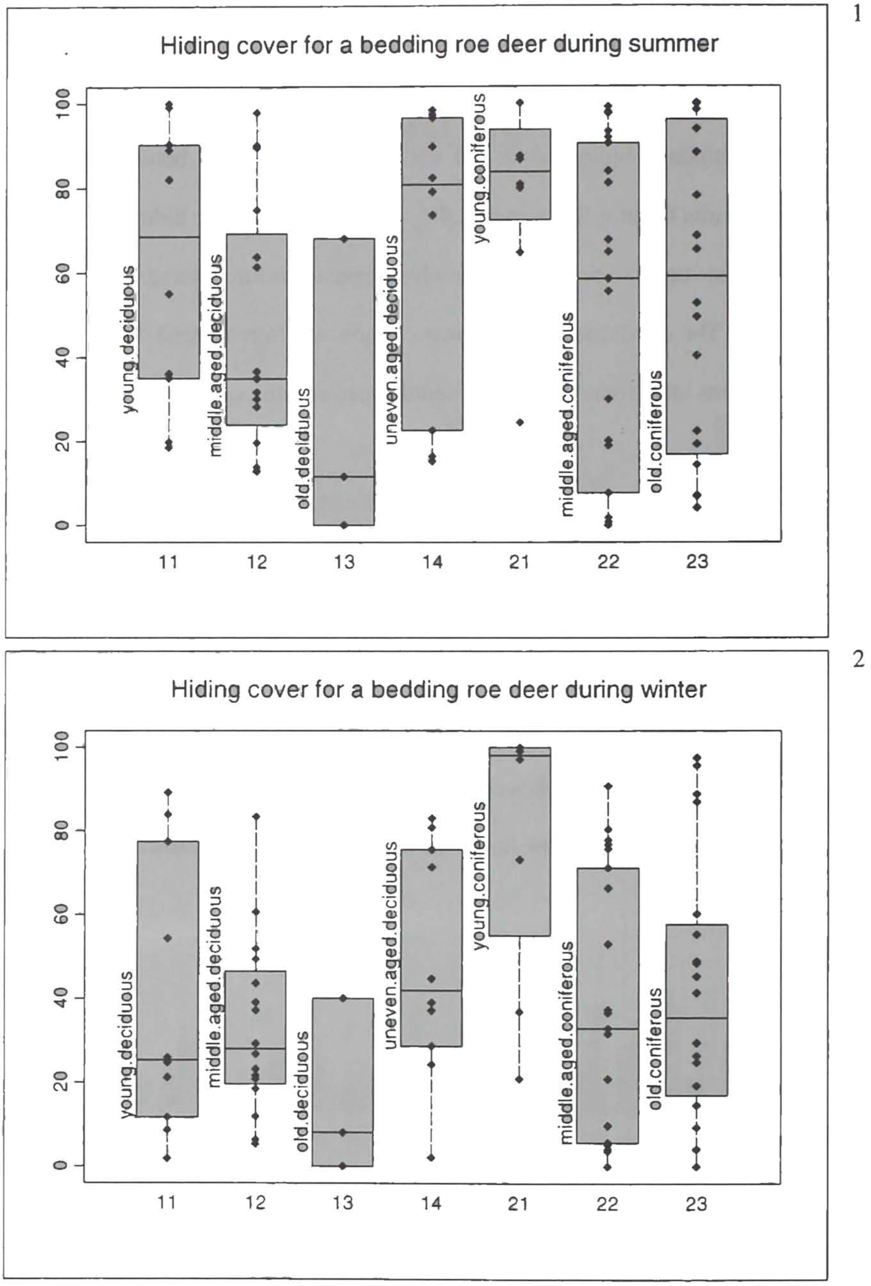
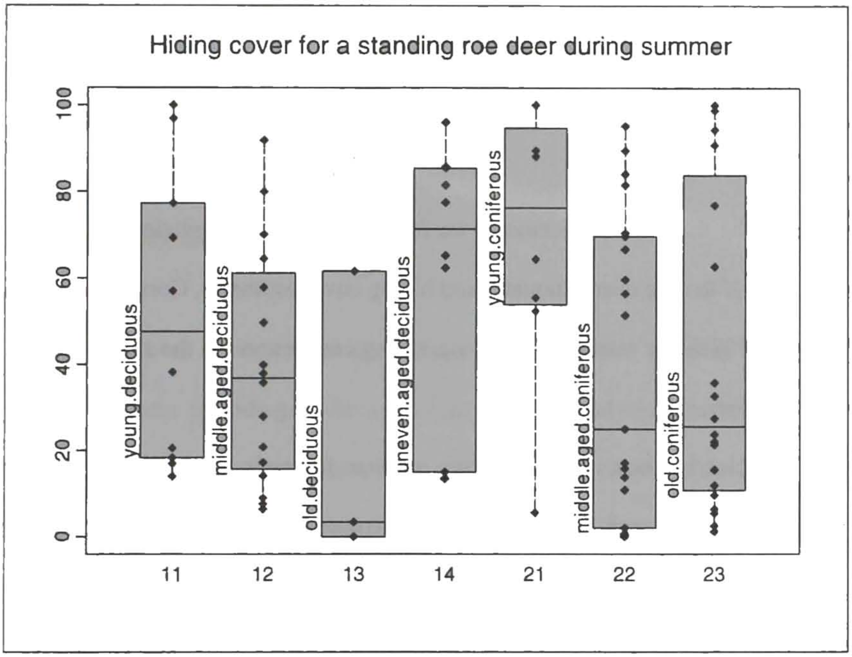


Figure III.4.a: Hiding cover estimates for a bedding roe deer during summer (1) and winter(2) in the different forest classes. Dots represent the cover estimates.

1



2

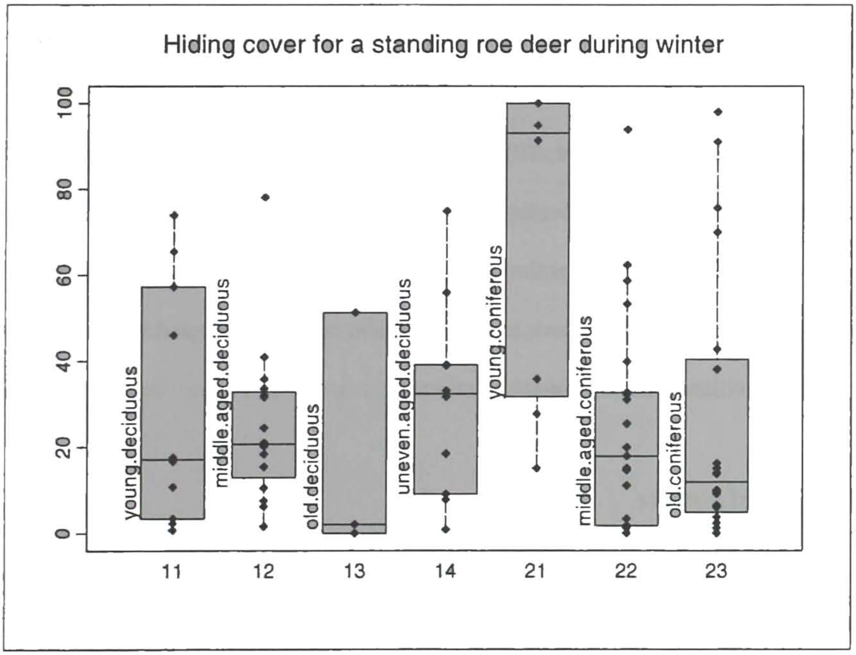


Figure III.4.b: Hiding cover estimates for a standing roe deer during summer (1) and winter (2) in the different forest classes. Dots represent the cover estimates.

III.F Discussion

III.F.1 Processing the observed concealment values

For each of the three tested distances, we found significant correlations between the concealment of the roe deer silhouette and hiding cover estimates. Contrary to Griffith and Youtie (1988) our results also show a strong correlation for the silhouette of the bedding roe deer.

Our results clearly show that, (*i*) using smaller intervals and (*ii*) weighting the obstruction values of each height interval by the proportion of the animal potentially visible in this interval, greatly improves the accuracy of the hiding cover estimation. These findings clearly confirm our working hypothesis that omitting the intermediate step, of calculating concealment values for each 0.5 m interval, improves the method to estimate the hiding cover.

Contrary to what we expected (*iii*) there was no a significant improvement when weighting for the number of cardinal directions in which obstruction was observed. Although this approach is still anthropocentric we believe that an objective, repeatable and observer independent method, as presented above, is a prerequisite to study of the role of visual obstruction in habitat selection.

III.F.2 Optimal distance

The best correlations were found for a distance of 10 meters and the optimal distance to achieve a uniform distribution seems to be a little below 10 meters for the bedding and a little more than 10 meters for the standing roe deer. Therefore we consider 10 meters to be a good standard distance to measure the visual obstruction for roe deer in forest stands in our study area. This is less than the distance determined by Nudds (1977), who found that 15 meters gave the greatest variation in foliage density readings.

III.F.3 Applying the developed method

The hiding cover estimates for the different forest classes showed that there were large differences in hiding cover availability. When analysing the characteristics of the canopy and the presence of hiding cover, it becomes clear that the light conditions on the forest floor, by influencing the ground vegetation, largely determine the hiding cover in the forest stand. These light conditions are mainly influenced by the canopy closure and by the tree species composition. The large variations in hiding cover within one single forest class together with the large overlap in hiding cover values between different forest classes, poses serious doubt on the possibility of translating forest inventory maps directly to cover maps. Therefore we seriously question the assumption that cover varies throughout the landscape and is constant within a habitat type. The use of other variables such as soil type, topography (Mysterud and Ostbye 1999) and management options could help to translate more accurately forest inventory maps into hiding cover maps (see also Reimoser and Zandl 1993).

III.G Final conclusions and research implications

Our results clearly indicate that a 2m cover pole can be used to measure visual obstruction for wildlife habitat studies. When calculating the percentage of an animal species potentially visible in each of the 20 0.1 m height intervals and using this information to compute the hiding cover estimates, the same field measurements can be used to calculate the visibility (concealment) of different animal species, or different positions of the same animal species.

Although the correlation coefficients did not improve when weighting for the number of cardinal directions in which obstruction occurred this does not mean that it cannot be useful to measure the visibility from more than one direction. The visibility of the silhouette as well as of the cover pole did vary significantly within some forest stands depending on the direction of the measurement. The directional variation in hiding cover can be very important for roe deer in the process of selecting bedding sites (Mysterud and Ostbye 1995, Mysterud and Ostbye 1999), and should therefore be estimated. The cover pole proved to be a powerful tool for this purpose.

We do not state that 10 meters is 'the' distance to measure cover for any animal, wherever in the world. We do believe however that this study shows that determining a standard distance, that returns the maximum range in hiding values for the species studied, within a specific study area, is an important aspect that cannot be omitted from any pilot study for a research project studying the role of cover for the species concerned.

Finally we suggest that to study the functional relationship between hiding cover and roe deer habitat selection one should use a different approach than the classical habitat selection methodology based on 'habitat types'. We suggest that a better understanding on the relationship between hiding cover and other environmental characteristics is needed. After establishing this relationship, this information could be used to map the spatial and temporal distribution of hiding cover in the study area. Finally, the comparison of the distribution of hiding cover and the space use of the animals will allow establishing the functional relationship between hiding cover and space use by roe deer.

I would like to thank Atle Mysterud and Charles Wilson for comments on previous drafts of this manuscript.

IV Collecting animal locations

IV.A Introduction

Whatever the question one wants to resolve by using information on the space use of a species, animal locations (fixes) are to be collected. Contrary to comparative home range studies (e.g. Cederlund 1983, Guillet et al. 1996), studying detailed habitat use, or studying the behaviour of individual animals, requires frequent, highly accurate animal locations. In this chapter we analyse the potential use of GPS (Global Positioning Systems) collars as an alternative for classical radio tracking of medium sized mammals.

Manual field telemetry can be very labour intensive and consequently expensive (Priede 1992). Furthermore, it can be risky or impossible to collect animal locations under severe conditions, e.g. in bad weather, during the night or in difficult terrain. To achieve a more or less continuous recording of the animals' positions is therefore hardly feasible using manual field telemetry. Moreover, there is the disturbance the operator may cause when getting close to the animal (Angerbjorn and Becker 1992).

Satellite telemetry has been used for many years to follow the migration of large animals, or species using large home ranges (e.g. Gorman et al. 1992, for wild dogs), marine species (Taillade 1992, Sakamoto 1997), and birds (Ancel et al. 1992). Several attempts were made to create automated radio telemetry systems in order to continuously and accurately localise smaller mammals. These systems were either based on rotating Yagi antennas in fixed stations (Deat et al. 1980), on hyperbolic antenna systems (Lenmell et al. 1983) or on a Doppler technique (Angerbjorn and Becker 1992). None of these attempts has yet resulted in a commercially available automated location system.

Nowadays, Global Positioning System (GPS) technology has become available for wildlife telemetry studies. The GPS unit can be built into a collar and combined with a VHF radio transmitter, the latter to allow classical radio tracking. Depending on the manufacturer, there is a bi-directional radio link between the GPS collar and a mobile or fixed receiver (Lotek), a one-way communication from the GPS collar to a receiver to transmit the data (Televilt), or there are no communication possibilities and the data have to be downloaded after retrieving the GPS collar (Advanced Telemetry Systems, Inc). The latter system is equipped with a drop-off mechanism to enable remote release of the collar to collect the stored information. The use of remote releasing systems allows the reduction of collar weight, since no radio modems are needed. Controlling the functioning of the GPS collar becomes, however, more difficult. The option of differentially correcting the collected raw measurements forms another important distinguishing feature when cross-comparing commercially available GPS collars. Table IV.1 gives an overview of the existing GPS collars and their characteristics. Telonics manufactures a system that combines GPS technology with the ARGOS (Taillade 1992) satellite system. The GPS unit records the positions of the animal and the ARGOS system transfers the collected animal positions by satellite to a distant ground station.

Table IV.1: Currently available GPS collars (January 2000)

Company / Name	Weight	Data transmission	Differential correction	Tests / Literature	Information / Websites
Lotek / GPS-1000	1800 gr.	Bi-directional	Yes	Remel & Rodgers 1997 Moen et al. 1997 Edenius 1997	www.lotek.com
Lotek / GPS-2000	875 gr				www.lotek.com
Televilt / GPS simplex	475 gr	One way	No	Own tests	www.televilt.com
Televilt / GPS simplex		One way	Yes		
ATS, Inc	920 gr	No	No	Merrill et al. 1998	www.atstrack.com
Telonics	1.7 kg	??	??		www.teleonics.com

The first documented results of testing GPS collars highlighted the influence of the habitat type on the probability of obtaining a successful location fix. The satellite visibility for the receiver unit is the main problem whenever the GPS collar is located in dense forest stands. In order to get a 3 dimensional (3D) fix (= a geographic position of the animal) the GPS receiver needs to detect at least four satellites simultaneously. If the GPS receiver detects less than four satellites, the search time to find a fourth satellite can be extended. This results, however, in a greater battery drain. Alternatively a 2-dimensional (2D) location can be stored, leading to a loss of precision (Moen et al. 1997).

According to the same authors, the fact whether the animals were moving or stationary had no impact on the location type (2D or 3D) nor on the success-rate. They also stated that the position of the GPS collar (vertical or inclined) influenced the proportions of 3D, 2D or failed observations. Other researchers do not come to the same conclusions (Edenius 1997, Bowman et al. 2000).

Field experiments demonstrated a significant influence of the DOP (Dilution of Precision) on the accuracy of the 2D locations but less so on the accuracy of the 3D fixes (Rempel et al. 1995, Edenius 1997, Rempel and Rodgers 1997). Field use of GPS collars that allowed post-processing differential correction of the collected fixes, illustrated the expected gain in precision (Moen et al. 1997, Rempel and Rodgers 1997).

Because of the limits on the weight of radio collars (upper threshold of approximately 3% of the animals body weight (Kenward 2001)) only the Televilt collars could be used for roe deer research. No results of field-tests of this GPS collar were available when this work was carried out (1998/99). Moreover, all previous tests of GPS collars (except for preliminary results of Janeau et al. 1998) took place in boreal forest conditions (Remple et al. 1995, Moen et al. 1996, Edenius 1997, Moen et al. 1997, Dussault et al. 1999).

Habitat preference is analysed by comparing the use (percentage of the observations) and the availability (percentage of the total area) of a certain habitat. The occurrence of habitat-related differences in the probability of obtaining a GPS observation (fix) may therefore strongly bias the results of habitat preference studies. Even more because interactions between habitat use and external factors (weather, disturbance, ...) are common. Moen et al. (1996) illustrated this by showing the interaction between ambient temperature and habitat selection by moose on the one hand and the proportions of 3D and 2D locations and failed attempts, on the other hand. With increasing ambient temperature, moose shifted their preference to closed canopy habitats, resulting in an increase in the number of failed location attempts from 1% to 16%. Similar findings were reported by Bowman et al. (2000). Researchers consequently need to understand the character and the magnitude of the observation bias before deciding on using GPS telemetry, and bias has to be corrected for before interpreting the data. Rumble and Lindzey (1997) suggest that modelling the influence of the habitat type on the GPS observation rate could be a method to do this.

We therefore decided to test the performance and accuracy of a prototype GPS collar, for roe deer in temperate forest in Flanders. Using statistical model building, we estimate the difference in observation rate related to the forest type and observation angle. Because the search period (programmed to be 240sec for each location attempt) strongly influences the total life-time of the GPS collar, we analyse the time-distribution of the 3D and 2D locations in order to optimise the search period for future use of GPS collars in temperate forest conditions.

To increase the accuracy of GPS fixes, several researchers (e.g. Moore et al. 1997) suggested using a linear correction method as an alternative for differential correction of GPS data. In the second part of this chapter, we present the results of our field experiments showing why this method of correcting GPS fixes is not recommended.

IV.B Testing the GPS simplex (Televilt)

IV.B.1 Abstract

We tested the performance and accuracy of a GPS collar in temperate forest ecosystems. The results in temperate forests corroborate with those of tests done in boreal forests. Observation angle and habitat type influence the success-rate of a GPS collar. The DOP has a greater influence on the accuracy of two-dimensional observations (2D) than on the accuracy of three-dimensional observations (3D). The observation angle does not influence the accuracy of the GPS observation. Using the

derived observation probability model, we illustrate the influence of habitat related bias on habitat preference studies.

IV.B.2 Study area

The GPS simplex was tested on seven sites all situated south of Leuven (Flanders, Belgium). Three sites were located in beech (*Fagus sylvatica* L.) stands, two sites in pine forest (*Pinus pinaster* Ait.), and one was located in a small spruce stand (*Picea abies* Karst). As a reference, we used an open area in a military camp. The distance between the individual sites and the base station in Leuven was maximum 13 km.

IV.B.3 Material and methods

We tested a GPS–Simplex (Televilt) in stationary mode. The collar was placed around a horizontally oriented filled water bottle replacing the animal's neck. The bottle was fixed on a pole so the GPS antenna was at a height of 70-cm (approx. height of the neck of a roe deer).

The frequency of the location attempts and the search time (the period during which the GPS will attempt to determine its location) have to be programmed by the user. This is done using programming software supplied by Televilt while the collar is connected directly to a PC.

According to the manufacturer, the battery allows a total of 400 attempts using a maximum search time of 90 seconds. Since we originally intended to perform 2016 attempts, we changed the battery system and connected a rechargeable battery.

The collar was programmed to attempt one location every hour. We set a maximum search period of 240 seconds. Whenever a 2D location fix succeeded, the collar continued searching for a fourth satellite, in order to get a 3D location, and this during 12 seconds.

The collar was placed on a test-site for 24 hours. After each 24-hour session the locations were downloaded to a PC. Because there were some technical malfunctions we decided to revisit the same test-site for another 24-hour session whenever none of the 24 location attempts had been successful. To avoid (as much as possible) confounding effects between meteorological circumstances and the performance of the collar, we moved the collar after each successful 24-hour session to another test-site.

Table IV.2 summarises the main characteristics of the different test-sites. For each of the seven test-sites there are three successful 24-hour sessions (minimal one location attempt succeeded) with the GPS collar in a vertical position (90° to the horizontal). To test the influence of the observation angle of the collar, we repeated the tests a second time, placing the collar at an angle of 50° to the horizontal (see Figure IV.1).

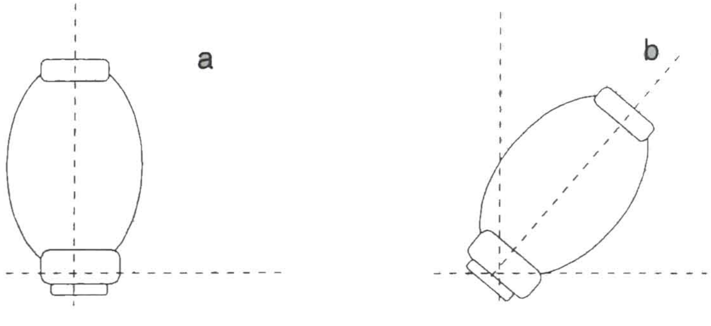


Figure IV.1: GPS collar in vertical (a) and inclined (b) position.

Table IV.2: Main characteristics of the seven test-sites.

Test-site	Number of trees (n/ha)		Basal area (m^2/ha)		Average height (m)	
	Upper storey	Understorey	Upper storey	Understorey	Upper storey	Understorey
Decid. 1	95	0	47.36	0	43.00	0
Decid. 2	64	1051	41.29	1.32	43.30	4.15
Decid. 3	95	127	34.26	0.35	31.82	5.90
Conif. 1	764	350	40.82	2.22	21.27	4.40
Conif. 2	828	0	52.27	0	22.83	0
Conif. 3	2293	0	47.73	0	10.60	0
Open	0	0	0	0	0	0

The geographic co-ordinates of the test-sites were obtained using a Trimble ProXl, applying post-processing differential correction. This method enabled us to have a reference location with an accuracy better than 1 m (Sigrist et al. 1996).

The location error of the GPS collar was determined as the Euclidean distance between a measured position of the GPS collar and the geographic co-ordinates (Casaer et al. 1999b).

The performance of the collar (success-rate) was determined as the percentage of successful location attempts in a 24-hour session (maximum 24 locations).

To assess both performance and accuracy, we first performed a graphical explorative data analysis. Subsequently statistical model building was applied to determine the factors explaining the observed data structure best. The statistical model building was based on stepwise linear modelling (both directions), starting from the most complex model possible (including interaction terms between all possible factors). Both an automated stepwise modelling procedure (S-plus 2000) and the comparison of different possible models (anova-function, S-plus 2000) were used.

The dimension of the observation (2D or 3D) was included as a factor in the model explaining the probability of obtaining an observation. This enabled us to analyse the difference between considering only the 3D locations as successful observations compared to considering both 3D and 2D as successful location attempts.

To obtain a normal distribution of the dependent variable (probability of a successful location attempt) and to compensate for the heteroskedasticity in the data, we used an arcsine-transformation. The transformed dependent variable was called 'suca'.

The input model for the stepwise analysis (including all interaction terms) therefore had following structure (model formulation according to Chambers and Hastie 1992):

$$\text{Suca} \sim \text{dimension} * \text{observation angle} * \text{test-site}$$

To analyse the factors influencing the accuracy of the obtained locations, the starting model of the stepwise analysis included DOP, test-site, observation angle and dimension of the observation (and all possible interactions). The dependent variable was log–transformed. The resulting input model for the analysis therefore was:

$$\text{Log}_{10}(\text{error}) \sim \text{observation angle} * \text{test-site} * \text{dimension} * \text{DOP}$$

Before starting the stepwise analysis we compared (for the accuracy as well as for the performance of the GPS collars) the models including the seven test-sites as factor with the models using the type of test-site (deciduous, coniferous and open) as factor (anova, Splus 2000).

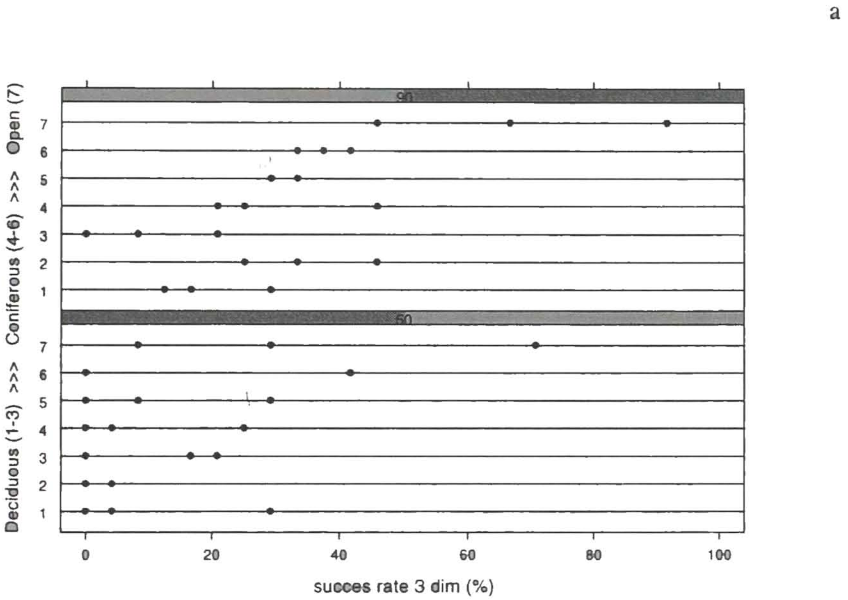
IV.B.4 Results

IV.B.4.a The probability of obtaining a successful location

A total of 83 days were needed to have 42 days with minimal one successful location attempt. This means that only 50% of the 24-hour sessions resulted in at least one successful fix.

On the remaining 42 days (6 days for each of the seven test-sites) 686 location attempts were successful. Since for each 24-hour session the maximum possible number of locations is 24, this represents an overall success-rate of 68%. Figure IV.2 shows for each of the test-sites the success-rate for each 24-hour session. When including the 2D observations as successful locations there was a major increase in the number of successful observations for all test-sites. Both within one test-site and within the same habitat type (deciduous, coniferous, open) the success-rate varied strongly. The probability of obtaining a location was greater on the open site than on the forested sites. The number of successful location attempts was for all possible test-sites higher when the collar was standing vertical (90°) than in the inclined (50°) position (Figure IV.1).

Table IV.3 shows for each test-site the number of successful 2D and 3D locations, the median, minimum and maximum location error and the standard deviation and 95^{the} percentile of the location-error distribution.



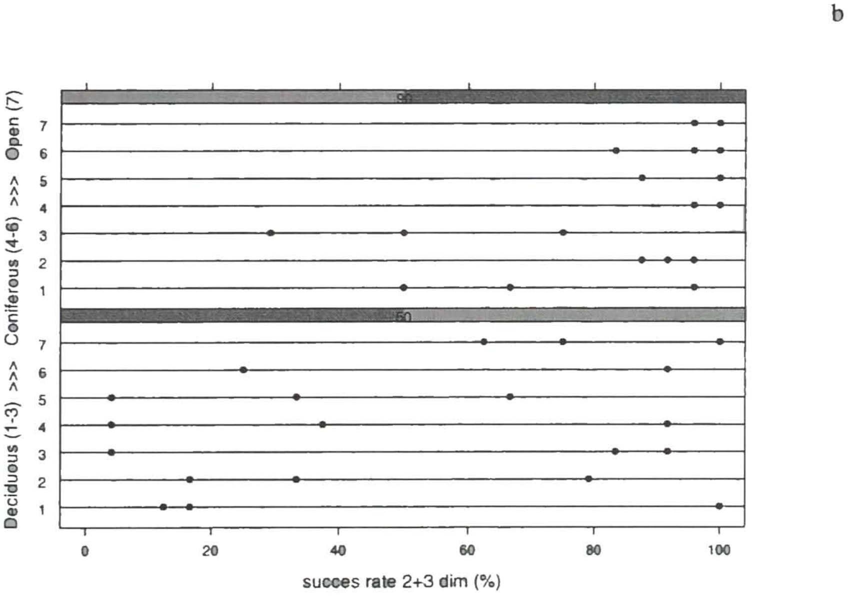


Figure IV.2: Success-rate for each of the test-sites, and observation angles (90° upper part of each figure, 50° lower part of each figure), when considering only the 3D observations as successful (a) and when considering both 3D and 2D as successful (b). Each dot represents one 24-hour session.

Table IV.3: The number of observations and the characteristics of the location errors for each of the test-sites and observation angles.

Site	Observation angle	Dimension	Number of successful location attempts.	Median of the location errors (m)	Standard deviation of the location error	Minimum location error (m)	Maximum location. Error (m)	95_{the} percentile of the location errors (m)
Decid. 1	50	2D	23	95.22	101.03	8.92	404.31	383.36
		3D	8	44.22	48.88	20.28	165.43	165.43
	90	2D	37	71.09	125.49	11.68	669.7	358.96
		3D	14	68.08	72.44	18.19	297.62	297.62
Decid. 2	50	2D	30	70.20	88.34	19.6	480.47	348.08
		3D	1	36.32	36.32	36.32	36.32	36.32
	90	2D	41	91.10	100.7	4.29	410.81	340.23
		3D	25	38.04	45.94	5.62	189.55	179.6
Decid. 3	50	2D	34	74.14	161.41	15	813.64	518.48
		3D	9	56.23	29.65	16.62	105.12	105.12
	90	2D	30	86.98	106.12	18.69	426.53	407.24
		3D	7	62.61	30.3	38.23	129.57	129.57
Conif. 1	50	2D	25	221.36	78.54	120.22	505.63	451.91
		3D	7	258.37	47.19	145.22	291.41	291.41
	90	2D	49	228.20	95.97	29.33	675.97	415.94
		3D	22	242.17	59.97	107.9	417.31	405.39
Conif. 2	50	2D	16	224.02	99.08	170.55	548.43	548.43
		3D	9	254.92	84.84	89.59	394.07	394.07
	90	2D	46	255.01	109.82	102.64	700.82	464.01
		3D	23	221.54	65.68	33.63	392.59	373.3
Conif. 3	50	2D	24	278.29	120.72	33.62	527.42	527.42
		3D	10	223.74	75.15	139.49	375.82	375.82
	90	2D	40	227.94	96.28	73.29	551.29	438.01
		3D	27	242.31	65.22	148.19	442.22	428.1
Open	50	2D	31	62.98	84.2	7.01	376.09	327.71
		3D	26	38.73	40.72	15.19	217.2	179.38
	90	2D	22	67.64	108.82	7.07	464.86	441.6
		3D	49	43.22	42.75	8.36	264.94	115.99

Comparing the model using the seven test-sites (Decid.1, Decid.2, Decid.3, Conif.1, Conif.2, Conif.3 and Open) as a factor with the model using the type of the test-site (deciduous, coniferous and open), revealed that the latter model should be preferred over the mover complex one (Δdf=16, F-value = 0.506, p= 0.933). Therefore we chose the model using the type of test-site as input for the stepwise analysis. The analysis indicated that we could use a model without any interaction factors to model the influence of the dimension (2D+3D/3D), observation angle and habitat type on the probability of obtaining a successful location (Δdf = 7, F-value = 1.31, p = 0.256). The resulting model (R^2=0.64, p<0.001) therefore included no interaction terms. Since there were no interaction terms included in the model we can analyse the effect of the dimension (2D+3D/3D), of the type of test-site (deciduous, coniferous or open) and of the observation angle (50°/90°) separately.

Using multiple comparisons we calculated (multicomp, Splus 2000) the contrasts between different levels for each of the factors (α = 0.05) (Table IV.4).

Table IV.4: Estimates and confidence interval for each of the contrasts between the different factor levels.

Factor	Contrast	Estimate	Std. error	Lower bound	Upper bound
Dimension	2+3 / 3	0.382	0.041	0.299	0.464
Observation angle	50° / 90°	-0.248	0.041	-0.331	-0.166
Habitat type	Conif. / Decid.	0.082	0.045	-0.025	0.189
Habitat type	Conif. / Open	-0.206	0.063	-0.357	-0.055
Habitat type	Decid. / Open	-0.288	0.063	-0.439	-0.137

When the collar was at an angle of 50° the predicted probability was reduced from 61% tot 32%. Including the 2D observations as successful observations increased the overall predicted probability from 22% to 71%. The probability of obtaining a location was greater on the open site than under canopy cover and there was a slight greater probability of obtaining a location on coniferous stands than on deciduous forest stands.

IV.B.4.b Accuracy of the observations

We started the graphical explorative data analysis by analysing if the expected relationship between DOP and the accuracy was influenced by the habitat type, dimension and observation angle. Figure VI.3 shows for each habitat type the relationship between DOP and the logarithm of the location error. Furthermore the figure is split according to the dimension of the observations. There was a remarkable and systematic difference between the accuracy of the locations on the coniferous test-sites compared to the other test-sites.

Comparing the model using the different test-sites as factor and the one using the habitat type of test-site showed that the use of the latter as input for the stepwise analysis was justified ($\Delta df = 28$, F-value = 1.04, p = 0.40). After a first stepwise linear modelling analysis the resulting model still included the habitat type, the dimension and the DOP (and their interaction terms), however the observation-angle (and its interaction terms) were rejected from the model ($\Delta df = 15$, F-value = 0.54, p = 0.92). Because the graphical data-analysis revealed a possible relationship between DOP and the location error for the deciduous and the open test-site but apparently no relationship for the coniferous test-sites we split the further statistical model analysis in these two subgroups.

For the coniferous test-sites no relationship between DOP and location error could be detected. The model including both DOP and the dimension and their interaction-terms did not explain the observed variation in location error better than a model including only a constant term ($\Delta df = 3$, F-value = 0.56, p = 0.64).

For the open en deciduous test-sites the model including both Dim and DOP as factors but without the habitat type as factor nor any interaction-term, appeared to be the best one (Δdf =5, F-value = 1.12, p =0,34), all model parameters being highly significant ($p < 0.001$).

$$\text{Log}_{10}(\text{error}) = 1.57 - 0.23*\text{Dim} + 0.0862 * \text{DOP}$$

with Dim = 0 for a 2D observation and
Dim = 1 for a 3D observation

This model indicates that the relationship between the DOP value and Log_{10} of the error depends of the dimension of the observation (see discussion). Because the internal variation in accuracy for each habitat type - dimension - DOP combination is large, the predictive value of the relationship found is limited ($R^2 = 0.29$).

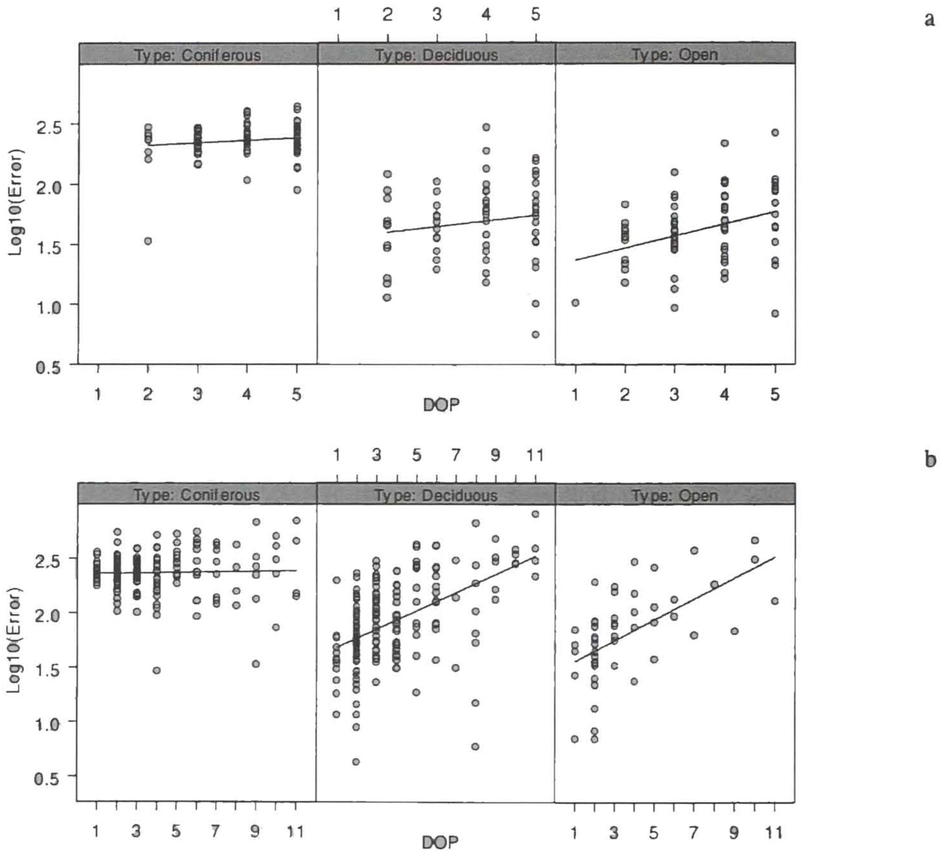


Figure IV.3: The observed location errors in relation to the DOP for the different habitat types. Figure IV.3.a shows the location errors of the 3D observations. Figure IV.3.b of the 2D observations.

IV.B.4.c Search period

The search period was programmed to be 240 sec. Almost 80 % of all the observations took place in the first two minutes. From the observations made during the last two minutes 75 % were 2D observations. Meanwhile 85% of the 3D observations took place in the first two minutes. There was a clear difference in the distribution of the observations over time when comparing the open and the forested test-sites (Figure IV.4)

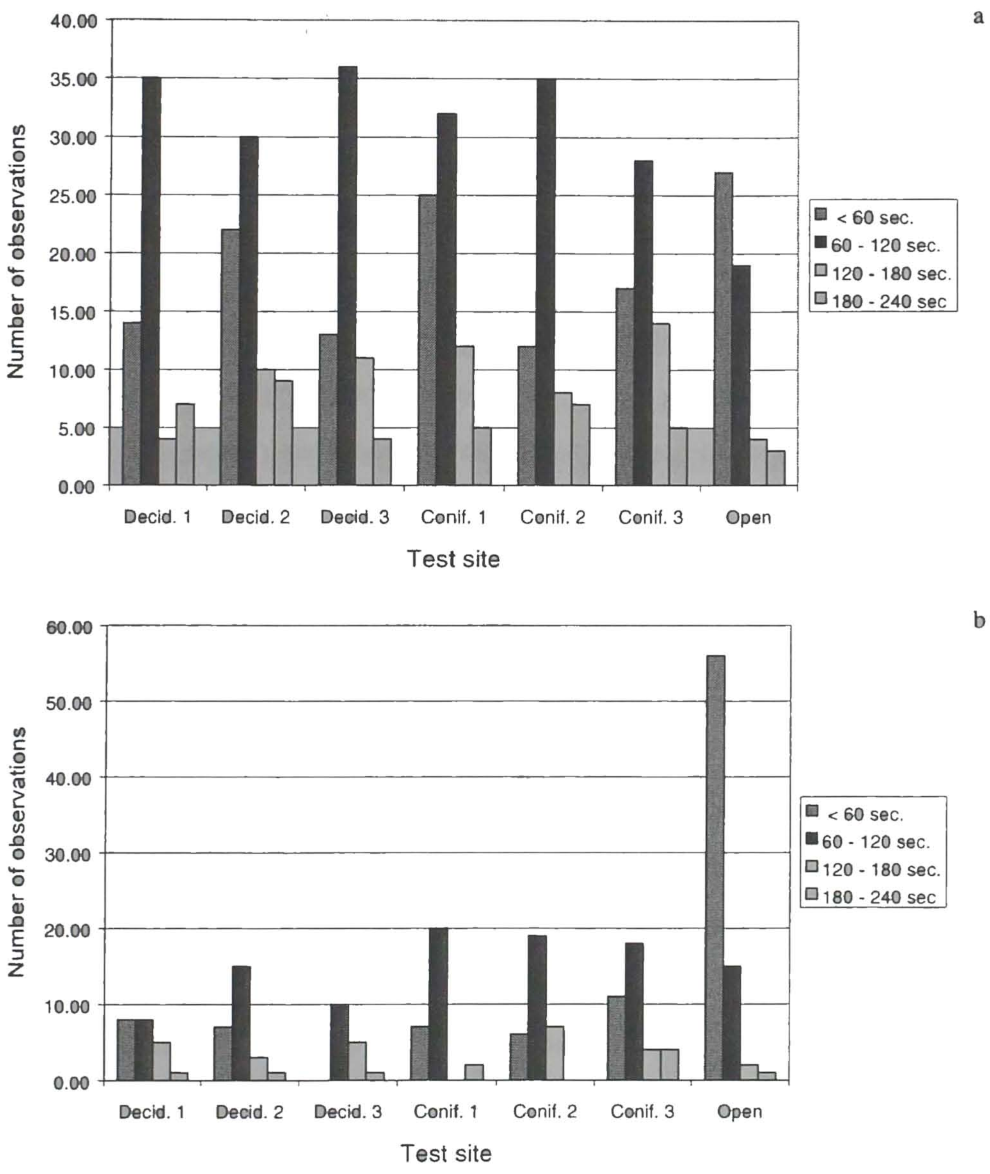


Figure IV.4: Distribution of 2D (a) and 3D (b) observations over time, for each of the seven test-sites.